Received: 30 August 2022 | Accepted: 4 April 2023
DOI: 10.1111/jfb.15398

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Factors influencing the downstream passage of European silver eels (*Anguilla anguilla*) through a tidal sluice

Jeroen B.J. Huisman[1,2] | Leander Höhne[3] | Reinhold Hanel[3] | Henry Kuipers[2] | Peter Paul Schollema[4] | Leopold Nagelkerke[1]

[1]Wageningen University & Research, Aquaculture & Fisheries Group, Wageningen, The Netherlands

[2]Van Hall Larenstein University of Applied Sciences, Leeuwarden, The Netherlands

[3]Thünen Institute of Fisheries Ecology, Federal Research Institute for Rural Areas, Forestry and Fisheries, Bremerhaven, Germany

[4]Water authority Hunze en Aa's, Veendam, The Netherlands

Correspondence
Jeroen B.J. Huisman, Van Hall Larenstein University of Applied Sciences, Leeuwarden, The Netherlands, Agora 1, PO Box 1528, 8901 BV Leeuwarden, The Netherlands.
Email: jeroen.huisman@hvhl.nl

Funding information
Waddenfonds, Grant/Award Number: 01709068/WF-2019/200914; Van Hall Larenstein Applied Sciences University; Lower Saxony Ministry of Food, Agriculture and Consumer Protection; European Maritime Fisheries Fund, Grant/Award Number: NI-1-18-004

Abstract

Tidal sluices are a frequent element in the tidal regions of Europe's rivers and may hinder downstream migrating European eels *Anguilla anguilla*. Sea level rise will reduce the possibility for tidal sluices to freely discharge water, further compressing windows of opportunity for the passage of eels. Understanding how eels utilize the discharge events of tidal sluices and which conditions facilitate successful passage is pivotal for the design of effective fish migration measures. To investigate eel migration at a tidal sluice, acoustic receivers were placed at the tidal sluice Nieuwe Statenzijl and in its tributary of the Westerwoldse Aa, the Netherlands. Of the 30 tagged eels, 26 eels reached the tidal sluice and passage success was 100%. The mean migration speed of eels in the unobstructed part of the tributary was slow (0.14 m s^{-1}). The eels were delayed in their migration by the sluice and delay was right-skewed distributed with most eels showing moderate delays (<2 days), while about 10% of the tagged individuals experienced extensive delays of more than 3 weeks. The number of missed sluicing events prior to successful passage was influenced by biological characteristics such as migration speed in the tributary, weight and condition. In addition, sluicing events with rapidly increasing and high maximum discharge levels increased the success rate of an individual eel to pass the sluice. Compromising sluicing duration in favour of higher and faster increasing discharge could facilitate eel migration at tidal barriers and contribute to the recovery of this endangered species.

KEYWORDS
European eel, fish migration, passage behaviour, tidal barriers, tidal sluices

1 | INTRODUCTION

Diadromous fish species rely on successful and timely migration to fulfil their life cycle. However, diadromous fish around the world increasingly face man-made barriers (Belletti *et al*. 2020) that are

* Jeroen B.J. Huisman and Leander Höhne should be considered as joint first authors.

hindering migration and contributing to their decline (Baras & Lucas, 2001; Limburg & Waldman, 2009). Tidal barriers such as sluices, weirs and pumping stations are of especial importance to migratory fish as they govern access to and departure from estuarine areas and rivers (Lucas *et al*., 2009; Nunn & Cowx, 2012). Removal or mitigation of barriers is one of the big five considerations in conserving diadromous species but fundamental knowledge is needed to further support management (Verhelst *et al*., 2021). However, removal of barriers in populated coastal areas is often not possible and therefore basic knowledge on how to design and utilize mitigation measures for diadromous fish in coastal zones is necessary.

The population of the catadromous European eel *Anguilla anguilla* L. 1758 has steeply declined and it is listed as a critically endangered species (ICES, 2021; IUCN, 2021). The primary causes of the decline include fisheries, pollution and migration barriers (Castonguay & Durif, 2016; Hanel *et al*., 2019). Measures to recover the eel stock primarily aim to increase the number of potential spawners, *i.e*., silver eel migrating towards the sea (EU, 2007). Enabling successful downstream migration of silver eels at tidal barriers is of importance as it focuses on the last physical barrier before the marine phase. Moreover, Lennox *et al*. (2018) stated that the coastal zone could be an important focus in protecting European eels. Eels are particularly affected by tidal barriers, as successful and timely movement in both upstream and downstream directions is essential to complete their life cycle.

Pumping stations, tidal gates and tidal sluices are common elements in the landscape of coastal ecosystems such as the Wadden Sea. These structures are primarily built to manage water levels and prevent tidal influence or the ingress of salt water in tributaries but may also hinder or delay fish migration. Delay of silver eels at tidal barriers may affect migration timing (Bolland *et al*., 2019; Lucas & Baras, 2001) and could deplete the energy reserves essential for successful spawning migration (Belpaire *et al*., 2009). Moreover, delays may lead to an aggregation of individuals in constrained areas, where they may become more vulnerable to predation or fishing mortality (Chaput *et al*., 2014; Garcia de Leaniz, 2008; Venditti *et al*., 2000; Wright *et al*., 2015). While mortality and migration delays of eels at pumping stations has received more attention in recent years (Baker *et al*., 2021; Bolland *et al*., 2019; Buysse *et al*., 2015; van Keeken *et al*., 2020) less is known about similar effects at tidal sluices. Silver eel passage has been studied at tide gates, revealing a potential for substantial migration delays for eels, although tide gates open automatically every tide (Wright *et al*., 2015). Indeed, Bourgeaux *et al*. (2022) highlighted the importance of regular discharge events to facilitate eel migration. In contrast to tide gates, tidal sluices may not be opened for multiple tides and may therefore impact silver eel migration.

The frequency and duration at which tidal sluices are opened depend on the amount of excess water in the tributary and on water levels on the sea side that enable free discharge, and this is highly site-specific. Little is known about how eels utilize discharge events of tidal sluices, including the potential delays that this barrier type might induce. A study by Piper *et al*. (2013) indicated that seaward migrating eels were delayed up to 68.5 days in a complex of water control structures including a tidal sluice. In another study, Piper *et al*. (2015) ascribed migration delays at a hydropower station to the exploratory behaviour of eels. Similarly, Jellyman and Unwin (2019) observed that eels (*A. dieffenbachii*) were generally attracted towards the outlet areas of a power station but showed hesitancy to exit. Behrmann-Godel and Eckmann (2003) found that some eels retreated upstream after arrival at a hydropower dam before approaching the structure again and similar observations have been made at a pumping station (Baker *et al*., 2021). To explain the varying degrees of delay experienced at a barrier, some studies suggest a stepwise response to different cues that may be present (van Keeken *et al*., 2020) which depend on individual characteristics or site-specific environmental cues. Vergeynst *et al*. (2021) concluded that the success of passing a barrier depends on an interplay of intrinsic fish characteristics and environmental conditions. Some pumping stations also possess the ability to freely discharge water, depending on the difference between polder water levels and the tide. A study by Baker *et al*. (2021) showed that free discharge at a pumping station may assist silver eel migration and as such may prove to be an interesting mitigating measure. Likewise, Vergeynst *et al*. (2021) stated that increased flow at a navigation lock could attract silver eels and therefore facilitate passage. In the light of sea level rise more tidal barriers will be built and the frequency, duration and magnitude of sluicing events at existing sites will diminish (Bormann *et al*., 2020). It is therefore crucial to understand the factors that contribute to the passage of fish and eels in particular at tidal sluices.

Empirical information on escapement success, migration delay of eels and which individual characteristics of eels or site-specific environmental cues (*e.g*., discharge) influence passage at tidal sluices is scarce. This study aimed to increase our knowledge on (a) passage efficiency and potential migration delays at a tidal sluice and (b) the characteristics of migrating eels and sluicing events that are associated with timely passage.

2 | MATERIALS AND METHODS

2.1 | Study area

The Westerwoldse Aa is a small river and canal system in the north-west of the Netherlands and a tributary of the Ems River (Figure 1). Recent monitoring (Vis, 2021) indicated this tributary contains a high biomass of eel (9 kg ha^{-1}) and could therefore substantially contribute to the escapement of eels from the Ems catchment. The Westerwoldse Aa is heavily modified by measures ensuring flood protection (*e.g*., canalisation, dikes and weirs) and consist of two parts, a small brook system upstream and a regulated canal system of ~25 km that flows into the Dollard estuary at Nieuwe Statenzijl. The tidal sluice at Nieuwe Statenzijl (latitude 53.2316N, longitude 7.2090E) regulates water levels in the Westerwoldse Aa. The sluice has four hydraulically operated doors that can be opened or closed vertically depending on the amount of excess water that needs to be discharged. Each sluice door is 4.9 m wide and 6.6 m high. Maximum discharge of the sluice depends on the water level difference between both sides of the sluice but is estimated by the water authority at 1,5 - 2 x 10^6 m^3 per tide. Adjacent to the discharge sluice lies a shipping lock that is extensively used for recreational boating. The

JOURNAL OF FISH BIOLOGY fsbi

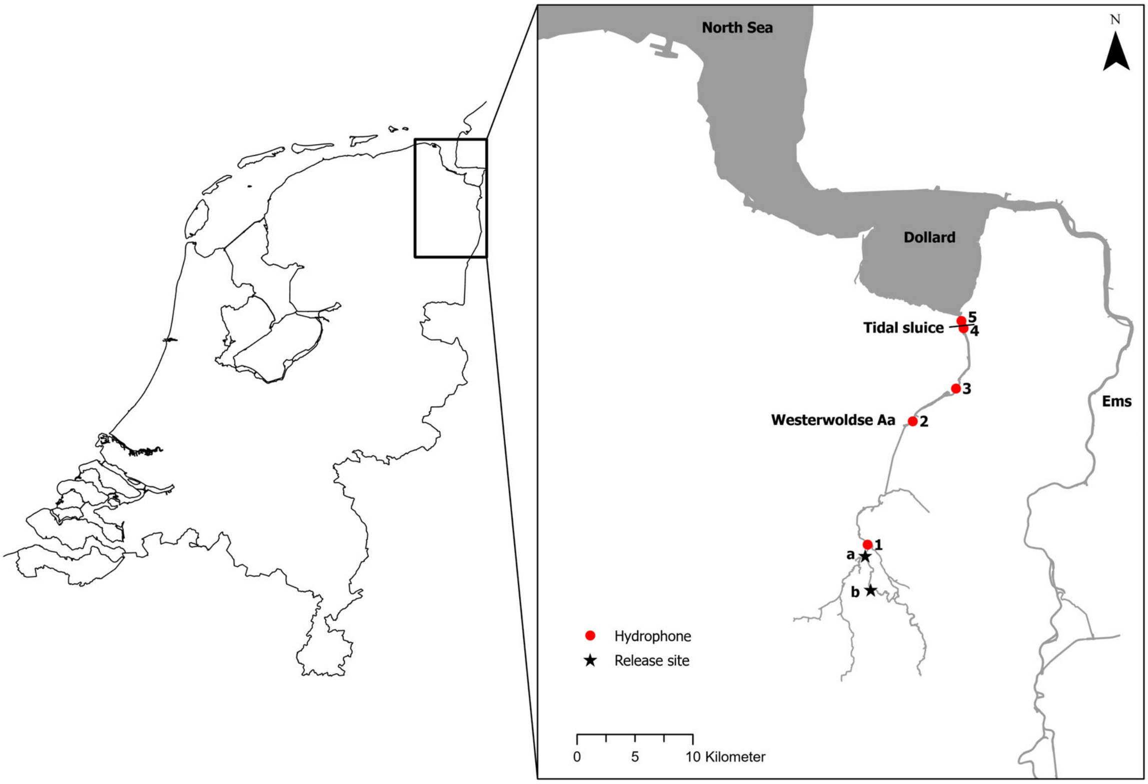

FIGURE 1 Map of the Westerwoldse Aa, the Netherlands. Receiver locations are indicated with dots and numbers. Release sites of eels (*Anguilla anguilla*) are indicated by a and b

TABLE 1 Distribution of the maturation stages of eels (*Anguilla anguilla*) (following Durif *et al*., 2005) with the number of individuals (*n*) and associated morphological variables available

Stage	Degree of silvering	*n*	TL (mm)	BW (g)	*K*
Yellow	F2	2	600 ± 14.1	430 ± 40	0.20 ± 0.004
Pre-migrant	F3	2	685 ± 63.6	673 ± 163	0.21 ± 0.007
Migrant	F4	5	830 ± 57.0	1143 ± 138	0.20 ± 0.018
Migrant	F5	21	680 ± 60.6	620 ± 160	0.19 ± 0.018

Note: TL, total length; BW, body weight; *K*, Fulton's condition factor. Means and standard deviations are indicated.

lock is only operated when the tide is higher than the polder water levels. The canal system varies in width between ~30 m (upstream) and ~90 m (close to the sluice) and has a mean depth of ~2.5 m.

2.2 | Receiver and tagging data

Acoustic telemetry is a proven and useful tool to investigate the migration behaviour of silver eels and to quantify the impacts of migration barriers (Béguer-Pon *et al*., 2017). Five acoustic receivers (VR2W-69 kHz; Innovasea, Halifax, Canada, http://www.innovasea.com) were placed in September 2017 and retrieved in April 2018 (Figure 1). Four receivers were placed in the Westerwoldse Aa upstream of the tidal sluice Nieuwe Statenzijl, creating three inter-receiver sections (station 1–station 2 = 14 km, station 2–station 3 = 5 km, station 3–station 4 = 6 km). One receiver (station 5) was placed on the seaside of the sluice. Silver eels for this study were caught using fyke nets near the sluice. One eel was caught in the riverine section of the Westerwoldse Aa. Eels were anesthetized using benzocaine at a concentration of 40 mg L^{-1} and tagged on 17 October 2017. A V13-2L (ping interval of 20–50 s, weight in water 6 g; Innovasea) transmitter was then placed in the abdominal cavity by making a mid-ventral incision of about 2–3 cm. The incision was closed by two to three sutures (absorbable, braided Vicryl 3/0, FS2 needle). Once anaesthetized, each eel was measured (total length, left pectoral fin length, left eye horizontal and vertical diameters, all in mm, weight in grams) to determine the maturation stage according to Durif *et al*. (2005) (Table 1). Mean total length was 700 mm, S.D. ± 83.9 mm and mean weight was 697.8 g, S.D.± 254.7 g. Based on length all tagged eels were considered females (Durif *et al*., 2005). To avoid tag signal collisions, eels were released at two different sites not far apart (release site a = 53.0523N, 7.0772E and release site b = 53.0257N, 7.0825E) in the upstream part of the tributary (Figure 1). The distance from the release sites to the sluice was between 25.6 and 30.3 river-km.

2.3 | Data and statistics

Discharge (measured as the elevation height of the sluice doors in centimetres) was measured every 10 s, and water levels (15-min intervals) and the number of opened sluice gates, including the duration of opening, were logged by the water authority Hunze en Aa's. Day-time or night-time at the moment of sluice opening was defined as a binary variable based on times of sunrise and sunset, extracted through the 'getSunlightTimes' function from the package 'suncalc' (Thierumel, 2019) in the R-software environment (R-Core-Team, 2022). Fulton's condition factor (K) was calculated for every eel as $K = 100 \times$ weight (g)/total length (cm)^3 (Cone, 1989). Migration speed was calculated for each individual eel and for each inter-receiver section using two metrics. First, to compare migration speed between inter-receiver sections (including eventual delays), speed was calculated as the time difference from the first detection of a receiver to the last detection on the consecutive receiver, divided by the distance in river-km between the two receivers (*i.e.*, first-to-last detection; following Verhelst, Buysse *et al.*, 2018). Second, to study the relationship between migration speed in the unobstructed part of the tributary and the number of missed sluicing events before passage, the migration speed of eels was calculated as the mean migration speed across the three inter-receiver sections upstream of the sluice (as first-to-first detection), thus excluding delays at the sluice. The distance between two stations in river-km was determined using a shapefile of the river catchment and functions from the R-package 'actel' (Flávio & Baktoft, 2021). Following Piper, Wright *et al.* (2013), the migration delay of an eel at the sluice was calculated as the time difference between the first and last detection on station 4 (*i.e.*, the receiver on the canal side of the sluice).

Differences in migration speed across inter-receiver sections were examined by conducting a nonparametric Friedman's test. Following identification of a significant difference, pairwise comparisons were carried out using a paired Wilcoxon signed-rank test. P values were adjusted using the Bonferroni correction for multiple testing.

To investigate if the biological variables of eels (weight, condition factor and migration speed) were correlated with the number of sluicing events missed by eels, representing migration delay, we used data from all 26 eels that passed the sluice. We first used simple Pearson correlation coefficients (r) to examine the linear relationships between the biological variables. This procedure allowed us to identify potential multicollinearity among variables. An $|r| > 0.7$ indicates that multicollinearity starts having notable consequences (Brun *et al.*, 2020). There was no strong collinearity among these predictor variables (all $|r| < 0.22$). We then used a generalized linear model in R (glm.nb function from the 'mass' package version 7.3-55; Ripley *et al.*, 2013) with negative binomial error and a log link function to assess the effects of eel characteristics on the response variable. For every eel, all sluicing events were considered during which the eel was present in vicinity of the sluice, indicated by its detection on receiver station 4. Thus, our global model featured the characteristics weight, condition and speed of the eel in the tributary, and as a response variable we used the number of missed sluice events before passage. The StepAIC ('mass' R package) stepwise regression, both forward and backward selection procedure, was used to achieve the model with the lowest Akaike information criterion (AIC) value. As a control variable we also included the release site to verify possible differences between the two release sites.

To investigate the relationship between the discharge characteristics of any sluicing event and the passage of eels, we used the data from 25 of the 26 eels that passed the sluice. We excluded one eel that passed the sluice much later in the year than all other individuals and at a discharge level that was substantially higher compared to the main migration period, causing an outlier observation (Supporting Information Figure S1). To describe the discharge characteristics of any sluicing event, we defined a set of four variables: (a) discharge level at 15 min after sluice opening, (b) discharge level at 30 min, (c) maximum level of discharge and (d) duration of discharge in minutes. The maximum level of discharge within a sluicing event and the discharge at 15 min (as another measure of flow increase that was explored) were both highly correlated with the discharge at 30 min (both $|r| > 0.76$). Therefore, only the discharge at 30 min was retained because this variable had the strongest univariate relation with the dependent variable. There was no strong collinearity among the discharge at 30 min and the duration of a sluicing event ($r = 0.33$). We then used a generalized linear mixed-effect model in R (glmmTMB version 0.2.3; Brooks *et al.*, 2017) with binomial error and a logit link function to assess the probability of a sluice passage by an eel in relation to the characteristics of the sluice event. Individual differences between study animals were accounted for by fitting random intercepts for each individual eel. More eels could be present at the same sluice event so we also included crossed random intercepts for each event. However, the distribution of the number of sluice events that an individual encountered before passage was very skewed. This led to an imbalance of the random factor 'individual', with few individuals contributing a vast number of observations (four out of 26 eels contributed 149 out of 202 observations in total). For reasons unknown to us, the mentioned individuals may have temporarily ceased their migration (Breukelaar *et al.*, 2009) but resided in the sluice area. However, these eels finally did pass the sluice and to include them in our analyses and deal with the imbalance, we used only their latest eight observations. Eight observations were chosen as a threshold as this corresponds to the mean number of encountered sluice events before the passage of all 26 eels. A logarithmic transformation was applied on the discharge at 30 min to account for outliers in this variable (Zuur *et al.*, 2010). Our global model therefore featured the following sluice event characteristics: discharge level at 30 min after sluice opening (log-transformed), duration of the sluice event in minutes and if it was day or night at the time of sluice opening. Our binary response variable indicated whether the eel did not successfully pass (= 0) or did successfully pass the sluice (= 1) within a given event. As before, a StepAIC ('mass' R package) stepwise regression, both forward and backward selection procedure, was used to achieve the model with the lowest AIC value.

Residual diagnostics on the analyses of delays and passage events were performed by using the 'DHARMa' R package version 0.2.6 (Hartig, 2017). Predictor effect plots were used ('effects' R package; Fox, 2003) to visualize the partial effect of each predictor of the final model on the response variable with the other predictors set to the median.

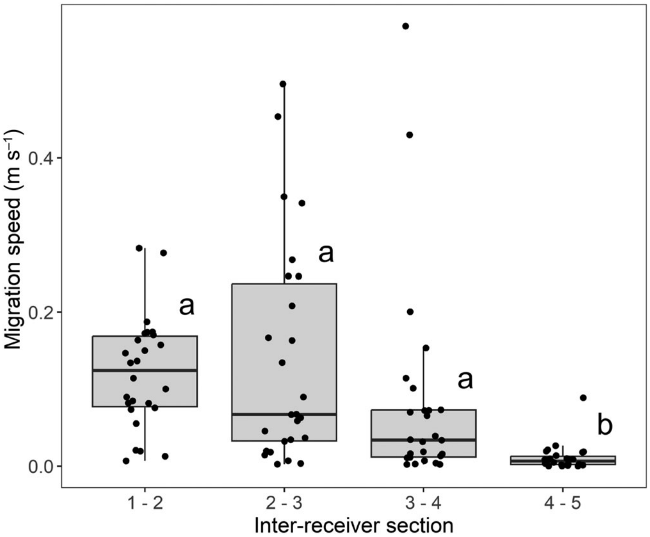

FIGURE 2 Migration speed (m s^{-1}) of 26 eels (*Anguilla anguilla*) in the Westerwoldse Aa between inter-receiver sections. Inter-receiver section 4-5 included the sluice Nieuwe Statenzijl

2.4 | Animal welfare

The tagging experiment was approved by the Dutch Board on Animal Experiments (Project AVD223000002015110, experiment nr. VA2017_26). Eels were caught by a professional fisher. The surgical procedure was done by trained and experienced professionals of VisAdvies.

3 | RESULTS

3.1 | Migration in the tributary

Of the 30 eels released, 26 eels were detected at the sluice, while four eels were lost after being detected at station 1. Mean migration speed in the unobstructed part of the tributary (*i.e.*, arrival at station 1 to arrival at station 4) was 0.14 m s^{-1} (S.D. = 0.09). The mean migration speed of 26 eels across the studied river stretch including the sluice (*i.e.*, arrival at station 1 to departure from station 5) was 0.07 m s^{-1} (S.D. = 0.07). There was a significant difference in migration speed between inter-receiver sections in the Westerwoldse Aa (Friedman, χ^2 [3] = 42.62, $P < 0.001$). Median migration speed decreased towards the sluice. Pairwise comparisons showed that the migration speed of eels in the river stretch between stations 4 and 5 was significantly lower than in the other three inter-receiver sections (Figure 2).

3.2 | Passage and delay at the sluice

All 26 eels that arrived at the tidal sluice passed successfully, that is, passage efficiency was 100%, and no eels used the shipping lock. The degree to which eel migration was delayed at the sluice (*i.e.*, the time difference between the first and last detections at station 4) was right-skewed distributed. Seventeen of 26 eels (65%) experienced delays of less than 2 days and the median delay of eels at the sluice was 1.3 days (mean = 4.7 days, S.D. = 8). Three eels were extensively delayed by 23–29 days. Eels encountered a median of two sluice events between arrival at station 4 and passage (mean = 7.8 events, S.D. = 14.5), while the aforementioned three eels missed 38–53 sluice events before passage. Seven eels (27%) passed the sluice during the first opening of the sluices on arrival.

Of all eels that passed the sluice, 24 eels (92%) passed the sluice during the night and two eels during the day (Figure 3a). Individual eels usually passed quickly within a sluice event, with 22 out of 26 individuals passing the sluice within ≤90 min after gate opening (Figure 3b). Fourteen eels passed during periods of increasing discharge (defined as the time period from the opening of the sluice up to 0.9 × maximum discharge level), 10 eels used peak discharge (defined as discharge larger than 0.9 × maximum discharge level) and two eels passed during decreasing discharge. Three eels retreated about 6 km upstream and arrived at station 3 after being detected at the sluice (station 4), likely representing an upstream retreat after initial failure to overcome the barrier.

3.3 | Eel characteristics related to migration delay and passage at the sluice

Weight, condition factor and migration speed in the unobstructed reach were retained in the best model to explain the number of sluice events that an eel encountered before passage (Table 2). Weight and condition factor had a positive significant relationship with the number of missed events (Figure 4a,b). The migration speed of eels in the tributary showed a positive but not significant relationship with the number of sluice events (Figure 4c). The characteristics of passage events (discharge at 30 min, duration of the sluice events and day–night) in relation to the passage of 25 eels were also analysed. Of all sluicing event variables, only the discharge level at 30 min after sluice opening was retained in the final model. The probability that an eel passed the sluice increased with higher discharge at 30 min ($\chi^2(1, N = 83) = 6.11$, $P = 0.013$) (Figure 5).

4 | DISCUSSION

This study investigated silver eel migration behaviour in a regulated tributary and passage through a tidal sluice. Tidal sluices only open if there is a need to discharge excess water and thus offer only temporary opportunities for downstream migration of silver eels, potentially inducing delay. It is important to understand the factors that facilitate eel passage at tidal barriers to inform water managers in the design of suitable management measures supporting eel migration.

Water levels in the canal part of the Westerwoldse Aa are managed by the tidal sluice at Nieuwe Statenzijl. This results in negligible flow, unless the sluice is opened, resembling conditions found in highly regulated canal and polder systems. As a result,

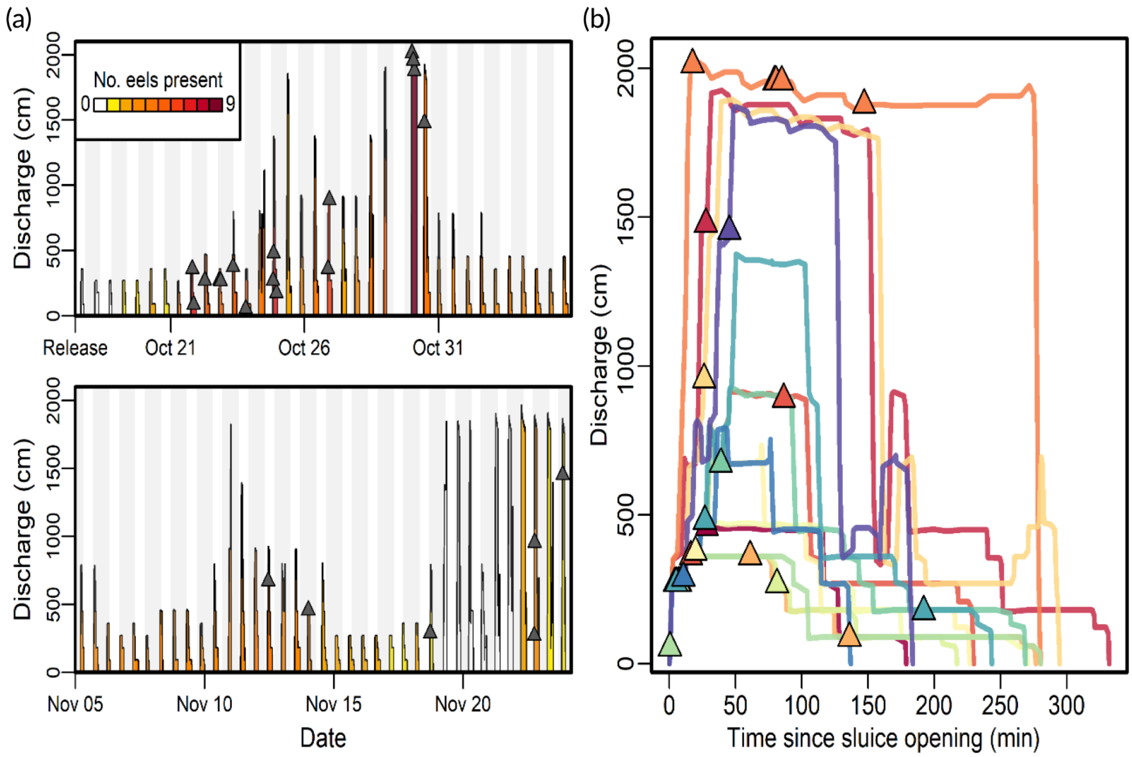

FIGURE 3 Discharge levels through a sluice and passage events of individual eels (*Anguilla anguilla*, $n = 25$) indicated by triangles. Shaded areas indicate night-time. The colour of the sluicing events indicates the number of eels present at a given sluice event (a). Passages of individual eels ($n = 25$) within the successful sluice events (b). Triangles indicate eel passages and their colour in (b) is consistent with the sluicing event during which they occurred. For representation purposes, one eel that passed very late in the study period is excluded in the figure. , eel passage

TABLE 2 Estimated regression parameter *B* with SE, *z* value, *P* values and Exp(B) with 95% CI of the final negative binomial model for the number of sluice events an eel missed before passage.

Parameters in final model	*B*	SE(B)	*z* value	*P* value	Exp(B)	95% CI for Exp(B)
Intercept	1.20	0.30	4.06	***<0.001***	3.34	1.91–6.14
Weight	1.09	0.29	3.73	***<0.001***	2.99	1.70–5.72
Condition factor	0.62	0.31	2.02	***0.043***	1.87	0.91–4.07
Speed	−0.61	0.31	−1.93	*0.053*	0.54	0.24–1.21

Note: All predictors were standardized to allow for comparison of effect sizes. *P* values < 0.05 are highlighted italic and bold. B, model parameter estimate; CI, 95% confidence interval of exp(B); Exp(B), incidence rate ratio; *P* value, significance value; SE(B), standard error of the model parameter; *z* value, z score of the statistical test.

the mean migration speed of eels across the unobstructed part of the canal was slow (0.14 m s^{-1}). The migration speed of silver eels in the rivers Meuse (in Belgium and the Netherlands), Finn (Ireland) and Gudenaa (Denmark) have been reported to be 0.62, 0.45 and 0.27 m s^{-1}, respectively (Aarestrup *et al*., 2008; Barry *et al*., 2016; Verbiest *et al*., 2012), which is considerably higher than found in this study. Progression rates across the studied river reach including the sluice were even slower (0.07 m s^{-1}). This value is comparable with the reported low swimming speeds (<0.06 m s^{-1}) found in a shipping canal in Belgium by Verhelst, Baeyens, *et al*. (2018). In general, downstream migration speed of eels is faster in river habitats with continuous discharge, as opposed to habitats with absent, very low and/or intermittent discharge (Lenihan *et al*., 2019).

All eels that arrived at the sluice ($N = 26$) migrated successfully to sea, that is, passage efficiency was 100%. Four eels were lost in the tributary, two of which were classified as nonmigratory yellow eels. The fate of these four eels is unknown, but predation and postponed migration may explain the loss of tagged eels (Verhelst, Buysse, *et al*., 2018; Verhelst, Reubens, *et al*., 2018). Eel passage efficiency at Nieuwe Statenzijl is in line with eel passage efficiency (98.3%) (Wright *et al*., 2015) and for juvenile sea trout (95.8%–100%) observed at tide gates (Wright *et al*., 2014), and suggests that tidal sluices do not constitute an impassable barrier for fish. However, the downstream migration of eels in this study was delayed at the sluice. Reported delays that eels experience at tidal barriers are highly variable and the difference in the types of tidal barriers (pumping stations, weirs, sluices, etc.) will contribute to these differences. Piper *et al*. (2013)

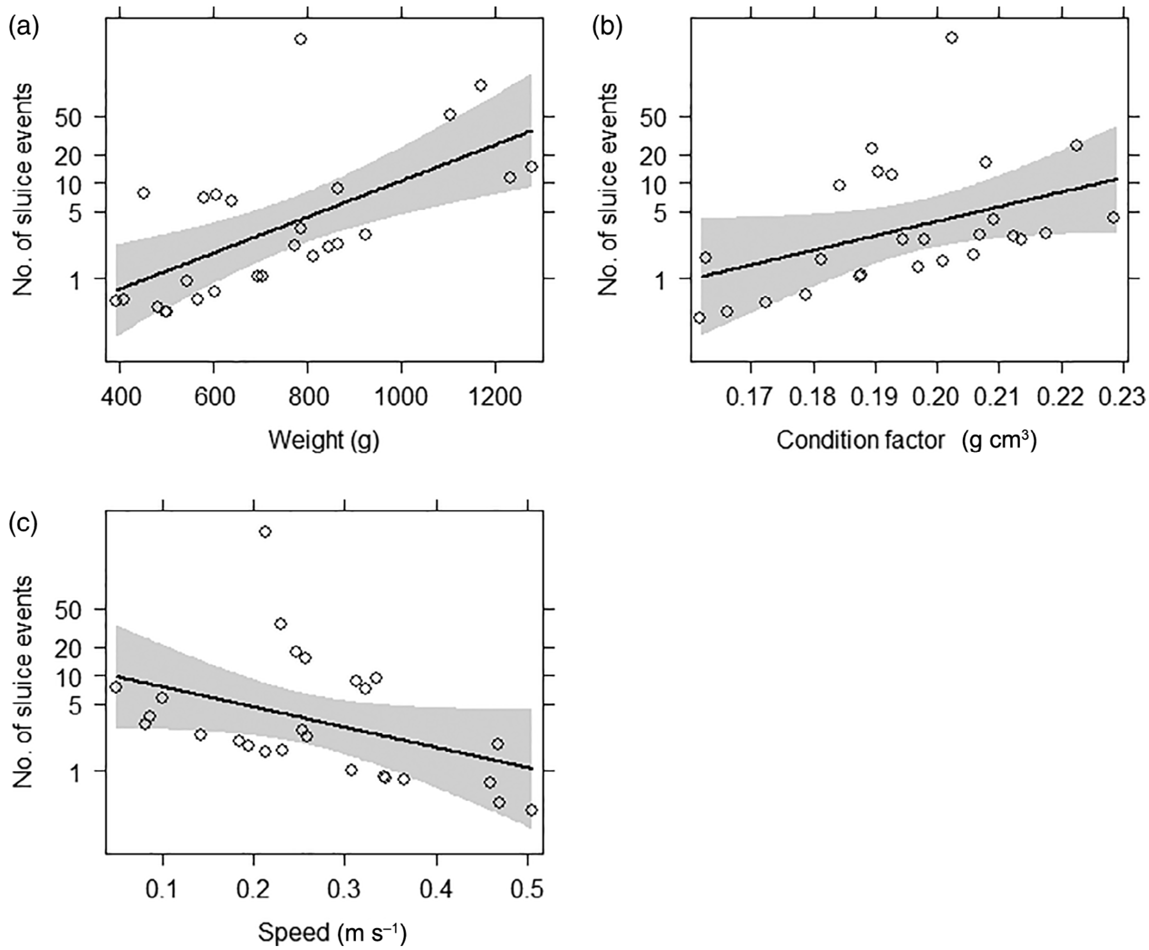

FIGURE 4 Predictor effect plots with partial residuals for the best model predicting the number of sluice events an eel missed before passage ($n = 26$). Predictor variables include the (a) weight (g), (b) condition factor (g cm^{-3}) and (c) speed (m s^{-1}) of the eel in the tributary. Shaded areas represent 95% confidence intervals, reflecting the variance in the fixed effects

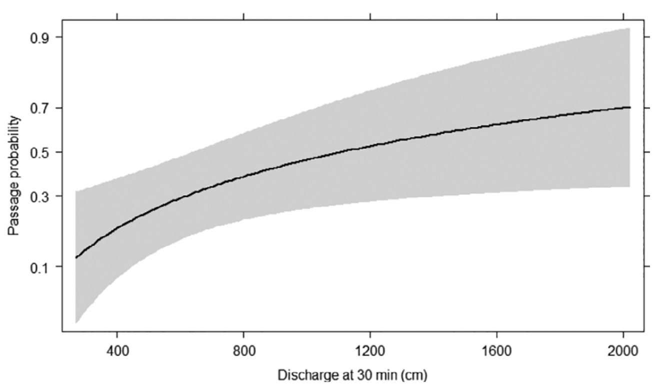

FIGURE 5 Predicted probability of an eel's (*Anguilla anguilla*) passage through the sluice in relation to the discharge level at 30 min after sluice opening. Shaded areas represent 95% confidence intervals

found that eels were delayed for up to 68.5 days at several structures, including a tidal sluice, in a heavily regulated river. In contrast, van Keeken *et al.* (2021) found that most silver eels were delayed less than a day after arriving at a pumping station. Baker *et al.* (2021) observed long passage delays (up to 21 days) at a pumping station equipped with a gravity sluice and found that it took two eels 3 h to 2.35 days before passing the gravity sluice. Most eels in this study experienced moderate delays of less than 2 days, but extensive delays exceeding 3 weeks were found for three individuals (= 10%). Eels encountered on average eight sluice openings (median = two events) and up to 54 events for successful passage, while only seven eels (27%) passed within the first sluice event. This indicates that temporarily providing an opening for eels to utilize may not be enough to facilitate migration. Indeed, Besson *et al.* (2016) found that eels only successfully migrated across a high dam near the estuary of the Fremur river at highly advantageous hydrological conditions.

Condition and weight influenced delay of eels at the tidal sluice, suggesting that bigger and well-conditioned individuals are affected most by the sluice. One possible explanation may be that size differences in eels may lead to a different stimulus threshold value, as stated by Piper *et al.* (2015), and thus how individual eels experience discharge events. In addition, the asset-protection principle by Clark (1994) relates higher fitness of individuals to an increase in avoidance of risks. In this study eels in better condition missed more sluice events, suggesting that eels consider passing the sluice as a higher risk than momentarily delaying their migration. As fecundity in eels is positively correlated with size (MacNamara & McCarthy, 2012), this result could have severe implications for eel management. Although no significant relationship was found between migration speed in the unobstructed reach and the number of missed sluicing events, this study suggests that faster eels may pass the barrier within fewer sluicing events after arrival. This may be related to the trade-off between migration speed and safety (Lennox *et al*., 2018). Faster progressing individuals might accept more risks during downstream migration and therefore might also more boldly explore and overcome an unknown structure such as a sluice. Our observation of faster swimming eels overcoming the sluice sooner could also be environmentally influenced as rainfall and downstream tide height influence the frequency and size of discharge of sluice events and migration speeds simultaneously.

Peaks in discharge often start the onset of eel migration (Buysse *et al*., 2014; Marohn *et al*., 2014; Teichert *et al*., 2020; Verbiest *et al*., 2012). Similarly, sluicing events with steeply increasing discharge levels and higher peak discharge fostered successful eel passage in our study, validating that the amount of discharge (related to current velocity) is also an important migratory cue at barriers (Egg *et al*., 2017). We further observed that eels preferentially passed during the early parts of sluicing events and mostly before the maximum level of discharge was actually reached. This indicates that the pace at which discharge increases rather than the maximum discharge level might be the decisive mechanism in guiding eels to overcome the barrier. This is in accordance with findings by Verhelst, Baeyens, *et al.* (2018), who observed that low flow velocities were not strong enough to attract migratory eels. In contrast, it has been reported that too fast and sudden a change in water movement might lead to rejection behaviour and upstream retreat, suggesting that there might be an upper threshold to the positive relation between flow velocities and passage success (Piper *et al*., 2015).

Nocturnal migration behaviour of eels at barriers is well known (Egg *et al*., 2017; Lowe, 1952; Piper *et al*., 2017; Vøllestad *et al*., 1986). Twenty-six eels migrated through the tributary towards the sluice, of which 24 passed the sluice during the night. Two individuals used sluicing events during the day, further validating the importance of the nocturnal migratory behaviour of eels at barriers. Thus, night-time sluicing events are of particular importance for the escapement of eels.

This study shows that eels are able to successfully pass tidal sluices, but that these barriers can cause migration delays. Findings from this work suggest that to assist eel migration the duration of discharging excess water could be reduced in favour of discharging excess water more quickly and at higher volumes. However, the amount of water to be discharged through sluices is usually determined by climatic conditions and specific traits of tributaries. We therefore suggest that water managers devise a site-specific trade-off between day and night-time sluicing and between the number of sluicing events and the amount of water discharged as a suitable management option to assist migration of eels. Further studies should focus on the site-specific compromises between eel behaviour and sluice management.

AUTHOR CONTRIBUTIONS

J.H. and P.S. conceived and designed the experiment. J.H. obtained funding. J.H. and P.S. executed the field work. L.H., J.H. and H.K. performed the data analyses. J.H., H.K., L.H., R.H. and L.N. interpreted the results. J.H. and L.H. wrote the first draft. All authors contributed to the writing and further manuscript preparation and approved this version.

ACKNOWLEDGEMENTS

The company VisAdvies assisted with the tagging. This work was supported by the water authority Hunze en Aa's. We would like to thank three anonymous reviewers for their constructive feedback, which has greatly improved the paper.

FUNDING INFORMATION

The research was financed by the Waddenfonds (01709068/WF-2019/200914) and the Van Hall Larenstein Applied Sciences University. This work was supported by the water authority Hunze en Aa's. L.H. was supported by the Lower Saxony Ministry of Food, Agriculture and Consumer Protection and the European Maritime Fisheries Fund (EMFF-ID: NI-1-18-004).

CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

ORCID

Jeroen B.J. Huisman https://orcid.org/0000-0002-8055-629X
Leander Höhne https://orcid.org/0000-0002-6009-4665

REFERENCES

Aarestrup, K., Thorstad, E., Koed, A., Jepsen, N., Svendsen, J. C., Pedersen, M. I., … Økland, F. (2008). Survival and behaviour of European silver eel in late freshwater and early marine phase during spring migration. *Fisheries Management and Ecology*, *15*(5–6), 435–440.

Baker, N. J., Wright, R. M., Cowx, I. G., Murphy, L. A., & Bolland, J. D. (2021). Downstream passage of silver European eel (*Anguilla anguilla*) at a pumping station with a gravity sluice. *Ecological Engineering*, *159*(106), 69.

Baras, E., & Lucas, M. C. (2001). Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *International Journal of Ecohydrology & Hydrobiology*, *1*(3), 291-304.

Barry, J., Newton, M., Dodd, J., Lucas, M., Boylan, P., & Adams, C. (2016). Freshwater and coastal migration patterns in the silver-stage eel *Anguilla anguilla*. *Journal of Fish Biology*, *88*(2), 676–689.

Béguer-Pon, M., Dodson, J. J., Castonguay, M., Jellyman, D., Aarestrup, K., & Tsukamoto, K. (2017). Tracking anguillid eels: Five decades of telemetry-based research. *Marine and Freshwater Research*, *69*(2), 199–219.

Behrmann-Godel, J., & Eckmann, R. (2003). A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany. *Ecology of Freshwater Fish*, *12*(3), 196–202.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436-441.

Belpaire, C., Goemans, G., Geeraerts, C., Quataert, P., Parmentier, K., Hagel, P., & De Boer, J. (2009). Decreasing eel stocks: Survival of the fattest? *Ecology of Freshwater Fish*, *18*(2), 197–214.

Besson, M. L., Trancart, T., Acou, A., Charrier, F., Mazel, V., Legault, A., & Feunteun, E. (2016). Disrupted downstream migration behaviour of European silver eels (*Anguilla anguilla*, L.) in an obstructed river. *Environmental Biology of Fishes*, *99*(10), 779–791.

Bolland, J. D., Murphy, L. A., Stanford, R. J., Angelopoulos, N. V., Baker, N. J., Wright, R. M., … Cowx, I. G. (2019). Direct and indirect impacts of pumping station operation on downstream migration of critically endangered European eel. *Fisheries Management and Ecology*, *26*(1), 76–85.

Bormann, H., Kebschull, J., & Ahlhorn, F. (2020). Challenges of flood risk management at the German coast. In: Negm, A., Zelenakova, M. & Kubiak-Wójcicka, K. (Eds.), *Water Resources quality and Management in Baltic Sea Countries* (pp. 141–155). Cham: Springer. https://doi.org/10.1007/978-3-030-39701-2_8

Bourgeaux, J., Teichert, N., Gillier, J.-M., Danet, V., Feunteun, E., Acou, A., … Trancart, T. (2022). Modelling past migrations to determine efficient management rules favouring silver eel escapement from a large regulated floodplain Lake. *Journal for Nature Conservation*, *67*(126), 192.

Breukelaar, A., Ingendahl, D., Vriese, F., De Laak, G., Staas, S., & Klein Breteler, J. (2009). Route choices, migration speeds and daily migration activity of European silver eels *Anguilla anguilla* in the River Rhine, north-west Europe. *Journal of Fish Biology*, *74*(9), 2139–2157.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, *9*(2), 378-400.

Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R. O., Wang, Z., & Zimmermann, N. E. (2020). Model complexity affects species distribution projections under climate change. *Journal of Biogeography*, *47*(1), 130–142.

Buysse, D., Mouton, A., Baeyens, R., & Coeck, J. (2015). Evaluation of downstream migration mitigation actions for eel at an Archimedes screw pump pumping station. *Fisheries Management and Ecology*, *22*(4), 286–294.

Buysse, D., Mouton, A., Stevens, M., Van den Neucker, T., & Coeck, J. (2014). Mortality of European eel after downstream migration through two types of pumping stations. *Fisheries Management and Ecology*, *21*(1), 13–21.

Castonguay, M., & Durif, C. M. (2016). Understanding the decline in anguillid eels. *Ices Journal of Marine Science*, *73*(1), 1–4.

Chaput, G., Pratt, T. C., Cairns, D. K., Clarke, K. D., Bradford, R. G., Mathers, A., & Verreault, G. (2014). *Recovery potential assessment for the American eel (Anguilla rostrata) for eastern Canada: Description and quantification of threats*. Ottawa: Canadian Science Advisory Secretariat.

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159–170.

Cone, R. S. (1989). The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society*, *118*(5), 510–514.

Durif, C., Dufour, S., & Elie, P. (2005). The silvering process of *Anguilla anguilla*: A new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, *66*(4), 1025–1043.

Egg, L., Mueller, M., Pander, J., Knott, J., & Geist, J. (2017). Improving European silver eel (*Anguilla anguilla*) downstream migration by undershot sluice gate management at a small-scale hydropower plant. *Ecological Engineering*, *106*, 349–357.

EU. (2007). EU (European Union). 2007. Council Regulation (EC) No. 1100/2007 of September 18, 2007 Establishing Measures for the Recovery of the Stock of European Eel. Brussels.

Flávio, H., & Baktoft, H. (2021). Actel: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. *Methods in Ecology and Evolution*, *12*(1), 196–203.

Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of Statistical Software*, *8*, 1–27.

Garcia de Leaniz, C. (2008). Weir removal in salmonid streams: Implications, challenges and practicalities. *Hydrobiologia*, *609*(1), 83–96.

Hanel, R., Briand, C., Diaz, E., Döring, R., Sapounidis, A., Warmerdam, W., Andrés, M., Freese, M., Marcelis, A., Marohn, L., Pohlmann, J.-D., van Scharrenburg, M., Waidmann, N., Walstra, J., Werkman, M., de Wilde, J., & Wysujack, K. (2019). *Research for PECH Committee – Environmental, social and economic sustainability of European eel management, European Parliament, Policy Department for Structural and Cohesion Policies*. Brussels. https://www.europarl.europa.eu/RegData/etudes/STUD/2019/629189/IPOL_STU(2019)629189_EN.pdf

Hartig, F. (2017). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) RegressionModels*. R package version 0.2.0. https://CRAN.R-project.org/packages/DHARMa

ICES. (2021). European eel (*Anguilla anguilla*) throughout its natural range. In Report of the ICES Advisory Committee, 2021. ICES Advice 2021, ele.2737. nea, https://doi.org/10.17895/ices.advice.7752.

IUCN. (2021). IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-3. https://www.iucnredlist.org. Accessed on 1 June 2022.

Jellyman, D., & Unwin, M. (2019). Fine-scale swimming movement and behaviour of female silver eels, *Anguilla dieffenbachii*, within a lake affected by hydro-power generation. *Fisheries Management and Ecology*, *26*(1), 57–69.

Lenihan, E. S., McCarthy, T. K., & Lawton, C. (2019). Use of an acoustic camera to monitor seaward migrating silver-phase eels (*Anguilla anguilla*) in a regulated river. *Ecohydrology & Hydrobiology*, *19*(2), 289–295.

Lennox, R. J., Økland, F., Mitamura, H., Cooke, S. J., & Thorstad, E. B. (2018). European eel *Anguilla anguilla* compromise speed for safety in the early marine spawning migration. *Ices Journal of Marine Science*, *75*(6), 1984–1991.

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, *59*(11), 955-965.

Lowe, R. H. (1952). The influence of light and other factors on the seaward migration of the silver eel (*Anguilla anguilla* L.). *The Journal of Animal Ecology*, *21*, 275–309.

Lucas, M., & Baras, E. (2001). *Migration of freshwater fishes*. John Wiley & Sons. https://doi.org/10.1002/9780470999653

Lucas, M. C., Bubb, D. H., Jang, M. H., Ha, K., & Masters, J. E. (2009). Availability of and access to critical habitats in regulated rivers: Effects of low-head barriers on threatened lampreys. *Freshwater Biology*, *54*(3), 621–634.

MacNamara, R., & McCarthy, T. K. (2012). Size-related variation in fecundity of European eel (*Anguilla anguilla*). *ICES Journal of Marine Science/Journal du Conseil*, *69*(8), 1333–1337.

Marohn, L., Prigge, E., & Hanel, R. (2014). Escapement success of silver eels from a German river system is low compared to management-based estimates. *Freshwater Biology*, *59*(1), 64–72.

Nunn, A., & Cowx, I. (2012). Restoring river connectivity: Prioritizing passage improvements for diadromous fishes and lampreys. *Ambio*, *41*(4), 402–409.

Piper, A. T., Manes, C., Siniscalchi, F., Marion, A., Wright, R. M., & Kemp, P. S. (2015). Response of seaward-migrating European eel (*Anguilla anguilla*) to manipulated flow fields. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1811), 20151098.

Piper, A. T., Svendsen, J. C., Wright, R. M., & Kemp, P. S. (2017). Movement patterns of seaward migrating European eel (*Anguilla anguilla*) at a complex of riverine barriers: Implications for conservation. *Ecology of Freshwater Fish*, *26*(1), 87–98.

Piper, A. T., Wright, R. M., Walker, A. M., & Kemp, P. S. (2013). Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. *Ecological Engineering*, *57*, 88–96. https://doi.org/https://doi.org/10.1016/j.ecoleng.2013.04.030.

R-Core-Team. (2022). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass'. *Cran r*, *538*, 113–120.

Teichert, N., Tetard, S., Trancart, T., de Oliveira, E., Acou, A., Carpentier, A., … Feunteun, E. (2020). Towards transferability in fish migration models: A generic operational tool for predicting silver eel migration in rivers. *Science of the Total Environment*, *739*(140), 69.

Thierumel, B. (2019). suncalc: *Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*. R packageversion 0.5.1. https://espejito.fder.edu.uy/cran/web/packages/suncalc/suncalc.pdf.

van Keeken, O. A., van Hal, R., Volken Winter, H., Tulp, I., & Griffioen, A. B. (2020). Behavioural responses of eel (*Anguilla anguilla*) approaching a large pumping station with trash rack using an acoustic camera (DIDSON). *Fisheries Management and Ecology*, *27*(5), 464–471.

van Keeken, O. A., van Hal, R., Winter, H. V., Wilkes, T., & Griffioen, A. B. (2021). Migration of silver eel, *Anguilla anguilla*, through three water pumping stations in The Netherlands. *Fisheries Management and Ecology*, *28*(1), 76–90.

Venditti, D. A., Rondorf, D. W., & Kraut, J. M. (2000). Migratory behavior and forebay delay of radio-tagged juvenile fall Chinook salmon in a lower Snake River impoundment. *North American Journal of Fisheries Management*, *20*(1), 41–52.

Verbiest, H., Breukelaar, A., Ovidio, M., Philippart, J. C., & Belpaire, C. (2012). Escapement success and patterns of downstream migration of female silver eel *Anguilla anguilla* in the river Meuse. *Ecology of Freshwater Fish*, *21*(3), 395–403.

Vergeynst, J., Pauwels, I., Baeyens, R., Mouton, A., De Mulder, T., & Nopens, I. (2021). Shipping canals on the downstream migration route of European eel (*Anguilla anguilla*): Opportunity or bottleneck? *Ecology of Freshwater Fish*, *30*(1), 73–87.

Verhelst, P., Baeyens, R., Reubens, J., Benitez, J.-P., Coeck, J., Goethals, P., … Mouton, A. (2018). European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal. *Fisheries Research*, *206*, 176–184.

Verhelst, P., Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., … Mouton, A. (2018). Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management. *Fisheries Research*, *199*, 252–262.

Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., & Moens, T. (2021). Toward a roadmap for diadromous fish conservation: The Big Five considerations. *Frontiers in Ecology and the Environment*, *19*(7), 396–403.

Verhelst, P., Reubens, J., Pauwels, I., Buysse, D., Aelterman, B., Van Hoey, S., … Mouton, A. (2018). Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area. *Ecology of Freshwater Fish*, *27*(1), 471–480.

Vis, H. (2021). KRW-visstandbemonstering Westerwoldse Aa Noord 2020 (Report) (p. 18). VisAdvies BV, Nieuwegein. Projectnummer VA2019_20.

Vøllestad, L., Jonsson, B., Hvidsten, N., Næsje, T., Haraldstad, Ø., & Ruud-Hansen, J. (1986). Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(10), 1909–1916.

Wright, G., Wright, R., & Kemp, P. (2014). Impact of tide gates on the migration of juvenile sea trout, Salmo trutta. *Ecological Engineering*, *71*, 615–622.

Wright, G., Wright, R., & Kemp, P. (2015). Impact of tide gates on the migration of adult European eels, *Anguilla anguilla*. *Estuaries and Coasts*, *38*(6), 2031–2043.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Huisman, J. B.J., Höhne, L., Hanel, R., Kuipers, H., Schollema, P. P., & Nagelkerke, L. (2023). Factors influencing the downstream passage of European silver eels (*Anguilla anguilla*) through a tidal sluice. *Journal of Fish Biology*, *103*(2), 347–356. https://doi.org/10.1111/jfb.15398