



ARTICLE

Migration of silver eel, *Anguilla anguilla*, through three water pumping stations in The Netherlands

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Abstract

European eel, *Anguilla anguilla* (L.), migrating to sea encounter many man-made structures that can hamper and delay migration or induce mortality. Three pumping stations in Friesland, the Netherlands, were covered with acoustic receivers. Ninety-three silver eels tagged with acoustic transmitters were released in the polders upstream of the stations and 89% were detected passing a pumping station. The majority of silver eels passed the stations within a day after arriving at the station. Four silver eels stayed for longer than 2 weeks before passage, and 18 were detected at the receiver downstream the pumping station for more than one day, with detections up to several weeks. These detections probably indicated a dead eel, but could also indicate a live eel remaining at the site. Most of the silver eels passed the pumping stations within a day after release, so fish-friendly pumps will benefit the migrating population most. In the Netherlands, there are several thousand pumping stations. Installing fish passages near these stations is not feasible due to high costs. Prioritising all these sites in relation to the degree of blockage, mortality rates and its relative importance for migratory fish, can maximise the effectiveness of measures and mitigation taken.

KEYWORDS

Anguilla, barriers, conservation, fish behaviour, fish migration, telemetry

1 | INTRODUCTION

European eel *Anguilla anguilla* (L.) stocks are in strong decline since the 1970s (ICES, 2018) as a result, amongst others, of migration barriers, fisheries, habitat loss and deterioration, pollution, parasites and changes in oceanic conditions (Buysse, Mouton, Stevens, den Neucker, & Coeck, 2014; Drouineau et al., 2018; Feunteun, 2002; Moriarty & Dekker, 1997; Palstra, Heppener, van Ginneken, Székely, & Van den Thillart, 2007; Verhelst, Buysse, et al., 2018; Westerberg et al., 2018). Man-made structures such

as pumping stations, sluices, weirs and hydropower stations form migration barriers for the catadromous eel and can cause migration delay or mortality (e.g., Buysse, Mouton, Baeyens, & Coeck, 2015; Buysse et al., 2014; Jansen, Winter, Bruijs, & Polman, 2007; Winter, Jansen, & Bruijs, 2006). It was estimated that about 91 tonnes of fish per year, one-third being eel, get damaged by structures in the Netherlands alone (Kunst et al., 2010). Van de Wolfshaar et al. (2018) estimated that about 35% of the eel population dies due to passage through pumps placed between polder waters to adjacent water bodies. The damage and related mortality due to

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passage are species (behaviour) and size dependent, and are caused by the type of pump blade, impact with the blades or other objects in the pumping station, abrupt changes in pressure, turbulence and fast water flows (Buysse et al., 2014; STOWA, 2012). The eel mortality rate of a pumping station depends on the type of turbine and ranges from 0% to 100% (STOWA, 2012).

In the Netherlands, there are several thousand larger and smaller pumping stations, which can delay or block silver eels during their migration from polders through larger canals, rivers and/or lakes towards sea. On their way to the sea, silver eels may have to pass several pumping stations. A delay in the migration of downstream migrating silver eels may be caused by sounds or vibrations from pumping stations or the physical barrier posed by the trash racks in front of the turbines (Bolland et al., 2019; van Keeken, van Hal, Winter, Tulp, & Griffioen, 2020). At a short distance from the pumping station, silver eels could hesitate to pass a station, caused by physical contact with the trash rack in front of the pumping station. Several studies have indicated exploration behaviour of silver eel in front of the trash rack (e.g., Behrmann-Godel & Eckmann, 2003; Bolland et al., 2019; Gosset, Travade, Durif, Rives, & Elie, 2005; van Keeken et al., 2020; Winter et al., 2006). Behrmann-Godel and Eckmann (2003) found three out of six tagged silver eels passed through the turbines of a hydropower station on day of arrival, while the other three approached the turbines, turned round and swam rapidly upstream near the riverbank up to 1 km, then they approached the structure again. This behaviour was repeated several times per day and on consecutive days until finally the silver eels passed through the turbines.

This paper focusses on the barrier function of pumping stations in polders for migrating silver eel and asks the question: Do pumping stations delay or block silver eel migration? The focus of most studies is on mortality caused by hydropower or pumping stations, but the barrier effects caused by these structures are often understudied and underrated. Insights into the factors that cause blockage are therefore needed, to avoid chances that installing fish-friendly pumps diminishes the mortality rates, but potentially results in blocking the migration instead. Estimates of the percentage of eels delayed or blocked by pumping stations during their migration can be used in models estimating the numbers and proportion of the population of silver eels migrating. Estimates of lethal damage of silver eel passing through different types of pumping stations in the Netherlands have already been assessed (e.g., Kunst et al., 2010; STOWA, 2012), but estimates of the percentage of migrating silver eel in a water body that eventually bypass a pumping station and delay times during their migration caused by pumping stations has not yet been investigated. A study on delay in migration has been conducted in Belgium near two pumping stations, a weir and tidal sluices and substantial delays and exploratory behaviour near barriers were observed (Verhelst, Buysse, et al., 2018). Long delays (up to 68.5 days) were also found in front of several structures in a

heavily regulated river in the UK (Piper, Wright, Walker, & Kemp, 2013).

Acoustic telemetry was used to study the barrier function of three pumping stations in Friesland, the Netherlands. The aims were to study (a) the success rate of eels passing the pumping stations and (b) migration delay of eels upstream the pumping stations.

2 | MATERIAL AND METHODS

Three study sites were chosen to assess the percentage of silver eels passing pumping stations: these were Miedema, Ropta and Schalsum in Friesland, the Netherlands (Figure 1). The selection of sites was based on location, pump type, pumping volume and the possibility of migration of silver eel from the polder system only through the pumping station to the sea. The pumping stations at Miedema and Ropta both consisted of two closed propeller pumps and a smaller third propeller pump, with total capacities of 630 and 460 m³/min, respectively. Schalsum consisted of two Archimedes screw pumps with a total capacity of 300 m³/min. Both Miedema and Ropta pumping stations are in direct connection to the Dutch Wadden Sea, while Schalsum is connected to a freshwater canal with two major exit points to the Wadden Sea at Harlingen and Dokkumer Nieuwe Zijlen. Water flow velocities were not measured directly, but were calculated by the regional water authorities based on measurements of the pumping station dimensions, theoretical capacity of the pumps and water level. The maximum velocities were 0.30 m/s for Miedema, 0.45 m/s for Ropta and 0.29 m/s for Schalsum.

Vemco coded V9-2L transmitters and VR2W receivers were used, operating at 69 kHz (Canada, <http://www.VEMCO.com>). In total 11 receivers were placed between 27 and 29 September 2011 and retrieved between 2 and 4 April 2012. Three receivers were placed near each of the pumping stations and two receivers at the exit point of Friesland towards the Wadden Sea: at Harlingen and Dokkumer Nieuwe Zijlen. At each of the pumping station sites, one receiver was placed 220–280 m upstream of the pumping station, one receiver just upstream of the pumping station 5–10 m from each pumping station, and one receiver immediately downstream of the pumping station 10–20 m from each station. Detection range tests indicated a detection range of approximately 200 m. Transmitter signals were emitted random between 40 and 70 s.

The silver eels used in this study were obtained from two commercial fishermen. Eels were caught with fykes, which were emptied the day before tagging. The eels that were tagged showed visible signs of silvering, that is, differentiated lateral line and white-silver ventral and black dorsal surfaces (Palstra, Guerrero, de Laak, Breteler, & van den Thillart, 2011). Morphometric features were measured to determine the sex and eel maturation stage according to Durif, Dufour, and Elie (2005): total length (total length to nearest mm), vertical and horizontal eye diameter (to nearest 0.1 mm) and pectoral

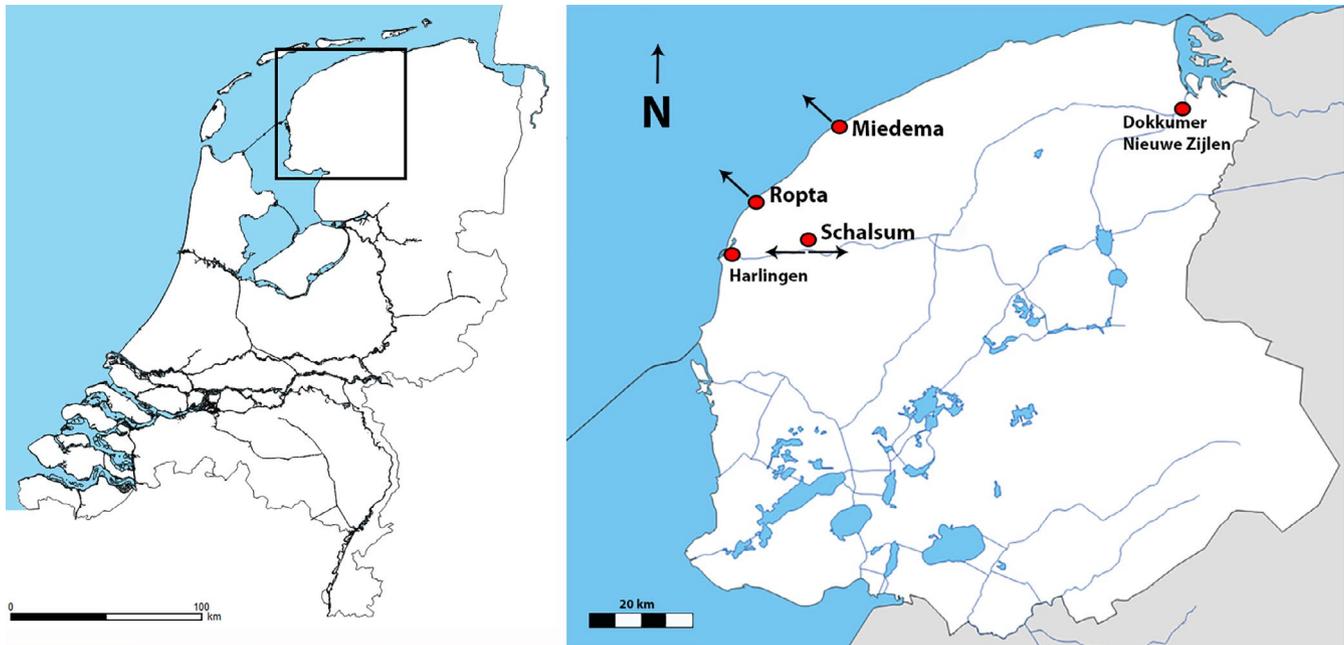


FIGURE 1 Map of Friesland, the Netherlands, with the three study sites and exit points. Ropta and Miedema exit into the Wadden Sea, Schalsum into a canal with connection to Harlingen and Dokkumer Nieuwe Zijlen

TABLE 1 Number of tagged eels per study area with morphometric measurements: minimum, mean and maximum total length (TL), horizontal (Eh) and vertical (Ev) eye diameter and pectoral fin length (PF). All measurements in mm with \pm SD

Pumping station	N eels	Mean TL (mm)	Min & max TL (mm)	Mean Eh (mm)	Mean Ev (mm)	Mean PF (mm)
Miedema	31	722 \pm 59.1	624–852	9.6 \pm 0.84	8.6 \pm 0.90	36.3 \pm 3.90
Ropta	31	728 \pm 57.4	615–861	9.6 \pm 0.83	8.9 \pm 0.87	36.7 \pm 3.94
Schalsum	31	723 \pm 59.5	612–940	9.8 \pm 0.85	9.3 \pm 0.87	35.9 \pm 4.02

fin length (to nearest 0.1 mm). In total 93 eels between 61.2 cm and 94.0 cm total length were tagged (Table 1). All eels were female, as males (max length 45–50 cm) do not grow that large before silvering and migrating (Dekker, 2000). All individuals were anaesthetised with 2-phenoxy-ethanol (0.9 ml/L). The eels were surgically implanted with a V9-2L transmitter in the body cavity by making a mid-ventral incision of 2–3 cm in the posterior quarter of the body cavity. The surgical procedure used was the best amongst five different procedures tested for European eel by Baras and Jeandrain (1998). The incision was closed by two sutures (absorbable, braided Vicryl 3/0, FS2 needle). Eels from Schalsum were also tagged with a floy tag, in case local fishermen would catch the eel, and they could return it to the water. Surgery lasted 3–5 min. Eels were observed in a recovery tank until swimming behaviour reappeared and then released at the study site upstream from the pumping stations. The eels were released in two batches: 15 eels per location on the 5 October 2011 and 16 eels per location on 19 October 2011. Release of the eels occurred at public accessible locations, which were 1,700 m upstream from the pumping station Miedema, 1,150 m upstream from Ropta and 3,000 m upstream from Schalsum. The eels were released around 13.00 p.m. at Miedema, 10.30 a.m. at Ropta and 15.30 p.m. at Schalsum during both occasions.

The number of eels at each receiver, and date and time of the first and the last detection at each receiver were calculated using the statistical software SAS (SAS version 9.3: SAS Institute Inc., 2011). Data from the receivers were corrected for time drift using a linear relationship, using Vemco VUE software (Vemco Users Environment, VEMCO Ltd, Canada). The Vemco receivers placed in the polder upstream close to the pumping station and further away from the pumping station overlapped partially in detection range and as a result eels were sometimes detected at the same time by both receivers when they were in the area between both receivers. Correction for time drift was used to set the correct time at both receivers. When a single detection was detected at both receivers at the same time, this detection was then labelled as “both receivers” and deleted from the list of detections of each individual receiver.

The success rate of eels passing the pumping stations was calculated as percentage of the eels passing the stations. To assess the delay of eels passing the pumping stations, the number of events when a pumping station was in operation and when a pumping station was not pumping water was assessed for each eel, when the eel was within the detection range of the upstream receiver close to the pumping station. An event could last from less than one hour to several days, depending on the water level in the polder. Water volume

data for each turbine was registered every 15 min. Differences in appearance at the receiver upstream of the pumping station were tested using a binomial distribution (R: www.r-project.org). A quasi-binomial GLM with a logit link function was performed to model the odds of silver eels passing the pumping station in relation to the volume of water pumped per day, with month and location as additional covariates. The number of silver eels that passed through the pumping stations being the binomial successes and the number of eels that did not yet passed the pumping station being the binomial failures. Water volume was expressed in mega-litres. Location was introduced in the model as a categorical covariate with three levels, with location Miedema as the reference level, and month introduced in the model as a categorical covariate with six levels (months 1, 2, 3, 10, 11 and 12) with the first month as reference level. Holm's correction for multiple testing (Holm, 1979) was applied on the *p*-values. Deviance residuals were used to assess the model diagnostics (using a residuals versus fitted plot, a half-normal plot, a non-linearity plot and an observed versus predicted plot), thereby checking for violations of any of the model assumptions. A significance level of $\alpha = 0.05$ was used.

3 | RESULTS

Of the 93 tagged silver eels, 91 were detected by at least one receiver (Table 2, Figure 2) and 81 of the tagged silver eels (89%) passed the pumping stations. Based on the data from the receivers, Ropta and Schalsum had success rates of 94% (29 eels) and 100% (30 eels) of eels passing the pumping station, while Miedema had a success rate of 73% (22 eels). In total, 77 silver eels were detected at the receivers downstream of the pumping station at any time during the test. However, four eels at Miedema and one eel at Ropta from the second batch were detected at the receiver close to the pumping station during the evening of 19 October. These eels were not detected at the receiver behind the pumping station, but were also not seen at any receiver in the polder at a later time. Assuming these eels passed the pumping station and were not being detected by the receiver behind the station, the success rate would increase to 87% for Miedema and 94% for Ropta. Additionally, four eels released upstream of the Schalsum pumping station were detected at the receiver at Harlingen, but were missed by the receiver directly downstream the pumping station.

Eighteen silver eels (60%) released upstream from the Schalsum pumping station and detected at any receiver in the polder were detected at the exit points, including 17 (57%) at Harlingen and one (3%) at Dokkumer Nieuwe Zijlen (Table 3). Four eels (13%) from Schalsum were caught at Harlingen and two eels (7%) were caught near the town of Welsrijp and Dongjum, which are close to Schalsum pumping station. The silver eels at Miedema and Ropta migrated from the polder into the Wadden Sea and were therefore not expected at Harlingen or Dokkumer Nieuwe Zijlen.

Silver eels tagged on 5 October 2011 were detected for the first time downstream of the pumping stations over a longer

TABLE 2 Numbers of eels detected at the receivers near the pumping stations

Pumping station	Eels tagged	Detected at any VR2W	Only at VR2W far upstream from station	VR2W in polder far upstream from station	Both VR2W in polder	VR2W close upstream to pumping station	VR2W downstream pumping station	N eel downstream station	% eel downstream pumping station
Miedema	31	30	2	30	16	24	22	22 (26)	73 (87)
Ropta	31	31	0	20	22	31	29	29 (30)	94 (97)
Schalsum	31	30	0	30	27	30	26	30	100
Total	93	91	2	80	65	85	77	81	89
%		100	2	88	77	93	85	89 (95)	

Note: Eels detected only at the VR2W far upstream from pumping station were not detected at any other VR2W. Four eels at Miedema and one eel at Ropta were not detected at the receiver behind the pumping station, but were all last seen at the 19th of October. There is a possibility that these eels were not detected at the receiver downstream the pumping station and are therefore included in the table.

FIGURE 2 Map of Friesland, the Netherlands, with the number of eels per location. P indicates the number of eels detected/number of eels released at each site

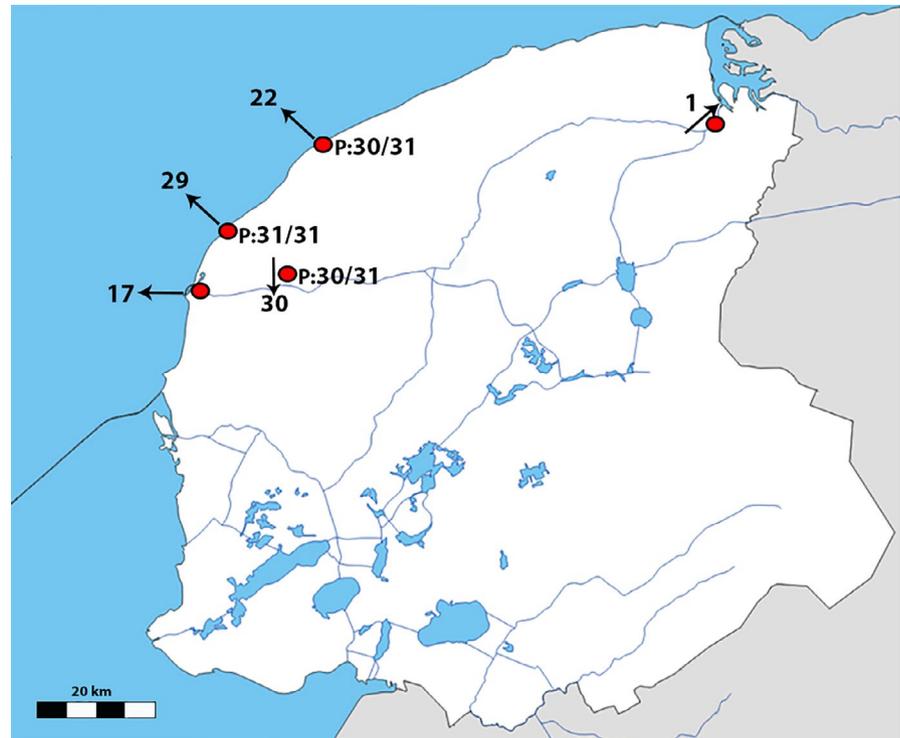


TABLE 3 Numbers of eels detected at Harlingen or Dokkumer Nieuwe Zijlen or caught by a commercial fisherman either inside or outside the polder

Pumping station	Detected at any VR2W	VR2W at Harlingen	VR2W at Dokkumer Nieuwe Zijlen	Caught and released outside the polder	Caught and released inside the polder
Miedema	30	0	0	0	1
Ropta	31	0	0	0	1
Schalsum	30	17	1	6 ^a	0
Total	91	17	1	6	2
Percentage	100	19	1	7	2

^aFour of these eels were also detected by the VR2W at Harlingen.

period of time; 13 eels took five days or more to pass the pumping station after first detection upstream the pumping stations, with one eel staying 84 days before passing. Silver eels tagged on 19 October 2011 were almost all detected downstream of the pumping station on the same day as release, with only three eels detected later than the tagging day (Figure 3a-b). For the silver eels released on 5 October 2011, the highest number of eels passing through a pumping station was three eels on 9 October at Schalsum, four eels on 12 October at Miedema and nine eels on 18 October at Ropta. The majority of silver eels passed a pumping station the same day after first detection at the receiver upstream of the pumping station (Figure 3c-d); 27 eels (60%) released on 5 October passed the pumping station the day of first detection upstream of the pumping station, while 41 eels (86%) released on 19 October passed the pumping station the same day.

There were two events when silver eels migrated through the pumping station at Miedema in higher numbers: 12 October with

four eels and 19 October with nine eels (Figure 4a). The latter event was during a period of rainfall with larger volumes of water being pumped through the pumping station. There were also two events at Ropta: 18 and 19 October with nine eels passing the pumping station each day (Figure 4b) during a period when large volumes of water were pumped. There were two events at Schalsum on 9 October with three eels and 19 October with 11 eels (Figure 4c), also during periods of larger volumes of water being pumped through the pumping stations.

The probability of a silver eel passing through the pumping station with increased volume of water pumped on any day was high (*t* test, effect size = 0.185, $p < 0.001$, Table 4), indicating more eels pass the pumping stations during periods of higher water volume discharged. There were also large differences found between the locations (*t* test, effect size Roptazijl: 2.399, effect size Schalsum: 3.448, $p < 0.05$, Table 4). The quasi-binomial dispersion parameter was estimated to be 2.758. The mean absolute deviation between

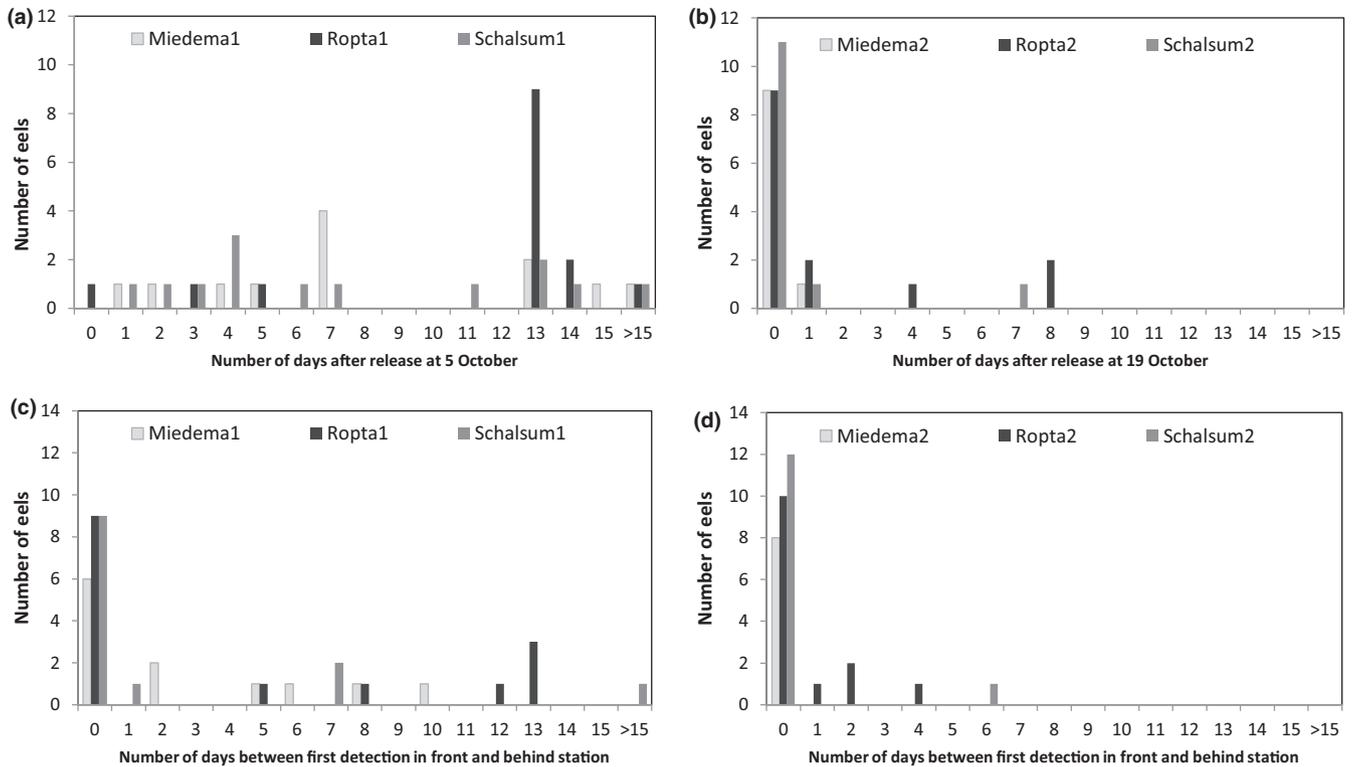


FIGURE 3 (a-d) Days between release and detection for the first time at the receiver behind the pumping station at polder side (a,b) and days between first detection at the receiver close to the pumping station at polder side and first detection at the receiver behind pumping station (c,d). Batch 1 = released at the 5 October 2011 (a,c), batch 2 = released at the 19 October 2011 (b,d)

the observed and predicted number of silver eels passing through the pumping station, used as a general check for the model fit, was computed to be 0.119. No noteworthy violation of the model assumptions were found.

Of the silver eels released on 19 October and detected passing a pumping station, 81% (30 eels) passed the pumping station during the first event when the pumping stations were in operation (Figure 5). Seven eels (19%) were in front of the pumping stations during more than one event. The highest number of events with a pumping station in operation and a silver eel having the possibility of passing the station was six (transmitter 2,805). From the silver eels released on 5 October and detected passing a pumping station, 33% (13 eels) passed the pumping station during the first event when the pumping stations were pumping. Of the silver eels that were in front of the pumping stations during more events, 33% (13 eels) were there during more than five events. The highest number of events with the pumping station in operation was 20 for this batch. Of the silver eels that did not pass a pumping station and were also not assumed to have passed the pumping station undetected (eels marked H and * in Figure 5), only one eel (transmitter 2,800) had a total of 12 events when the eel was close upstream the pumping station,

of which five were when the pumping station was in operation and seven when no water was pumped.

In total 85 silver eels were detected upstream of the pumping stations. Of these 33 were detected both day and night, seven were detected only during the day and 45 were detected only during the night (Figure 6.). A total of 52 detections were only during the day or the night. A binomial distribution (R-function dbinom) confirmed there was a greater probability of being detected during the night ($p < 0.05$; 45 of 52 detections). Thirty-five eels (87%) released on 5 October were detected at the receiver downstream of the pumping station between 20.00 p.m. and 06.00 a.m. (Figure 7a), and 31 eels (83%) from the 19 October batch between 16.00 p.m. and 23.00 p.m. (Figure 7b).

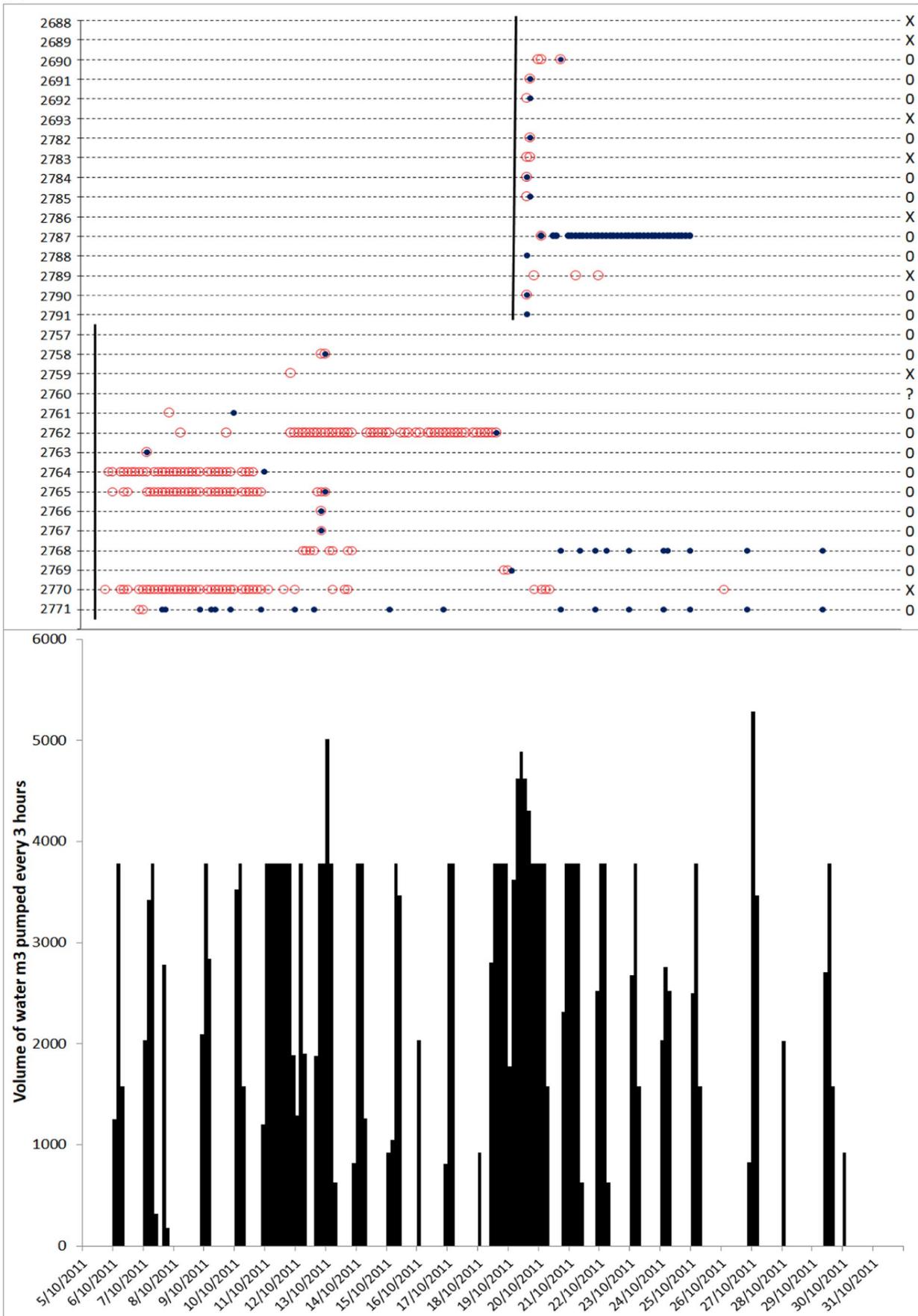
4 | DISCUSSION

The focus of this study was on the barrier function of pumping stations in polders for downstream migrating silver eel; to what extend mortality occurred due to passage through the pumping stations was not determined. While 94%–100% of the silver

FIGURE 4 (a-c) Detection of transmitter close in front (red open circle) and behind (blue closed circle) pumping station (top) and volume of water pumped by the pumping station per 3 hr (bottom) between the 5 and 31 October 2011 for Miedema (a), Ropta (b) and Schalsum (c). Vertical lines in top figure indicate release date. ?, eel not detected at any receiver X, eel detected but did not went through pumping station; O, eel went through pumping station during study; H, detected at Harlingen; L, detected at Dokkumer Nieuwe Zijlen

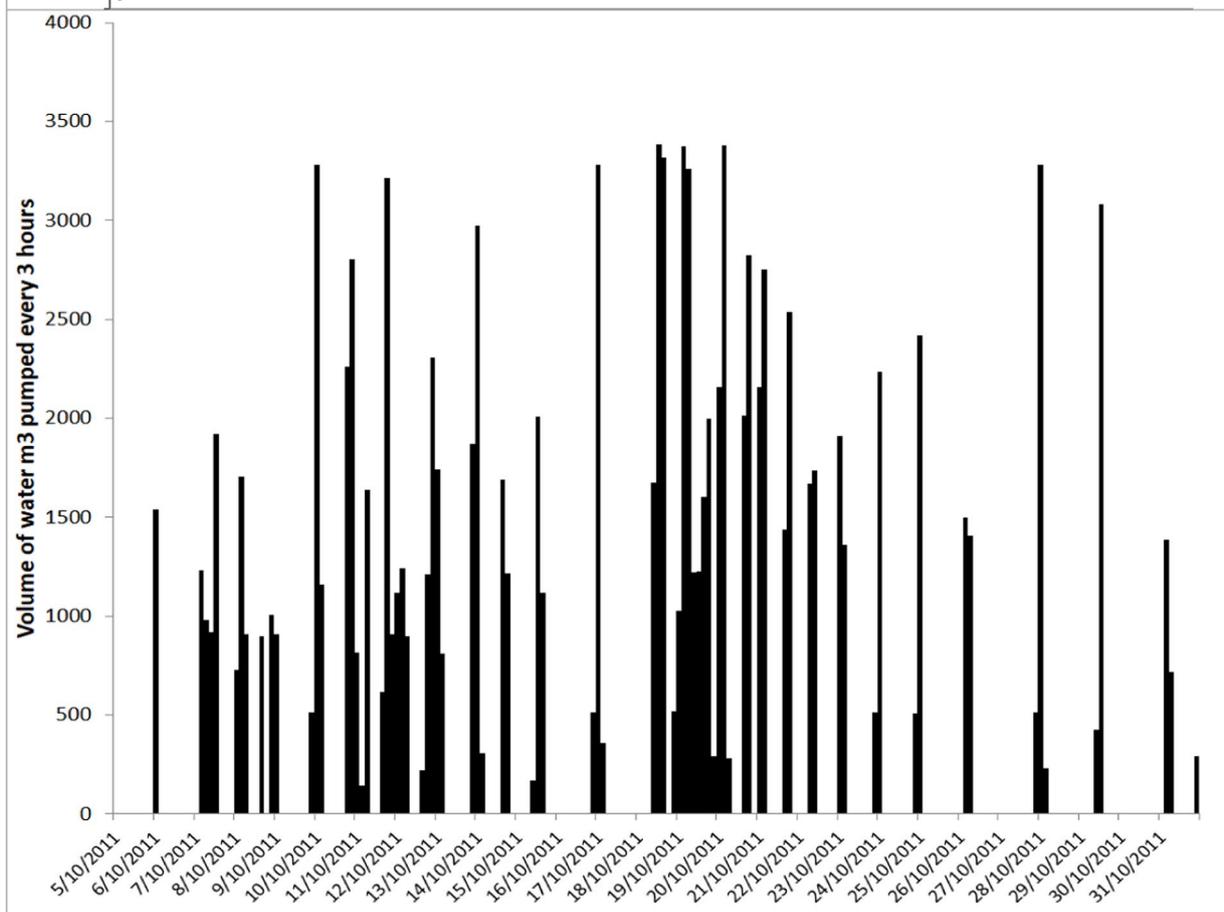
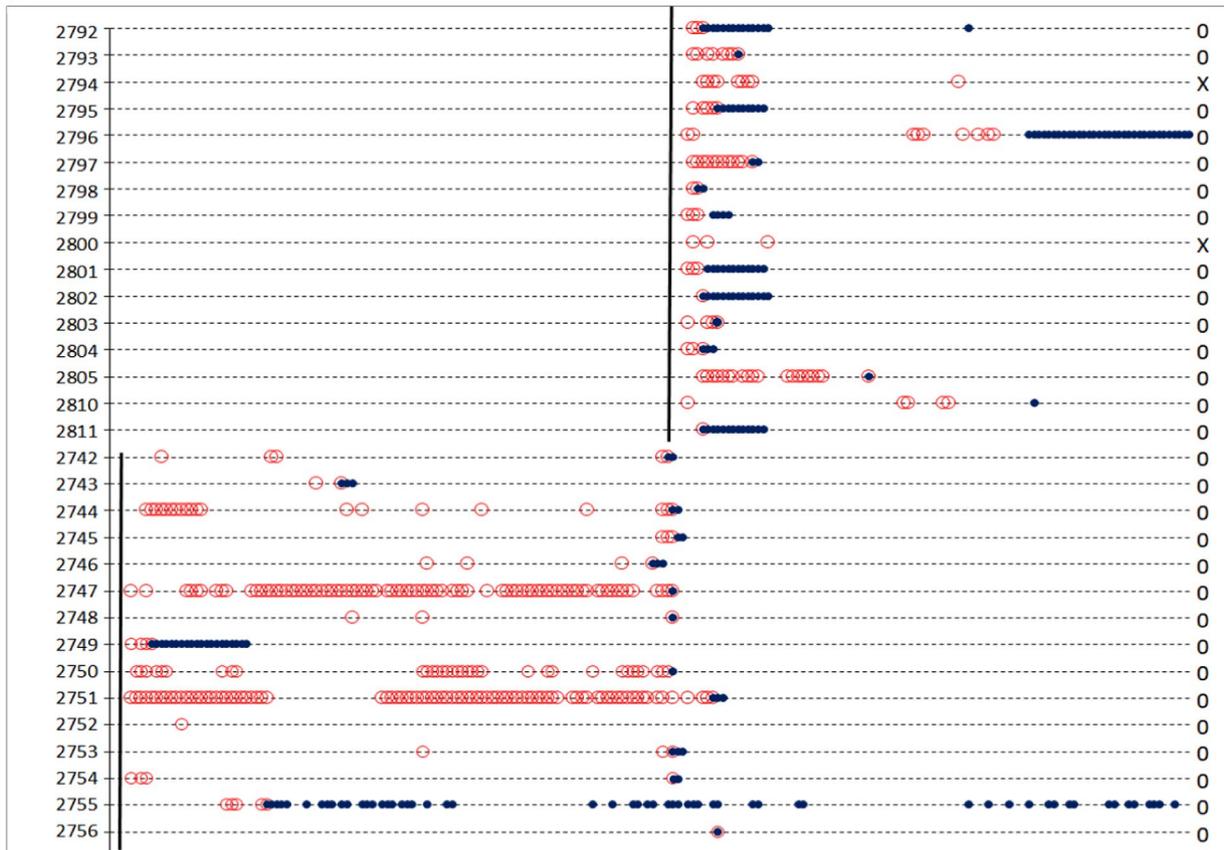


(a)



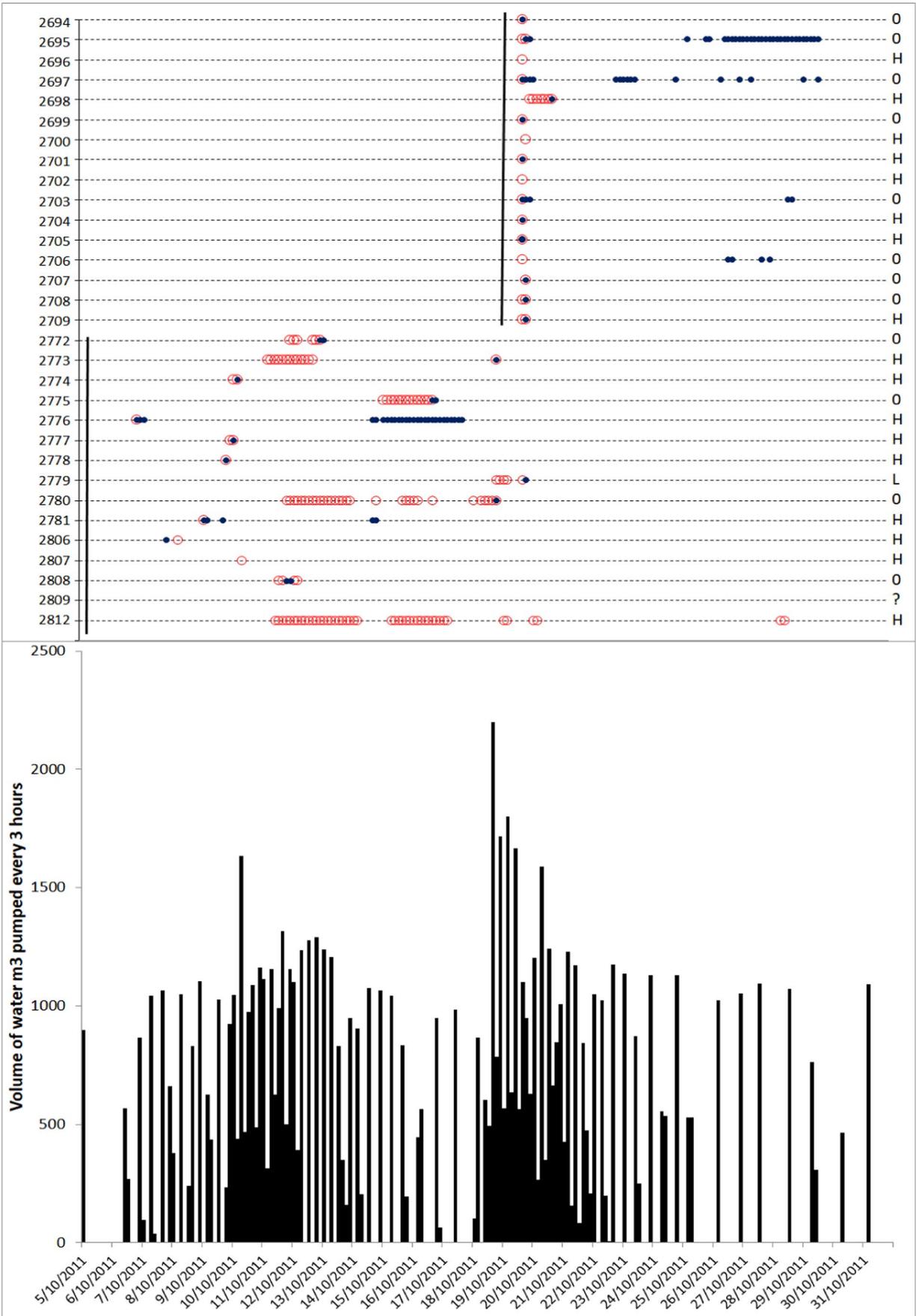


(b)





(c)



Coefficient	Estimate	Standard error	t value	Pr (>t)	Corrected p-value
Intercept	-12.396	2.400	-5.165	3.54E-07	3.19E-06
Volume water	0.185	0.039	4.736	2.87E-06	2.30E-05
Roptazijl	2.399	0.831	2.888	0.00405	0.020248
Schalsum	3.448	0.936	3.686	0.000254	0.001779
Month 2	-11.466	2,379.846	-0.005	0.996158	1
Month 3	4.624	2.588	1.786	0.074676	0.298703
Month 10	6.584	1.893	3.479	0.00055	0.003299
Month 11	-11.394	2,249.997	-0.005	0.995962	1
Month 12	1.385	2.406	0.576	0.565174	1

TABLE 4 Summary of the quasi-binomial GLM

Note: The covariate water volume was put into the model as mega-litres. Dispersion parameter for the quasi-binomial GLM was estimated to be 2.7515356. Corrected *p*-values were computed using Holm's correction for multiple comparisons. Holm's corrected *p*-values smaller than 0.05 are considered to be significant.

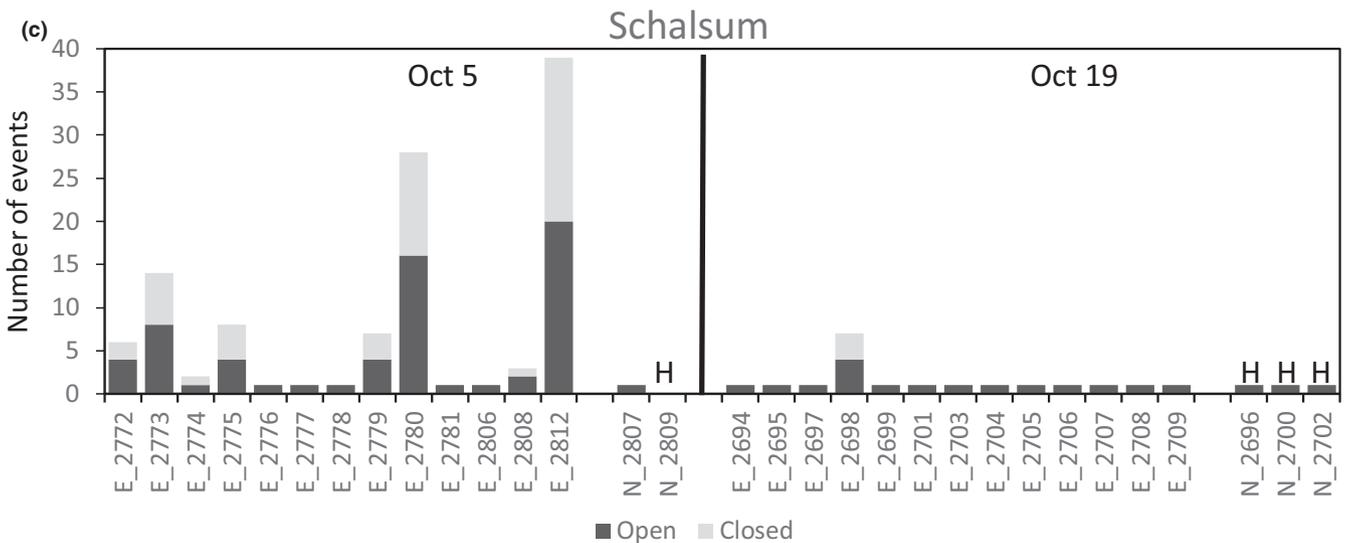
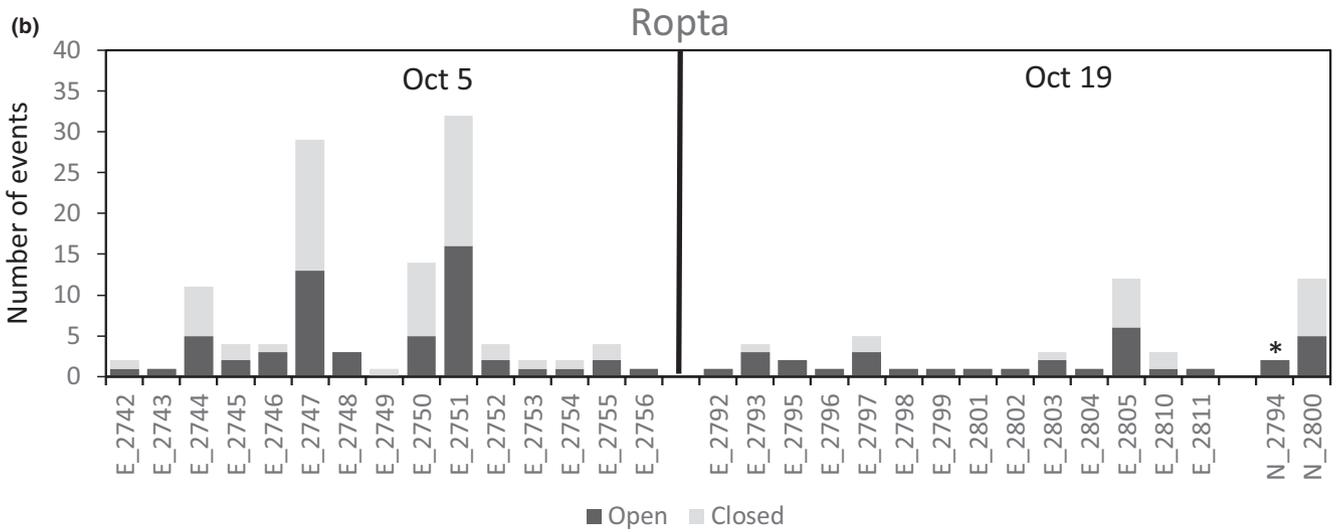
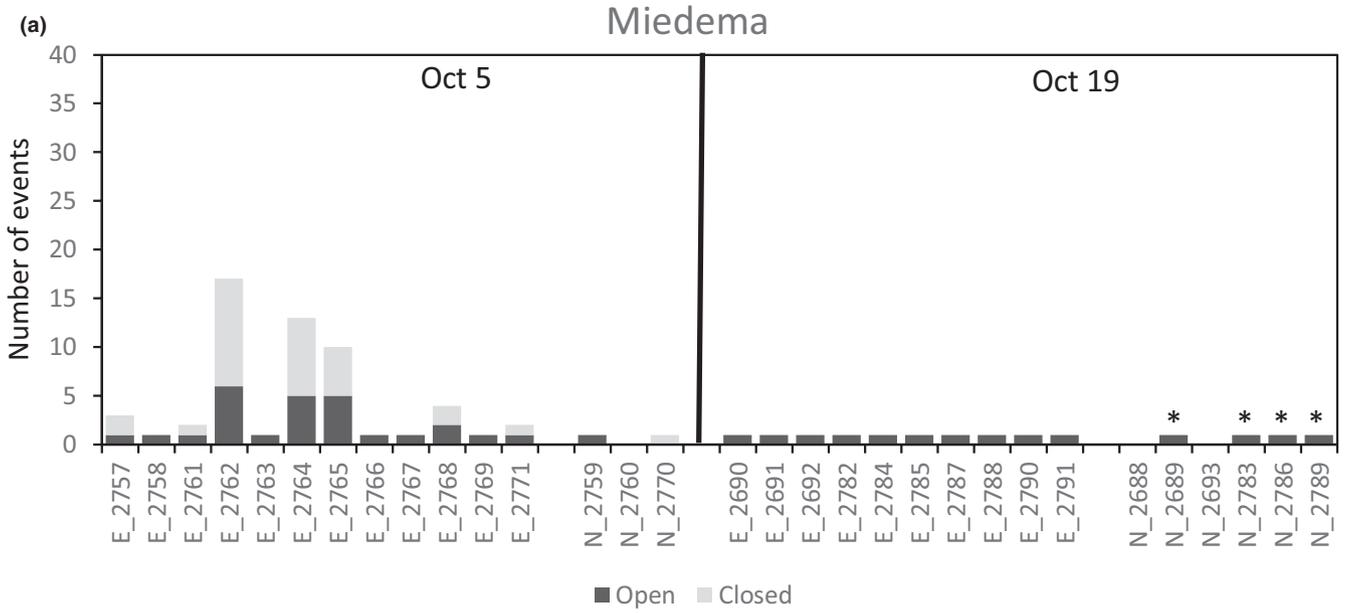
eels passed the pumps at Ropta (closed propeller pump) and Schalsum (Archimedes pump), 73% of the silver eels passed the pumps at Miedema (closed propeller pump). There is no clear explanation why less eel approached and passed the pumping station at Miedema compared with the other two pumping stations. However, silver eels could postpone their migration to later years. In a study in a polder in Belgium, a proportion of tagged eels also showed no migration in the same year (Verhelst, Buysse, et al., 2018) and these eels were detected in later years. Winter et al. (2006) also reported that eel equipped with transponders during a study at a large river in the Netherlands postponed the migration up to 2 years.

While silver eels from the first batch, released on 5 October 2011, arrived at the pumping station for the first time over a longer period of time, most eels from the second batch, released on 19 October 2011, arrived at the pumping station the same evening after release. The majority of the tagged silver eels passed the pumping station within a day after arriving at a pumping station during the first possible pumping event. Some silver eels even passed within minutes after being detected at the receiver upstream of the pumping station. However, some silver eels stayed upstream of the pumping stations for a prolonged period of time, even up to over two months before passing the pumping station and having multiple events with the pumping station pumping to pass. Eventually, most silver eels passed the pumping stations. Of 17 tagged eels detected at a large pumping station in the United Kingdom, 82.1% retreated back upstream and 58.8% eventually passed through pumps after delays (9.5 ± 11.0 days), with the shortest and longest delays of 53 min and 31 days respectively (Bolland et al., 2019). In a study with 50 eels tagged in

a polder in Belgium, Verhelst, Buysse, et al. (2018) found a mean resident time of 12.5 days \pm 23 days (range 0.01–91.7 days) for eel upstream an Archimedes screw pumping station. Of the 136 eels detected at the entrance of a hydropower station in the river Meuse by Winter et al. (2006), differences in time between first detection and passage also differed, with 60% of the silver eels detected once (one detection or a continuous series of detections with 2 min intervals), while 40% showed recurrence with larger intervals above 2 min, varying from several minutes to several weeks.

The fast migration of silver eels through the pumping stations after arrival could have been triggered by increased volumes of pumped water, caused by periods of rainfall, in combination with exploration behaviour of eels returned after tagging. This was seen most for silver eels from the second batch, which were tagged and released during a period with rainfall and pumping and passing the pumping stations the same day during the first possible event. However, to analyse initiation and intensity of silver eel migration properly in relation to pumping volume or water discharge, datasets including more years and sites are needed and is therefore beyond the scope of this study. As in other telemetric studies, episodes of active downstream migration of silver eels were intermittent, and occurred during "environmental windows" that were related to increased water discharge (Bruijs et al., 2003; Deelder, 1954; Durif, Gosset, Rives, Travade, & Elie, 2003; Travade, Larinier, Subra, Gomes, & De-Oliveira, 2010; Verhelst, Buysse, et al., 2018; Vøllestad, Jonsson, Hvidsten, & Naesje, 1994; Winter et al., 2006). Lowe (1952) concluded that silver eels migrated in major peaks on very few nights during a season. Vøllestad et al. (1994) found that water temperature and day length were important factors to initiate migration,

FIGURE 5 (a-c) Number of events for each eel, with pumping stations either pumping water during a period of time, or not being in operation. One event is the period a pumping station is either in or out operation. E_: eels detected going through the pumping station N_: eels not detected going through the pumping station *: eels from the second batch last seen at the 19 October at the receiver close upstream the pumping stations of Miedema and Ropta, and not being detected downstream the pumping station. Since however most eels of this batch passed the pumping station this day, these five eels could also have passed the receiver downstream unnoticed H: eels not detected at the receiver downstream pumping station Schalsum, but detected at the receiver at Harlingen



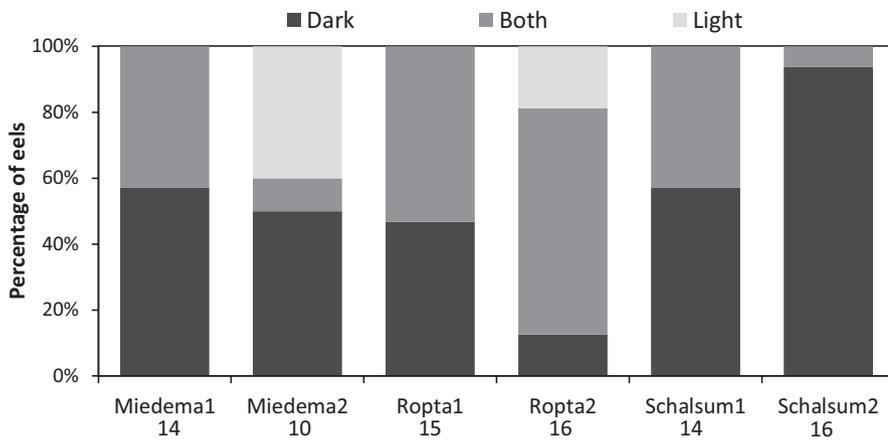


FIGURE 6 Percentage of number of eels per batch at the receiver upstream in front of a pumping station detected only during night (between sunset and sunrise), day (between sunrise and sunset), of both night and day. Number per batch indicates number of eels

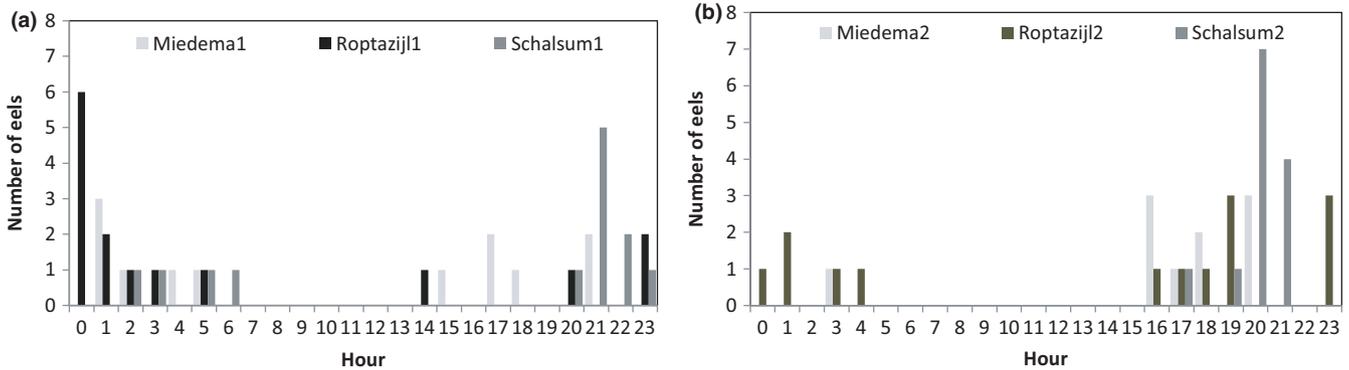


FIGURE 7 (a-b) Hour of first detection at receivers behind pumping station for batch released at the 5 October (a) and the 19 October 2011 (b)

whereas water discharge may influence the migratory speed once the “decision” to migrate is made. Downstream migration during high water discharge may be advantageous for many reasons; energy requirement for the migration is low and downstream passage is more rapid. If favourable conditions do not appear, the silver eels probably postpone the downstream migration one or more years (Vøllestad et al., 1994).

Time of day influenced migration through the pumping stations, with more silver eel movements and pumping station passage at night. On a circadian scale, timing of migration activities showed a higher number of detections at night, especially during the first half of the night (Bolland et al., 2019; Breukelaar et al., 2009; Riley, Walker, Bendall, & Ives, 2011; Travade et al., 2010; Verhelst, Buysse, et al., 2018; Verhelst, Reubens, et al., 2018; Winter et al., 2006). Riley et al. (2011) studied eels with pit tags over two years at the River Itchen, UK and found that the movement of silver eels was significantly correlated with the time of sunset, with 72% of the recordings during the hours of darkness. Also, Baras and Jeandrain (1998) found higher activity of eels in a Belgian tributary of the River Meuse after sunset during the first part of the night and eels ending their activity before sunrise. Some silver eels, however, left their diurnal residence before sunset, but only during low light conditions with rain and cloudy sky. Of 52 tagged eels in a polder system in Flanders, Belgium, 87% were detected at night, while only 62% were detected

during daylight (Verhelst, Reubens, et al., 2018). The lowest activity was observed during dawn and dusk with only 40% and 17% of the eels detected during those periods, respectively.

Four silver eels were not detected at the receiver downstream from the pumping station Schalsum, but these eels were detected at the receiver further downstream in Harlingen. Also, four silver eels at Miedema and one at Ropta were only detected during the evening of 19 October at the receiver just upstream of the pumping stations. These eels were not detected at the receiver downstream the pumping station, so these eels passed this receiver unnoticed. The silver eels all passed during a period when the pumping stations were active for long periods due to rainfall. The absence of detections could have been caused by either misdetections due to disturbance of the transmitter signal or to overlapping transmitter pings. The transmitter signal is acoustic and could be disturbed by small pockets of air in the turbulent water pumped behind the pumping station. Receivers behind the pumping stations were placed within the vicinity of the pumping stations and the acoustic signals from the transmitters could have been disturbed by turbulence. Another explanation could be overlapping signals from two transmitters. A transmitter sends a short acoustic pulse train and when all these pulses are received by the receiver a detection is recorded. When signals from two or more transmitters collide, a false detection is recorded (Pincock, 2012; Simpfordorfer et al., 2015). Because the



transmitters were programmed to give a signal randomly between 40 and 70 s, the chance of more than one overlapping detection in a row was low. Eels that were not detected at the receiver downstream the pumping stations passed when no other eel passed these stations at the same time. Therefore overlapping transmissions between two tags at the same time does not explain the lack of detections downstream the pumping stations for these eels.

At Schalsum, 30 silver eels passed the pumping station towards a larger canal, which eventually leads to the major exits to the sea near Harlingen and Dokkumer Nieuwe Zijlen. Of these 30 silver eels, 18 were detected at these two exit points, meaning the fate of these other 12 silver eels remained unknown. Instead of swimming towards the exit points, the eels could have chosen other migration routes going further into Friesland, which has many canals, lakes and small polders. A proportion of these eels could have eventually reversed their silvery state as mentioned earlier. Commercial fishing took place, but local fishermen were asked to look for floy tagged eels and return them. Six silver eels were reported caught and returned in the vicinity of Schalsum, of which four turned up at Harlingen.

During this study, a direct assessment of silver eel survival after passing the pumping station could not be made. Studies assessing direct pump mortality usually include catching silver eel after passing the pumps in fishing gear and assessing the direct damage and mortality suffered (e.g., Buysse et al., 2014). In this study, most silver eels were detected at the receiver downstream of the pumping station within 24 hr of passage, after which they were no longer detected at this receiver. However, three silver eels at Miedema, nine at Ropta and six at Schalsum were detected for more than one day behind the pumping station, with detections up to several weeks. Some of these eels were detected almost continuously, some eels were detected more scattered over time. These detections most probably indicated a dead eel, but eels being alive and remaining at the site for a longer time cannot be ruled out. Havn et al. (2017) studied the drift of dead eels downstream in three German rivers and found they drifted between 2.9 and 30.1 km (median 0.5 to 14.6 km), depending on release site and date. Median time from release to last recorded movement ranged from 5 to 55 days. Dead eels could also have been carried by the flow out of the detection range of the receiver within limited time. This would result in a similar detection pattern for live silver eels shortly after passage.

5 | IMPLICATIONS FOR MANAGEMENT

The proportion of silver eels that migrate from polders to sea, and thereby eventually contribute to the spawning population, depends on several factors. Pumping stations are pumping water from polders when water levels are high, because of, for example, high rainfall. Silver eels can migrate with the water flow through the pumps, but when the pumps are not operational migration is blocked. Even when the pumps are in operation, silver eels can hesitate to migrate through the turbines or delay their migration for a longer period or

even arrest their migration (e.g., Bolland et al., 2019; Verhelst, Buysse, et al., 2018; Verhelst, Reubens, et al., 2018; Winter et al., 2006). This delay could result in increased risk of predation, disease and depletion of energy stores (Piper et al., 2018; Tesch, 2003). Cumulative effects could occur when more than one of these man-made structures have to be passed. In the end, these delays could affect the migration during the oceanic phase and chances of eventually reaching the spawning sites and being in time to spawn. However, knowledge on eel migration and behaviour during the oceanic phase and eel spawning is still mostly lacking (Aarestrup et al., 2009; Miller et al., 2019).

Models estimating the population of silver eels migrating from polders through pumping stations have to take not only estimates of mortality into account, but also estimates of the percentage of the silver eel population that are willing or are able to migrate through these pumping stations. Passing the pumps can result in direct and indirect mortality. Damage is caused by contact with blades or other objects in the pumping station, abrupt changes in pressure leading to barotrauma, turbulence and fast water flows (Calles et al., 2010; Larinier & Travade, 2002; Russon, Kemp, & Calles, 2010; STOWA, 2012). Buysse et al. (2014), Buysse et al. (2015) reported mortality rates ranging from $17 \pm 7\%$ for large Archimedes screw pumps to $97 \pm 5\%$ for propeller pumps. STOWA (2012) reported mortality rates ranging from 0% (centrifugal pump, screw pump) to 100% (open propeller pumps), depending on the type of pump. Blockage can be a result of fish not being able to pass a pump, e.g. because of the pump being out of operation for a prolonged period of time. But fish could also refuse to pass, even though opportunities exist. From this study, while some eels were delayed, most eels eventually passed all three pumping stations, indicating that blockage was not a major factor to correct for in population models.

Measures that contribute to the migration of silver eel along a pumping station and/or increase eel survival are installing fish-friendly pumps or build fish passages. In this study, most silver eels passed the pumps within a day after release during the first possible event, so fish-friendly pumps will benefit the migrating population most. Installing new pumps is, however, costly and is usually done when the old pumps need to be replaced. Fish-friendly pumps will increase fish survival, but could still form a blockage during migration for some of the eels. Fish passages have been installed at many locations near man-made structures, such as turbines of hydropower stations, to benefit fish migration (e.g., Dainys, Stakenas, Gorfine, & Lozys, 2018; Fjeldstad, Pulg, & Forseth, 2018; Klopries, Deng, Lachmann, Schüttrumpf, & Trumbo, 2018; Økland et al., 2019; STOWA, 2012). However, the efficiency of fish migration facilities is not always as high as anticipated (Egg, Mueller, Pander, Knott, & Geist, 2017; Silva et al., 2018). In the Netherlands, there are several thousand small pumping stations and installing fish passages near all these stations is politically and financially not feasible due to the high costs. However, prioritising all these sites in relation to the degree of blockage and mortality rates suffered and their relative importance for migratory fish (e.g., Kemp & O'Hanley, 2010;



Nunn & Cowx, 2012), can maximise the effectiveness of measures and mitigation taken, such as installing new fish-friendly pumps or fish passes alongside pumping stations.

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