Received: 8 February 2023 | Revised: 10 August 2023 | Accepted: 11 August 2023

DOI: 10.1002/rra.4206

RESEARCH ARTICLE

WILEY

Assessing migratory bottlenecks and escapement of silver eel (*Anguilla anguilla*) in the highly urbanized North Sea Canal basin, the Netherlands

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Funding information
Ecologische Verbindingszone Noordzeekanaal en Ommelanden: Rijkswaterstaat West-Nederland Noord and Midden Nederland; Provincie Noord-Holland; Hoogheemraadschap Hollands Noorderkwartier; Hoogheemraadschap van Rijnland; Waterschap Amstel; Gooi en Vecht; Sportvisserij Midwest Nederland; Gemeente Amsterdam; Port of Amsterdam

Abstract

Habitat fragmentation and migration barriers have attributed to the decline of European eel (*Anguilla anguilla*). The migration of silver eels through pumping stations, ship locks, and migration facilities within the North Sea Canal basin using acoustic telemetry and overall escapement by mark–recapture was studied. A network of 61 acoustic receivers and three PIT-tag stations was built, and 305 silver eels were tagged with acoustic transmitters and 3923 with PIT-tags. Of all the silver eels that were detected, 55% passed barriers between the polders and the canal and 46% also passed the barrier complex at IJmuiden to sea, mainly via the ship locks. Overall, silver eel escapement to the North Sea per year averaged 81,629 silver eels and 14.3% suffered mortality in the pumping station at IJmuiden. Migration speed was lower for silver eels that initiated their migration upstream compared with silver eels further downstream, higher for silver eels passing barriers later in the migration period, and highest at sea. This study of silver eel movement and escapement in the North Sea canal basin indicated several bottlenecks. Passage success along barriers varied strongly between sites and types of barriers. While at two smaller locations, silver eels migrated through the pedal valves in the ship lock gates, a small passage facility and the pedal valves in a ship lock at complex IJmuiden did not enhance silver eel migration. The barriers and unnatural canal system caused additional delay during silver eel migrations. Mitigation measures for management could include installing fish-friendly pumps, using pumping stations only during the day, and in addition opening ship locks and pedal valves at the beginning of the night.

KEYWORDS
Anguilla, barriers, fish behaviour, fish migration, man-made barriers, silver eel, telemetry

1 | INTRODUCTION

The European eel population has strongly declined since 1980 (ICES, 2021). This decrease is caused by a cumulative effect of migration barriers, fisheries, habitat loss and deterioration, pollution, parasites, and changes in oceanic conditions (Buysse et al., 2014; Drouineau et al., 2018; Moriarty & Dekker, 1997; Palstra, Guerrero, de Laak, Klein Breteler, & van den Thillart, 2011; van Keeken, van Hal, Winter, Tulp, et al., 2020; Verhelst, Buysse, et al., 2018; Westerberg et al., 2018; Winter et al., 2023). During the silver eel stage, migration from freshwater to sea is severely hampered by barriers, such as hydropower and pumping stations, causing additional mortality and delay (e.g., Bolland et al., 2019; Buysse et al., 2014; Winter et al., 2007). In the Netherlands, there are several thousands of pumping stations, ship locks, and smaller barrages, such as small inlet sluices, to regulate water levels (Brevé et al., 2014). These man-made barriers can delay or block European silver eel during their migration from freshwater towards the sea (e.g., Vergeynst et al., 2021; Verhelst, Baeyens, et al., 2018). Opportunities for silver eel to pass a pumping station depend on environmental factors that will activate the operation of the pumping stations to maintain safe water levels, such as rainfall, and the availability of alternative routes (e.g., fish passes or sluices) alongside the pumping station. Passage of silver eels through a ship lock depends on commercial and recreational boating activity (Bolland et al., 2019; Travade et al., 2010; Verhelst, Buysse, et al., 2018; Verhelst, Baeyens, et al., 2018; Winter et al., 2006). Migration success is also related to variation in individual fish behaviour near barriers (Griffioen et al., 2015; van Keeken, van Hal, Winter, Tulp, et al., 2020).

Knowledge of silver eel escapement and bottleneck assessment on a catchment level is sparse. Many studies on eel migration focus on a single pumping station or hydropower plant, sometimes in combination with a single fish migration facility at these barriers (e.g., Baker et al., 2021; Buysse et al., 2014; Dêbowski et al., 2020; Egg et al., 2017; Gosset et al., 2005; Travade et al., 2010; van Keeken, van Hal, Winter, Wilkes, et al., 2020). Knowledge on silver eel migration through highly regulated water systems is becoming especially more relevant in areas below sea level, with the increasing number of summer droughts, sea-level rise, and other impacts from climate change (O'Briain, 2019; Vousdoukas et al., 2017). Areas below sea level may become more isolated, leaving potential habitats for eel more fragmented or unused. For migrating silver eels, highly regulated waterways, often lacking natural flows, potentially inducing conflicting behavioural cues, and hampering effective migration (Vergeynst et al., 2021; Winter et al., 2023).

The North Sea Canal basin, with a catchment area of 2300 km^2 (Van der Baan, van der Heijden & van Reen, 2023), contributes significantly to the Dutch silver eel escapement to the North Sea (van der Hammen et al., 2021). Waterways from the hinterland (e.g., Lake Markermeer, Amsterdam area, smaller canals, and multiple polders) towards the North Sea Canal and the adjacent Amsterdam-Rhine canal are highly regulated by pumping stations and/or ship locks. Data on overall silver eel escapement and passage rates at subsequent barriers, however, are currently lacking. In this study, the migration of silver eels through multiple major pumping stations, ship locks, and fish migration facilities along the North Sea Canal basin was studied by using acoustic telemetry and mark–recapture experiments using passive integrated transponders (PIT-tags).

The aims of this case study were to assess: (a) passage and migration success of silver eels at the various barrier locations; (b) timing, distribution, migration speed, and migration route choice of silver eel in this region towards the sea; (c) estimating the total number of migrating silver eel from the North Sea Canal area by a mark–recapture study (overall escapement); (d) indicating which potential management measures and optimizations can be used to mitigate identified bottlenecks for silver eel migration to the sea.

2 | MATERIALS AND METHODS

2.1 | Study area

Silver eel migration was studied in the North Sea Canal, the Amsterdam-Rhine canal (in open connection to the North Sea Canal), Lake Markermeer (connected through ship locks 'Oranjesluizen' to the North Sea Canal), and adjacent polder waters and canals in the Netherlands during autumn 2017–spring 2018 with acoustic tags, and during the autumn of 2016 and 2017 with PIT-tags. The North Sea Canal is fed by water coming from Lake Markermeer, while the Amsterdam-Rhine canal is connected in a southern direction by shipping locks to the River Lek. The water in the North Sea Canal flows towards the North Sea through a pumping station and discharge sluices complex at IJmuiden. Both the North Sea Canal and the Amsterdam-Rhine canal are important canals for shipping between the North Sea and the cities of Amsterdam and Utrecht.

A total of 61 Vemco VR2W receivers were placed in the study area (Figure 1, Table 1). Nine locations (Appendix A) with a pumping station, ship lock, or a combination of both were covered with receivers upstream and downstream (in canals leading to the North Sea Canal) of each barrier. The VR2W receivers were deployed starting September 2017 until March 2018 for inland sites and until June 2018 for sites further downstream near the North sea (IJmuiden, Markermeer). At each location, receivers were placed, so a distinction could be made for silver eels passing, for example, the pumping station or the ship lock. A VR2W receiver records the identification number and time stamp from acoustic transmitters with a frequency of 69 kHz as a tagged animal swims within the receiver range. Range tests were executed in the North Sea Canal to ensure that the receivers covered the full width of the canal, and the range was up to several hundred metres (Griffioen et al., 2017). The VR2W consists of a hydrophone, receiver, ID detector, data logging memory, and battery with a battery life of approximately 15 months, all housed in a submersible case. Data from the receivers were exported to a computer through a Bluetooth connection using the Vemco VUE software package (Canada, www.innovasea.com/fish-tracking). Data were processed using statistical software SAS (SAS version 9.3: SAS Institute

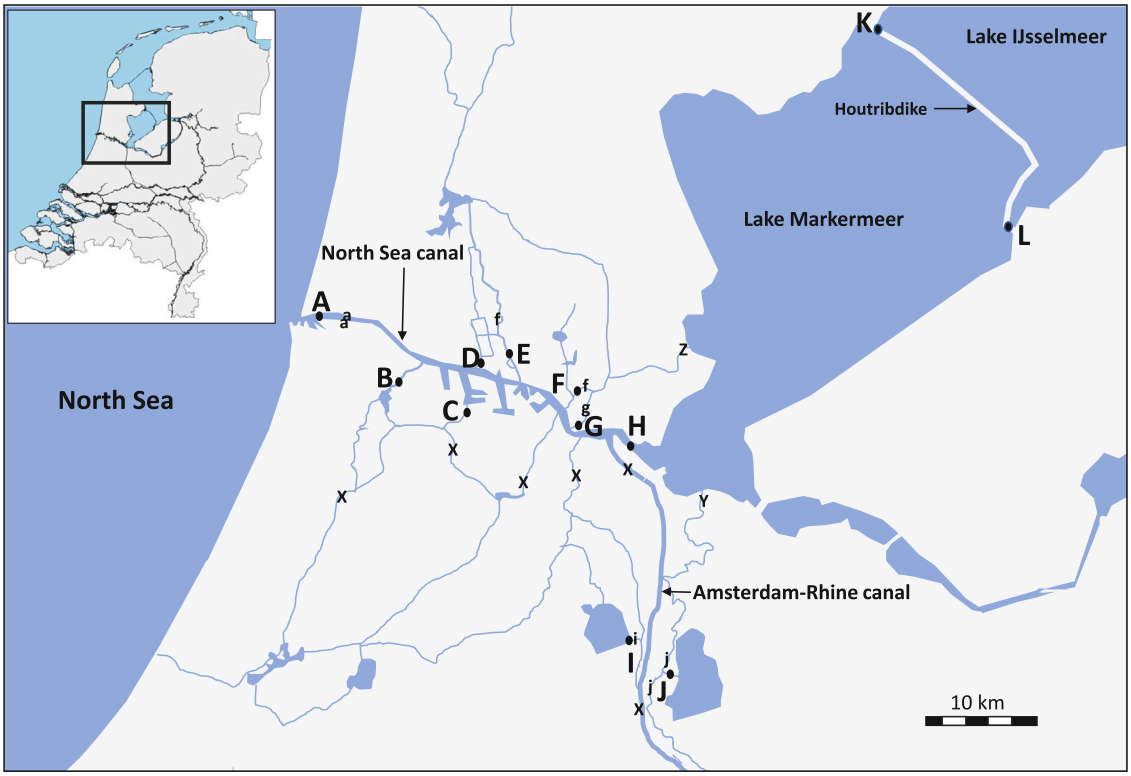

FIGURE 1 Map of the North Sea canal area. Locations are explained in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

inc., 2011) and R (R Core Team, 2021). The silver eels were caught upstream of the barriers, and at most locations, silver eels were tagged and released in two batches upstream of each pumping station and/or ship lock, at locations accessible by car, or by local fishermen by boat.

Kortenhoef (52.2428 N, 5.0468 E, Figures A1 and A2) and Vinkeveen (52.2202 N, 4.9731 E, Figures A1 and A3) lakes both connect to the Amsterdam-Rhine Canal by a pumping station and a small ship lock. Two receivers were placed upstream of the barriers, and one (Vinkeveen) or two (Kortenhoef) receivers were placed downstream the barriers. Two receivers were also placed in the Amsterdam-Rhine Canal, one in the southern and one northern part of the canal, one receiver was placed near Lake Markermeer on the River Vecht and one in a canal towards Amsterdam, to cover possible migration routes. At Kortenhoef, the silver eels were tagged during two sessions, while at Vinkeveen, the silver eels were tagged during five sessions, due to smaller catches. At these locations, fishermen catch mainly large eel; therefore, it was assumed that these locations are more difficult to pass for silver eels compared with the other locations. In addition to 15 silver eels released upstream of each location, 25 silver eels were released at 0.1 km downstream the ship lock/pumping station.

At the border of Lake Markermeer and Lake IJsselmeer, one receiver was placed near the city of Enkhuizen (52.6926 N, 5.2836 E) and two at Lelystad (52.5270 N, 5.4292 E) near the ship lock and discharge sluices, both on the Lake IJsselmeer side of the Houtrib dike dividing both lakes (Figure A4). At the Oranjesluizen ship lock complex (52.3816 N, 4.9605 E), six receivers (three on each side of the ship locks) were used to cover this complex. Also, one receiver was placed near pumping station De Poel, to detected silver eels migrating from Kadoelen and Willem I into Lake Markermeer. In addition, silver eels could also be detected by the Network of Sportvisserij Nederland at Lake Markermeer, which covered all entrances at this lake. The silver eels were released at two different locations during one session (12 and 13 eels released).

At Kadoelen (52.4088 N, 4.9093 E, Figures A5 and A6) and Willem I (52.3839 N, 4.9080 E, Figures A5 and A7), one receiver was placed upstream and one downstream of each barrier. In addition, four receivers were placed in the polder system between both barriers. Silver eels were able to migrate between both locations. At each location, 25 silver eels were tagged with transmitters and released upstream. To test the fish migration facility (a 'fish elevator') at Kadoelen and if silver eel swim through the pedal valves (a small panel in the ship lock gates that can be opened to let water into the ship lock for water levelling), underwater PIT-tag antennas were built at the exit of the fish passage and downstream of the pumping station exits at Kadoelen, and around the pedal valves at the gates on both sides of the ship locks of Willem I during September–October 2017, before the silver eels were released at the specific sites. The antennas at Kadoelen and Willem I consisted of 3 loops of 2.5 mm^2 metal wire, connected to Oregon single readers with autotuners. One hundred twelve silver eels were tagged with PIT-tags and released at Kadoelen, and 107 silver eels were tagged and released at Willem I upstream both objects during October–November 2017.

TABLE 1 Location name, number of receivers per location, type of barrier at location, indication of fish friendliness of a pump, distance of location to sea (km), and distance from release site to barrier (pumping station/ship lock).

Location	Location name	*N* receivers	Barrier	Fish-friendly pump	Distance to sea (km)	Distance release to structure (km)
A	IJmuiden	12 + 2 CU (a)	PS6B, DS7, LSH3, SSH1	−	0	2.5
B	Spaarndam	6	PS5W, MSH1, SSH1	+	12	2
C	Halfweg	2	PS3A, FM	+	15	1.9
D	Overtoom	3	PS2A, SSH1, FM	+	13	1.9
E	Zaandam	3 + 1 CU (f)	PS2H, LSH1, SSH1	+−	19	4.1
F	Kadoelen	2 + 3 CU (g)	PS2A, FM	+	22	0.3
G	Willem I	2 + 1 CU (h)	MSH1, FM	N/A	23	3.2
H	Oranjesluizen	6	LSH2, MSH2, FM	N/A	27	12.5[a]
I	Vinkeveen	2 + 1 CD (j)	PS2C, MSH1	−	52	0.8
J	Kortenhoef	2 + 2 CD (k)	PS2PA, MSH1	++	44	1
K	Enkhuizen	1	LSH2, MSH2	N/A	33	7.8[b]
L	Lelystad	2	DS6, LSH2	N/A	55	20.9[b]
x	Additional VR2W	6				
y	Additional VR2W Muiden	1	MSH2	N/A	37	
z	Additional VR2W De Poel	1	PS2C	+	54	

Abbreviations: A, auger; B, bulb pump; C, centrifugal; CD, additional receiver downstream from barrier; CU, additional receiver upstream from barrier; DSx, discharge sluices where x is the number of sluices; FM, fish migration passage; H, horizontal screw; LSHx, large ship lock, used frequently for large vessels, usually on a daily basis. x is number of locks; MSHx, medium ship lock, used frequently for recreational boats and also large vessels, more frequent during summer. x is number of locks; PA, pipe auger; PSx, pumping station where x is the number of pumps; SSHx, small ship lock, used only occasionally, for recreational boats, more frequent during summer and at daytime. x is number of locks; W, pedal wheel.
[a]Distance calculated from batch released at Lake Markermeer, batch Uitdam.
[b]Distance calculated from batch released at Lake Markermeer, batch Hoorn.

Overtoom (52.4310 N, 4.7841 E, Figures A8 and A9) and Zaandam (52.4394 N, 4.8255 E, Figures A8 and A10) both consist of a ship lock and a pumping station. At the small ship lock Overtoom, silver eel migration was facilitated by an automated paddle valve in the lock gate. Two receivers were placed upstream of each location close to the barriers. Because of the rather small location at Overtoom, both receivers were placed making use of an acoustic 'blind spot' near the ship lock for the receiver close to the pumping station, so ensure that a distinction could be made between both migration routes. In addition, one receiver was placed downstream the structures at each site, as well as one receiver more upstream in the canal de Zaan. Silver eels were able to migrate between both locations. At each location, 25 silver eels were released upstream.

At Spaarndam (52.4131 N, 4.6815 E, Figures A11 and A12), a total of six receivers were placed to make a distinction between the pumping station and the two ship locks. Three receivers were placed upstream and three downstream of the barriers. At pumping station Halfweg (52.3925 N, 4.7707 E, Figures A11 and A13), one receiver was placed upstream and one downstream of the barrier. In addition, three receivers were placed in canals upstream of both locations, to detect silver eel migration in other directions. Silver eels were able to migrate between both locations. At each location, 25 silver eels were tagged and released upstream.

At IJmuiden (52.4678 N, 4.6098 E), a total of 14 receivers were placed to cover four ship locks (smallest two are adjacent to each other) upstream (North Sea Canal side) and downstream (North Sea side) of the pumping station/discharge sluices complex, and the North Sea Canal at two positions upstream of the complex. A total of 50 silver eels were tagged and released in the North Sea Canal during five sessions. Next to the silver eels tagged with acoustic transmitters, 1998 silver eels were tagged with 23 mm and 32 mm PIT-tags between 18 October and 24 November 2016, and 1925 silver eels between October 16 and November 23, 2017, to estimate population numbers. Migration through the pedal valves of the smallest ship lock was also studied. The pedal valve at the upstream gate was covered using three loops 2.5 mm^2 metal wire, while the pedal valve at the downstream gate was covered using a single loop 4 mm^2 metal wire, both connected to Oregon multi-antenna HDX readers.

Migrating silver eels in the North Sea could also be detected at the Permanent Belgium Acoustic Receiver Network (PBARN) in the Belgium part of the North Sea (Reubens et al., 2019). These data were obtained from the European Tracking Network (ETN) database.

2.2 | Catch and tagging procedure

The silver eels used in this study were obtained from commercial fishermen. Silver eels were caught with fykes, which were emptied the same day of tagging or the day before tagging. Silver eels caught the day before tagging were kept in holding pens or nets overnight. The silver eels that were tagged showed visible signs of silvering, that is, differentiated lateral line and white-silver ventral and black dorsal surfaces (Palstra et al., 2011). Morphometric features were measured in order to determine the sex and eel maturation stage according to Durif et al. (2005): total length (total length to the nearest mm), vertical and horizontal eye diameter (to the nearest 0.1 mm), and pectoral fin length (to the nearest 0.1 mm). All silver eels tagged with acoustic transmitters were female with lengths ranging between 537 and 1130 mm (Table 2), as males (max length 45–50 cm) do not grow that large before silvering and migrating (Dekker, 2000). Because of the large numbers of silver eels that had to be tagged with a single PIT-tag at IJmuiden, no eye and fin length measurements were taken. Silver eels tagged with PIT-tags, including also males, ranged in length between 340 and 1080 mm.

To recapture the PIT-tagged eels released at the North Sea Canal, fykes were placed near the IJmuiden complex during September–December 2016 and 2017. A total of three large and six small standing fykes were placed near the complex. In addition, two sets of train fykes were placed upstream along the southern shore of the canal in 2017 and two standing fykes were placed more upstream of the canal. Because of safety restrictions for shipping, no fykes were placed near the largest ship lock. Fykes were emptied twice a week and the number of eels caught were counted. The catch was scanned for previously tagged silver eels, using an Oregon hand-held PIT-tag scanner.

A total of 255 silver eels were tagged with Vemco V9-2L coded transmitters (length 27.5 mm, weight 4.5 g in air, estimated battery life 344 days, 69 kHz), and 50 silver eels were tagged with V9-2L pressure transmitters (length 31 mm, weight 4.9 g in air, estimated battery life 202 days) during September–December 2017 (Table 2). All silver eels were also tagged with a 23 mm or 32 mm PIT-tag (Oregon). Each transmitter sends an acoustic pulse train (eight sounds in ~2.6 s) at present time intervals, for our study between 30 and 50 s. Each pulse train includes a specific ID number for each transmitter to track the individual fish.

All silver eels were anaesthetized with 2-phenoxy-ethanol (transmitter 0.9 mL L^{-1}, PIT-tag 0.5 mL L^{-1}). For the silver eels that had both an acoustic transmitter and a PIT-tag implanted, these tags were surgically implanted 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 among five different procedures tested for European eel by Baras and Jeandrain (1998). The transmitter and PIT-tag were inserted into the body cavity and the incision was closed by two sutures (absorbable, braided Vicryl 3/0, FS2 needle). Surgery lasted a maximum of 5 min. When only a PIT-tag was required, the tag was injected through a hollow needle into the body cavity and no suture was used. After the surgery, the silver eels were transferred to a recovery tank and were observed until swimming behaviour reappeared. After recovery, the silver eels were released at each of the study sites.

2.3 | Analysis

To examine which factors influence the time taken to traverse the North Sea Canal from each location, a generalized linear model was used to explain the time from the last observation after the passage of the last barrier at a location upstream of IJmuiden to the first observation in IJmuiden:

$$⟦\text{lday\_loij}⟧\_i = ⟦\text{km\_loij}⟧\_i \times \text{day}⟦\text{\_relo}⟧\_i \times \text{obstacle}⟧\_i + \text{ee}⟦\text{l\_cm}⟧\_i + ⟦\text{days\_msre}⟧\_i$$

The dependent factor was the log-transformed days (=0.1) between last object (lo) and IJmuiden (ij) that silver eel i took. The following explanatory factors were added to the model as fixed factors: distance between last object and IJmuiden (km_loij), days taken between release and last object (day_relo), the presence of an obstacle between the release location and the last object (obstacle), the silver eel length (eel_cm) and the days between the estimated start of migration (15th September) and release (days_msre). Because release location strongly correlated with most of the factors, this factor was not included in the model. The fixed factors were explored with regard to outliers and collinearity. Outliers did not play a role and collinearity among continuous fixed factors was never high, with a maximum of −0.3 between km_loij and days_relo. Presence of obstacle was positively correlated with both days taken between release location and the last object and with distance between last object and IJmuiden, and a three-way interaction term was included in the model. Various transformations of the dependent variable (log, 2nd, 3rd, 4th root) and error structures (Gaussian, Gamma with log or inverse link function) were compared with regard to model validation, and the best residual patterns were found for the log-transformed explanatory variable and with a Gaussian error structure with an identity link function. Nonsignificant factors were identified by an F-test and removed one by one.

To test differences in migration speed between silver eels migrating in the North Sea Canal compared with the North Sea, two analyses were undertaken. First, migration speed in the North Sea from the marine side of IJmuiden to the Belgium network was compared with the migration speed in the North Sea Canal for the same silver eels, using a two-sided t-test. Because only few observations were available for this test, a second test was performed, using data from two different groups of silver eels. Migration speeds were available for silver eels released in the hinterland upstream of barriers (or downstream for Vinkeveen en Kortenhoef), calculated from the last detection downstream to the first detection in IJmuiden. Migration speeds were also available for silver eels released in IJmuiden, calculated from the last detection at the North Sea side of IJmuiden to the first detection at the Belgium network. Because these data did

TABLE 2 Number of tagged silver eels per study area, release dates, distance of release site to location, and morphometric measurements: minimum, mean, and maximum total length (TL), horizontal (Eh) and vertical (Ev) eye diameter, and pectoral fin length (PF).

Release site	Number	Release dates 2017	Distance to barrier (km)	Total length (mm)	Eye horizontal (mm)	Eye vertical (mm)	Fin length (mm)
Kortenhoef upstream	15	11, 26 October	1	836 ± 61 (721–932)	10.93 ± 0.65 (9.5–11.9)	10.56 ± 0.71 (8.9–11.6)	45.27 ± 5.43 (39–58)
Kortenhoef downstream	25	11, 26 October	0.2 downstream	868 ± 61 (759–972)	11.10 ± 0.74 (9.7–12.3)	10.66 ± 0.71 (9.0–12.0)	46.16 ± 5.01 (37–55)
Vinkeveen upstream	15	29 September, 6, 13, 20 October, 3 November	0.5	864 ± 87 (685–1000)	10.55 ± 1.29 (8.0–12.7)	10.36 ± 1.29 (7.9–12.7)	45.67 ± 6.01 (33–59)
Vinkeveen downstream	25	29 September, 6, 13, 20 October, 3 November	0.2 downstream	872 ± 89 (670–1130)	10.86 ± 1.24 (8.3–13.0)	10.50 ± 1.22 (8.1–12.8)	45.40 ± 4.56 (36–54)
Markermeer	25	14 December	7 and 31 to Enkhuizen	829 ± 55 (741–944)	10.48 ± 1.17 (7.4–12.1)	9.91 ± 1.26 (6.7–13.0)	40.84 ± 4.23 (33–49)
Kadoelen	25	11 October, 8 November	0.3 and 0.9	809 ± 118 (595–1040)	10.37 ± 1.52 (7.3–12.7)	9.96 ± 1.38 (7.3–11.8)	40.24 ± 6.01 (30–51)
Zaandam	25	26 October, 1 November	1.4 and 3.8	820 ± 75 (634–983)	10.70 ± 1.14 (8.6–14.8)	10.17 ± 1.18 (7.9–13.4)	42.80 ± 4.65 (35–55)
Willem I	25	11 October, 8 November	3.3	787 ± 129 (566–966)	10.39 ± 1.46 (7.8–13.0)	10.02 ± 1.43 (7.7–12.2)	40.64 ± 6.58 (28–51)
Overtoom	25	6, 25 October	1.9	798 ± 83 (620–1005)	10.33 ± 1.25 (6.5–12.3)	9.90 ± 1.25 (5.7–11.4)	42.00 ± 4.24 (32–49)
Halfweg	25	12, 24 October	1.8	833 ± 100 (641–1024)	10.70 ± 1.15 (8.9–13.3)	10.29 ± 0.94 (8.6–12.1)	42.12 ± 5.29 (29–51)
Spaarndam	25	9, 26 October	1.6	821 ± 59 (691–915)	10.55 ± 0.74 (8.8–11.9)	10.06 ± 0.65 (8.6–11.1)	41.16 ± 4.18 (34–50)
North Sea Canal	50	16, 19, 23 October, 6, 13 November	5	791 ± 83 (537–960)	10.52 ± 0.85 (8.8–12.3)	10.09 ± 0.81 (8.7–12.1)	40.54 ± 4.51 (29–53)
Kadoelen PIT	107	11, 18, 25 October, 8, 29 November	0.3 and 0.9	765 ± 111 (381–955)			
Willem I PIT	112	11, 18, 25 October, 29 November	3.3	704 ± 112 (430–981)			
North Sea Canal PIT 2016	1998	18, 21, 25, 28 October, 1, 4, 8, 9, 11, 15, 18, 22, 24 November	5	699 ± 115 (340–1080)			
North Sea Canal PIT 2017	1925	16, 19, 23, 26, 30 October, 6, 9, 13, 15, 16, 20, 23 November	5	703 ± 112 (345–995)			

Note: All measurements in mm with ±*SD*.

TABLE 3 Per study area, the number of tagged and detected silver eels, the number of silver eels upstream and downstream a barrier, detected upstream and downstream IJmuiden, and detected at the Amsterdam-Rhine canal southern receiver, Houtrib dike, and in Belgium.

Location	Eels tagged V9	Eels detected	Upstream barrier	Passage barrier	IJmuiden upstream	IJmuiden downstream	Ark South	Houtrib dike	Belgium
Kortenhoef upstream	15	6	6	5	2	2	0	0	0
Kortenhoef downstream	25	25	-	-	14	14	0	0	1
Vinkeveen upstream	15	15	15	1	0	0	0	0	0
Vinkeveen downstream	25	24	-	-	13	13	3	0	0
Willem I	25	25	17	5	2	2	0	0	0
Kadoelen	25	25	19	6	3	3	0	0	1
Zaandam	25	25	19	16	11	11	0	0	0
Overtoom	25	17	17	13	12	11	0	0	1
Halfweg	25	25	24	14	13	13	0	0	2
Spaarndam	25	25	24	11	8	8	0	0	1
North Sea canal	50	50	49	47	48	47	0	0	5
Markermeer	25	9	6	5	1	1	0	3	0
Total	305	271	196	142	127	125	3	3	11
Percentage		89%	88%	55%	47%	46%	1%	1%	4%

Note: The percentages have been calculated to the number of silver eels detected at a receiver.

not comply with the assumption of normality of error, a Kruskal–Wallis test was performed.

A mark–recapture analysis was performed with the data of silver eels caught and released at IJmuiden in 2016 and 2017, using the 'unbiased modified Lincoln–Petersen' method (Pollock et al., 1990; Ricker, 1975). This method assumes that the ratio between recaptured tagged silver eels (R) and the total number of tagged and released silver eels (M) is equal to the ratio of total catch (C) and population size (N). Population size (N) can be estimated:

$$N = \frac{(M+1)(C+1)}{R+1} \tag{1}$$

To calculate the *SD* of the estimated population, *R* is treated as a binomial value and calculated following Seber (1970):

$$SD = \sqrt{\frac{(M+1)(C+1)(M-R)(C-R)}{(R+2)(R+1)^2}}. \tag{2}$$

3 | RESULTS

3.1 | Silver eel migration from upstream locations

Of 305 silver eels tagged with an acoustic transmitter, 271 (89%) were detected by at least one receiver (Table 3). Of the silver eels detected in front of a barrier, 123 (55%) were able to pass, with differences in success between the locations. For the Vinkeveen upstream batch, no silver eels were able to pass both barriers and only 7% (1/15) were able to leave Vinkeveen along a canal on the north side of the lake, while for the IJmuiden batch, the passage was 94% (47/50) at the IJmuiden complex.

For study locations that were in open connection to each other, that is, Halfweg/Spaarndam, Overtoom/Zaandam, and Kadoelen/Willem I, silver eels showed 'exploration' behaviour, where silver eels were swimming back and forth, being detected by receivers at pumping stations and ship locks at both locations, before passage to the North Sea Canal (Figure 2). At Spaarndam and Halfweg, for example, eight silver eels (32%) from Spaarndam passed the pumping station at Halfweg, and three silver eels (12%) from Halfweg passed the large ship lock at Spaarndam. Also, silver eels were detected travelling back and forth between both locations. At Kadoelen and Willem I, five silver eels (10%) passed the pumping station at Kadoelen, and four (8%) the ship lock Willem I. Again, silver eels from both release locations were detected travelling between both locations. One silver eel (2%) from Willem I migrated northwards and passed the pumping station de Poel towards Lake Ijsselmeer, continued its journey through the Oranjesluizen, eventually passing IJmuiden towards the North Sea.

A total of 127 silver eels (42%) reached the IJmuiden complex, but silver eels also used other migration routes towards sea. Of the silver eels that passed a barrier at locations closer to IJmuiden (Spaarndam, Halfweg, Overtoom, and Zaandam) 69%–93% were able to reach the IJmuiden complex, while for location at further distances from IJmuiden (Kadoelen, Willem I, Kortenhoef, Vinkeveen downstream), the percentages ranged between 0% and 54% (Table 3). None of the silver eels upstream of Vinkeveen reached IJmuiden. Three

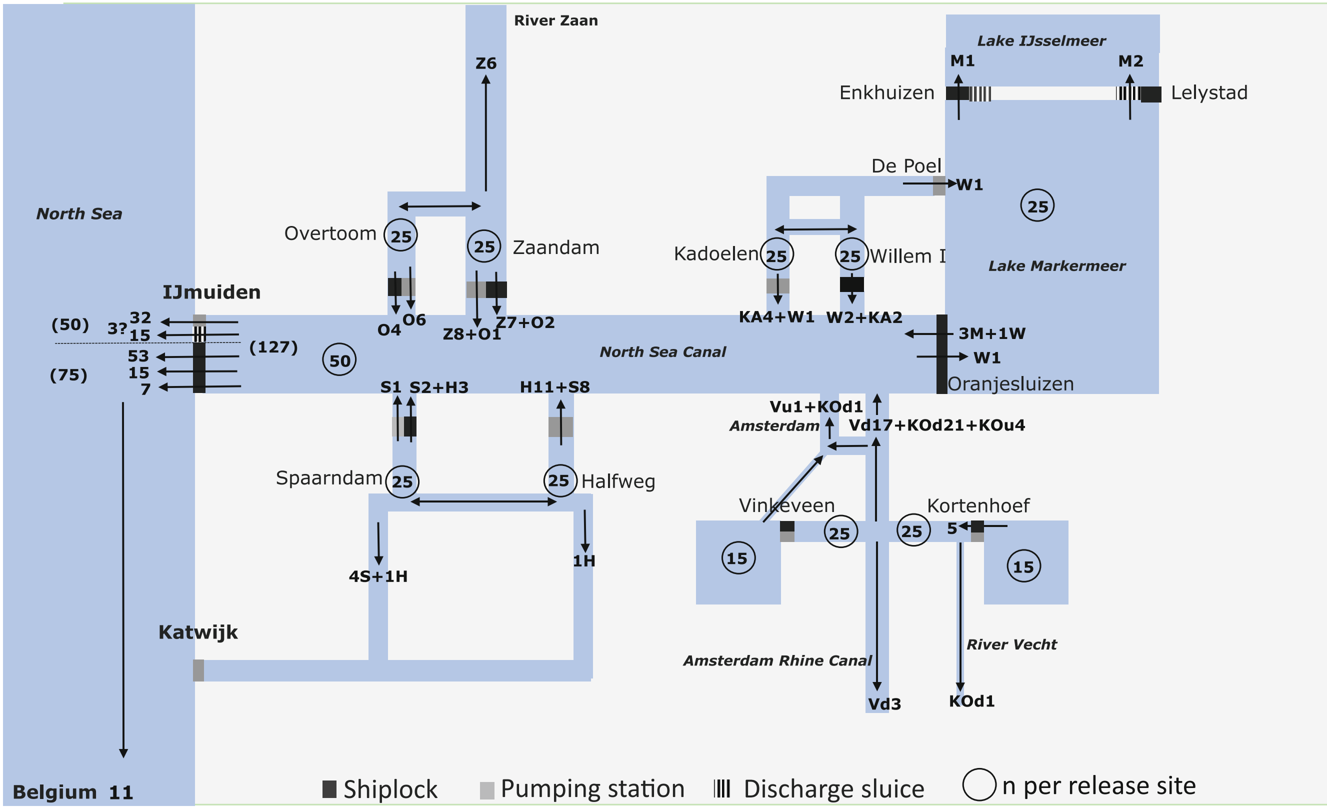

FIGURE 2 Schematic overview of numbers of silver eels released and number of silver eels (circled) that passed each barrier for the different locations. Before each number, the first letter(s) of the release location is given. Kortenhoef (KO), Vinkeveen (V), Markermeer (M), Willem I (W), Kadoelen (KA), Zaandam (Z), Overtoom (O), Halfweg (H), Spaarndam(S). For Kortenhoef and Vinkeveen, 'u' indicates silver eels released upstream and 'd' indicates silver eels released downstream a barrier. [Color figure can be viewed at wileyonlinelibrary.com]

silver eels (12%) from Lake Markermeer passed the Houtrib dike towards Lake IJsselmeer, while three silver eels (12%) from the Vinkeveen downstream batch swam southwards at the Amsterdam-Rhine canal towards the River Lek and one (4%) from Kortenhoef along the River Vecht southwards. From Zaandam, six silver eels (24%) also migrated northwards along the Canal de Zaan, while four silver eels (16%) from Spaarndam and two (8%) from Halfweg migrated southwards.

Mortality of silver eels during the experiment was confirmed for three silver eels (return of tag by fishermen) and probably for three others. Two silver eels were continuously detected behind the complex of Zaandam over a longer period of time, while one silver eel was detected at the receiver at the Amsterdam-Rhine canal north over a prolonged period of time.

3.2 | Passage to sea

Of the 127 silver eels tagged with an acoustic transmitter arriving at IJmuiden, 125 (98%) were able to pass the complex, which was 41% of all silver eels tagged with a transmitter (Table 3). It was possible to make a distinction between the different barriers at first arrival, barriers where exploration behaviour took place and eventually which barrier was passed at IJmuiden (Figure 3). The majority of the silver eels were first detected at the largest ship lock ($n = 58$, 46%) and the pumping station/discharge area ($n = 43$, 34%). For two silver eels, it was unknown where they arrived first, since they were only detected behind the complex. At each of the four sites, exploration behaviour occurred, with silver eels being detected by more than one receiver. Eventually 53 (42%) silver eels passed through the largest ship lock, 32 (26%) through the pumping station, 15 (12%) through the water discharge sluices, 15 (12%) through the middle-sized ship lock, and 7 (6%) through the two smallest of the four ship locks. For the remaining three silver eels (2%), a distinction between passing either the pumping station or the water discharge sluices could not be made. Out of the 125 silver eels that passed the IJmuiden complex, 11 (9%) were detected at the Belgium network.

3.3 | Timing of passage

Of the silver eels detected upstream from a barrier (excluding IJmuiden), 11 (16%) passed the barrier within an hour after first detection, while 18 (27%) passed within a day (Figure 4a). However, 27 (40%) silver eels passed after more than 14 days following first detection near a barrier. Of the eels not passing, 22 (22%) were detected only for a

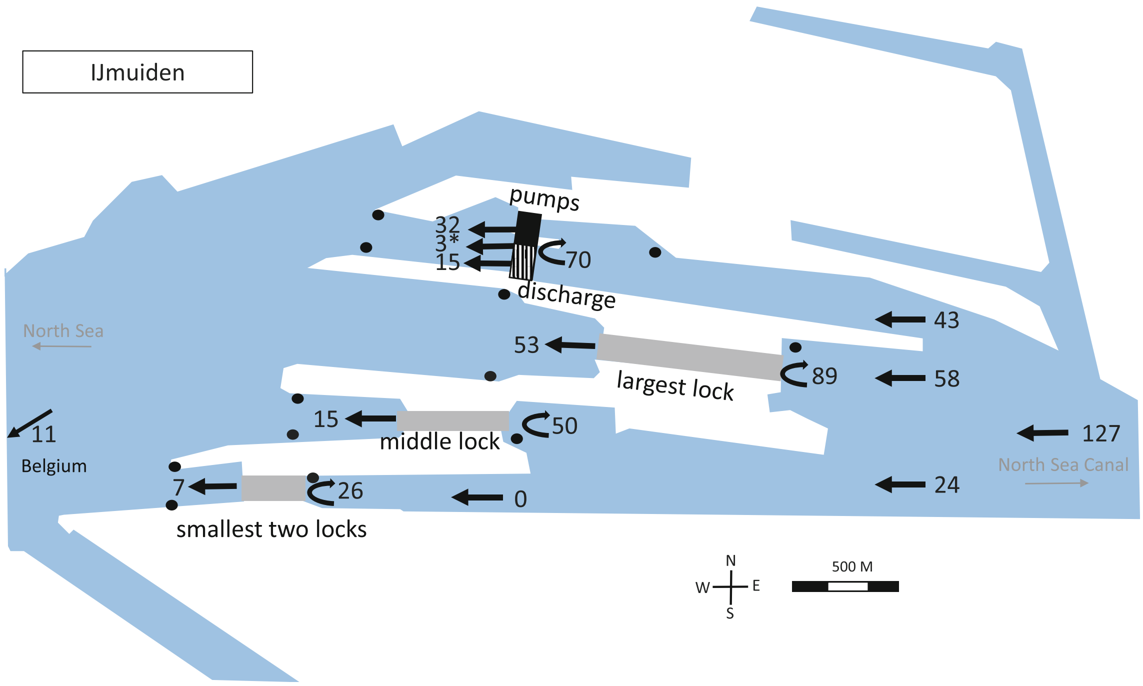

FIGURE 3 Numbers of silver eels detected first at a barrier at IJmuiden (location of first arrival), total number of silver eels detected at a receiver upstream the barriers (exploration behaviour, numbers next to returning arrow), and first detected at a receiver downstream (successful passage) at complex IJmuiden. For three eels (*), it was unknown if they migrated through the pumping stations or the discharge sluices. Pumping stations are indicated as black bar, discharge as black/white bar, and ship locks as grey bars. [Color figure can be viewed at wileyonlinelibrary.com]

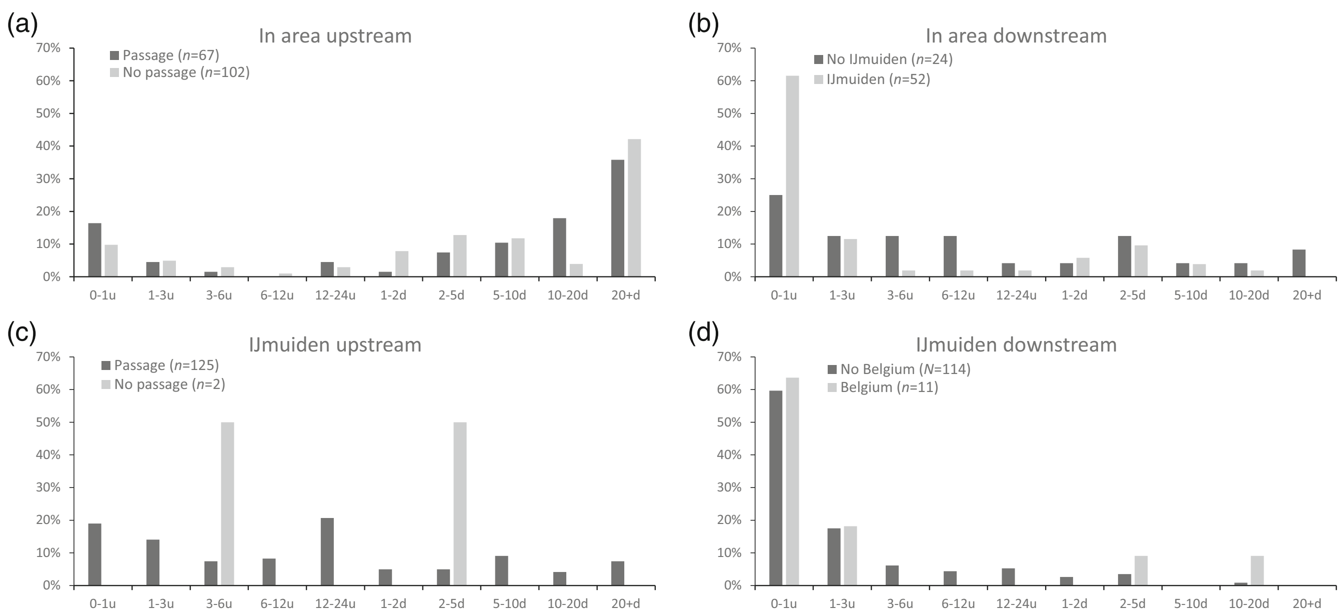

FIGURE 4 Duration between first and last detection of silver eels upstream (a) and downstream (b), a pumping station/ship lock at locations upstream IJmuiden and upstream (c) and downstream (d) at location IJmuiden.

day, while 45 silver eels (45%) were detected over more than 2 weeks between first and last detection. Of the silver eels that passed a barrier and that were detected later upstream of IJmuiden, 32 (62%) left the area behind a barrier within an hour, while for eels not detected at IJmuiden this number was six (25%). After 1 day, the numbers were 41 (79%) and 16 (71%), respectively (Figure 4d).

At IJmuiden 23 (19%) silver eels passed the complex within an hour and 84 (69%) passed within a day after first detection

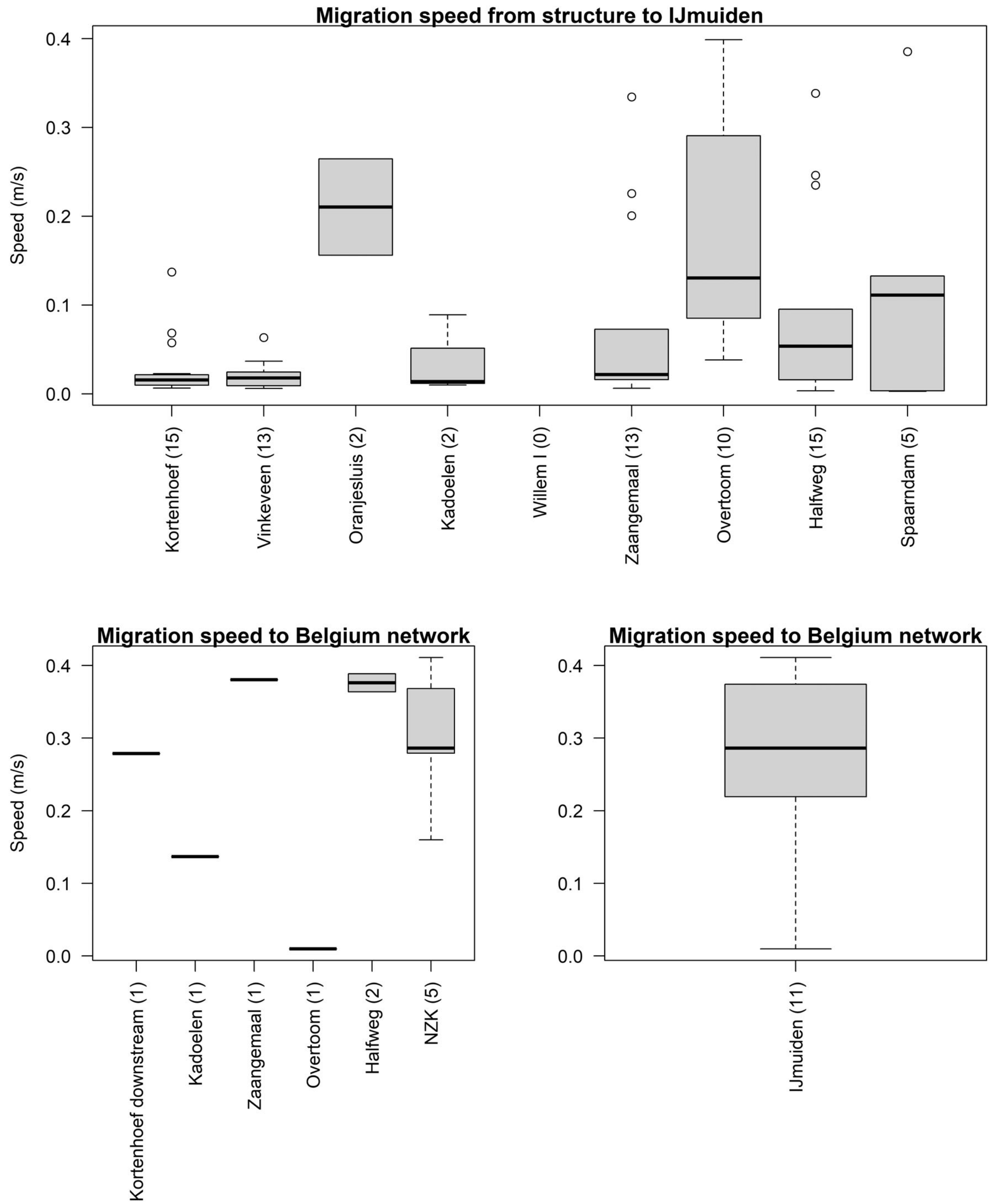

FIGURE 5 Migration speeds of silver eels between barriers upstream IJmuiden to IJmuiden, and downstream IJmuiden to Belgium.

(Figure 4b), while 21 (17%) took longer than 7 days after first detection. Of the two silver eels that did not pass IJmuiden, one was detected for between 47 days, while the other eel was only detected between 36 h. After passage 75 (60%) silver eels left the detection area within an hour while 115 (92%) left within a day after passage (Figure 4e). Nine (82%) of the 11 silver eels detected at the Belgium network left the IJmuiden complex within a day. Seven silver eels (5.6%) were detected after 2 days (Figure 4d), of which one went through the largest ship lock, three through the pumping station, two through the water discharge, and one through either the pumping station or the water discharge; this was not clear from the data.

Most silver eels passed the barriers at night with 68% of the detections during this study occurring during the night. A chi-square test of independence showed there was a significant association between circadian phase and the number of eels detected (X^2(3 df) = 59,422; $p < 0.05$). For the barriers at the different locations, 54 (59%) of the silver eels passed between 6 PM and 12 AM, while between 12 AM and 6 AM, 25 (27%) of the silver eels passed.

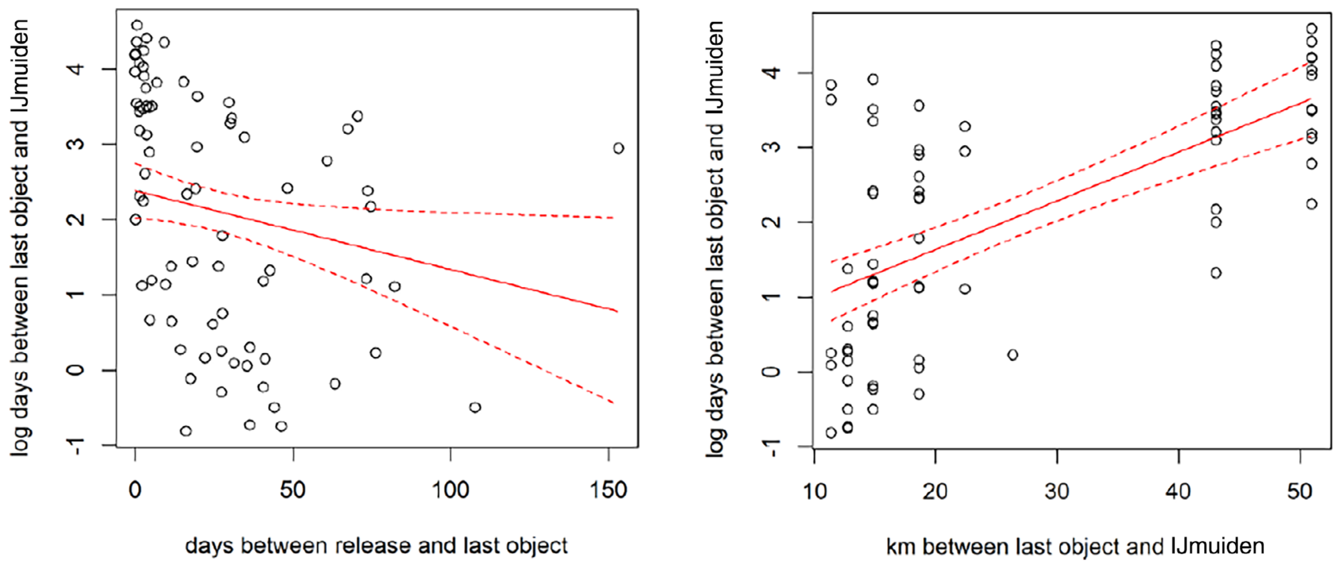

FIGURE 6 Scatterplot of distance between last detection downstream a barrier and first detection at complex IJmuiden versus the log-transformed days (+0.1) between last detection downstream a barrier and complex IJmuiden (a) and days between release and detection upstream a barrier and the log-transformed days (+0.1) between last detection downstream a barrier and complex IJmuiden (right). Red line (95% confidence interval in red dotted line) is the relationship between the two variables, as estimated in the final statistical model. [Color figure can be viewed at wileyonlinelibrary.com]

3.4 | Migration speeds

Migration speed was calculated as time taken divided by distance, from the last detection downstream of a barrier to first detection at the IJmuiden complex for silver eels from the hinterland, or last detection downstream of the IJmuiden complex to first detection in Belgium. The route of the one silver eel from Markermeer was unexpectedly long in duration and was excluded from the analysis; therefore, the migration speeds of 76 silver eels in the hinterland were calculated. Average migration speed after the passage of a barrier to IJmuiden was less than 0.02 ms^{-1} for Kortenhoef, Vinkeveen, Kadoelen, and Zaandam (Figure 5). For Halfweg, the migration speed was on average 0.05 ms^{-1}; for Spaarndam and Overtoom, 0.1 ms^{-1} and 0.2 ms^{-1} for two silver eels coming from the Oranjesluizen. Migration speed of silver eels at sea, swimming from IJmuiden to the Belgium network, for most silver eels ranged from 0.25 ms^{-1} up to 0.41 ms^{-1}. Only two silver eels, one from Overtoom and one from IJmuiden, showed lower average migration speed at sea of 0.01 ms^{-1} and 0.14 ms^{-1}, respectively. The overall migration speed in the North Sea Canal (Figure 6) between the last detection downstream of a barrier and the first detection at IJmuiden decreased with greater distance between both locations ($p < 0.001$). The overall migration speed increased with increasing time spent upstream from the last barrier from the polders into the North Sea Canal system ($p < 0.05$).

The migration speed of six silver eels migrating through the North Sea Canal, and the North Sea into the Belgium network could be compared. Although four out of these six silver eels had higher migration speeds in the North Sea compared with the North Sea Canal (average 0.26 ms^{-1} vs. 0.13 ms^{-1}), a two-sided t-test showed no significant difference between the two legs of their journey ($t = -1.3$, $p = 0.25$). This is probably caused by the low sample size. Migration speeds were also compared between silver eels released upstream from barriers (or downstream for Vinkeveen and Kortenhoef) in the hinterland, that passed the sluices at IJmuiden, and five silver eels released in IJmuiden, that migrated downstream of the IJmuiden complex to Belgium. This analysis excludes the six silver eels detected both at the North Sea Canal and the Belgium network in the North Sea. In this second analyses, the migration speed was significantly higher for eels in the North Sea migrating from IJmuiden to the Belgium network, compared with silver eels migrating in the North Sea Canal (0.30 ms^{-1} vs. 0.08 ms^{-1}, $\chi^2 = 10.79$, $p = 0.001$).

3.5 | PIT-tagged silver eel migration through migration facilities

At Kadoelen, no silver eel passed the fish migration facility, while at Willem I seven silver eels were detected swimming in the ship lock and six silver eels passed both the pedal valves downstream into the North Sea Canal. Of the silver eels tagged with a PIT-tag at Kadoelen and Willem I, including also silver eels with transmitters, four silver eels were detected at the entrance of the fish migration facility at Kadoelen and 29 silver eels were detected near the pedal valves upstream in front of the Willem I ship lock (Table 4). Of the four silver eels at Kadoelen, three originated from the Kadoelen batch (one with a transmitter) and one from the Willem I batch. Of 29 silver eels at the Willem I ship lock, 21 were from the Willem I batch and eight from the Kadoelen batch. Seven silver eels tagged and released at the North Sea Canal migrated through the pedal valves at the smallest ship lock at IJmuiden.

TABLE 4 Number and percentage of silver eels tagged with PIT-tags detected upstream Kadoelen and Willem I and that passed either the fish migration facility at Kadoelen or the pedal valves at Willem I.

Willem I ($n = 132$)	Detection upstream pedal		Passage downstream		
Kadoelen ($n = 137$)	N	%	N	% Location	% from total
Kadoelen (batch Kadoelen)	3	2%	0	0%	0.0%
Kadoelen (batch Willem I)	1	1%	0	0%	0.0%
Willem I (batch Willem I)	22	17%	5	23%	3.8%
Willem I (batch Kadoelen)	10	7%	1	10%	0.7%

3.6 | Population assessment silver eel escapement

Out of the 1998 eels released at IJmuiden with a PIT-tag in 2016, 76 (3.8%) silver eels were recaptured. Out of the 1975 eels released at IJmuiden with a PIT-tag in 2017, 74 (3.7%) silver eels, of which two silver eels also had a transmitter, were recaptured. Two silver eels in 2016 and one silver eel in 2017 were recaptured twice. In 2016, a total of 4171 silver eels and in 2017 a total of 3621 silver eels were caught in the fykes from September until December. Of the 50 silver eels tagged with a transmitter and released at the North Sea Canal, 48 (96%) reached the IJmuiden complex. Using this percentage on the number of PIT-tagged silver eels released at the North Sea Canal, the number of silver eels reaching the IJmuiden complex was estimated to be 1918 in 2016 and 1896 in 2017. Based on these numbers, the population of silver eels migrating to IJmuiden was estimated at 101,347 ± 10,990 silver eels in 2016 and 89,233 ± 9791 silver eels in 2017. To estimate to number of silver eels migrating through the IJmuiden complex into the North Sea, the migrating silver eel numbers were adjusted for the mortality rate of the pumping station turbines of 56% (Winter et al., 2020). Out of 125 silver eels tagged with a transmitter, 32 used the pumping station as a migration route, resulting in 14 eels surviving this route. The total mortality rate of the silver eel population passing the IJmuiden barrier-complex was therefore 14.3% ((32*0.56)/125), resulting in an escapement of 86,817 silver eel in 2016 and 76,441 in 2017 (average over both years 81,629).

4 | DISCUSSION

4.1 | Silver eel migration

There were large differences in passage success between the different study locations. At some locations, most silver eels were able to pass the barriers, such as the sluice-pumping station IJmuiden complex (98% passage) in the mouth of the North Sea canal. Some barriers had a 'blocking' effect, with low passage rates, higher resident times, and more exploration behaviour. This was most noticeable for inland locations at Vinkeveen (7% passage), Kadoelen (24%), and Willem I (20%). Silver eels were moving between connected locations such as Kadoelen and Willem I, which also indicated a blocking effect of the barriers at these locations. Other studies indicated a large variation in passage success. Verhelst, Baeyens et al. (2018) reported an escapement percentage of 34% from a heavily regulated shipping canal in Belgium. In the River Meuse in the Netherlands, Winter et al. (2006) reported that 37% of silver eels starting their migration reached the North Sea. By contrast, 89% of the silver eels passed three pumping stations in the polders in Friesland, the northern part of the Netherlands (van Keeken, van Hal, Winter, Wilkes, et al., 2020).

Passage of pumping stations and sluice barriers depends on the sequence and frequency of operation in time, which differed between locations. While pumping stations are used more frequently during periods after high rainfall, the operation of ship locks is dependent on local shipping activity in time. At some locations, the ship lock is used infrequently, for example, mostly during summer for recreational boating and not during night. At two such locations (Vinkeveen, Kortenhoef), no silver eels passed the ship lock. At Lelystad, there are two large ship locks, which are also in operation during night. However, only two silver eels were detected near Lelystad, and they both followed the spill gates route. At Ijmuiden, 60% (n = 75) passed via the ship locks, which facilitate intensive shipping during day and night. While 69% of the silver eels arriving at IJmuiden passed within a day, 17% took longer than a week to pass the complex. Verhelst, Baeyens et al. (2018) reported that migrating silver eels in Belgium were significantly delayed upstream of shipping locks.

Of the 71 silver eels that passed a barrier from a polder hinterland, 71% ($n = 51$) arrived at IJmuiden. Direct mortality could not be measured; however, some silver eels were detected continuously during longer periods at a receiver directly downstream from several pumping stations, indicating mortality caused by propeller collision when passing the pumping station. Silver eels can also suffer mortality during their migration within the canals, due to fisheries, predation by, for example, cormorants, or being struck by a propeller from a vessel. During September–November no commercial fishing is allowed, which was the most important period during the study for silver eels to migrate. At Lake Markermeer the silver eels were tagged and released in December, when fishing for eels was allowed, potentially leading to a lower escapement for this group than if silver eels were tagged and released earlier in the migration period.

In addition to the effects of barriers, in terms of mortality and delay, the lower average migration speeds in the upstream parts of the open canal system might indicate orientation problems. The highly regulated and unnatural nature of the flow regime could also result in a number of distracting cues silver eels encounter during their migration, such as lower or stagnant water flows or shipping activities. Silver eels from locations further upstream could encounter more of these distracting cues, which could result in lower migration speeds and eventually even in a lower percentage of silver eels reaching

IJmuiden. Verhelst, Baeyens et al. (2018) studied the migration of silver eel through the Albert canal (Belgium) and found an average migration speed of <0.06 m s^{-1}. The swimming speeds differed between different sections of the canal, with the maximum migration speed at 0.6217 ms^{-1}. This low average speed is comparable to other studies with open water and was caused by delays at ship locks and a lack of a consistent unidirectional water flow. Verbiest et al. (2012) found an average migration speed of 0.62 ms^{-1} for eels migrating along the river Meuse.

The migration speed of silver eels while traversing the North Sea Canal (without further obstructions) to IJmuiden increased significantly with the distance covered. The movement history of the silver eels before an obstruction significantly influences the migration speed after passage in the North Sea Canal. The more time silver eels spent between release and passage of a barrier, the higher the migration speed was from this barrier through the North Sea Canal to IJmuiden. This might be related to an increasing motivation (e.g., hormone driven) during the migration period by either higher swimming speed and/or changing their diurnal swimming pattern by migrating also during daylight more often. Migration delays can have serious impacts on silver eels because extra energy expenditure as such reducing the chance for a successful trans-Atlantic migration.

From other studies, it is known that a number of silver eels can cease their migration, even though the eels were in a silvery state during the tagging procedure (e.g., Okland et al., 2019; Verhelst, Buysse, et al. 2018; Winter et al., 2006). It is not known whether ceasing the migration is an effect of not being able to pass a barrier during a certain period, or could also be an effect of, for example, the handling and the tagging procedure (Okland et al., 2019). Eels can postpone their migration up to later years after the start of initial silvering (Durif et al., 2006; Verhelst, Buysse, et al. 2018; Winter et al., 2006). Even migration from freshwater to sea is reversible (Tambets et al., 2021). Given that the detection stations were in operation for up to 9 months (at IJmuiden), passage success at barriers might be underestimated when a fraction of the silver eels ceased their migration after having started. In our analysis silver eels that were not detected to start their migration were excluded, thus only eels that ceased their migration might have affected passage success. The overall escapement of silver eel estimates of the mark–recapture experiments, given their release at short distance from and high passage success at IJmuiden (98%), will not be affected by this.

Silver eels migrating at sea were detected in the Belgium network, confirming that silver eels used a southern migration route at the North Sea through the English Channel (Huisman et al., 2016). However, a portion of them could also have used a northern migration route going over the British Isles (Verhelst et al., 2022). This route was, however, not covered by receivers. In the recent study by Verhelst et al. (2022), 88% of migrating silver eels tagged with archival tags and released in Belgium, took the southern route, while 12% went in a northern direction. Of silver eels released in Germany, 83% migrated north and 17% southwestward. The silver eels had migration speeds ranging between 0.08 and 0.52 ms^{-1}. These differences in migration speeds were likely attributed to water currents, with silver eels that migrated through the English Channel being significantly faster than silver eels migrating northward. Huisman et al. (2016) reported that 20% of tagged silver eels released in Delfzijl (northern part of the Netherlands) were also detected in the Belgium detection network, indicating that at least a part of the Dutch silver eel population migrates in the North Sea southwards towards Belgium. These silver eels had an average migration speed in the North Sea of 0.23 ms^{-1}.

4.2 | Management

This study showed clear bottlenecks but also opportunities for enhancing silver eel migration along man-made barriers. With silver eel migrating mostly during the early evening, using fish-friendly pumps during this period of the night and pumps that cause higher mortalities during daytime could enhance safe passage. At IJmuiden, new pumps will be installed in coming years and this could offer the opportunity for higher silver eel migration survival. The ship locks at IJmuiden are used frequently and the newly constructed largest ship lock could also contribute to a safe migration along the complex at IJmuiden. Guiding silver eels away from the pumping station at IJmuiden could also increase survival but is difficult to accomplish at this large site. Methods for guiding eels away from barriers have been studied but gave mixed results. Also, due to the size of the IJmuiden complex, installing guiding systems that work properly might be challenging. Artificial light has been used to induce avoidance behaviour of eel species, mostly in experimental studies (e.g., Elvidge et al., 2018; Vowles & Kemp, 2021). Eels in the River Shannon (Ireland) showed avoidance behaviour to light barriers in a field experiment (MacNamara, 2012). For sound played under water, Sand et al. (2000) reported clear avoidance behaviour of silver eel to infrasound, Deleau et al. (2020) reported subtle avoidance behaviour, while Piper et al. (2019) and MacNamara (2012) reported limited to no avoidance behaviour of eels to infrasound. Miller et al. (2021) studied the effectiveness of electric barriers to block downstream migrating adult eel and concluded that the effectiveness is likely to be limited by water velocity, especially under very high velocities, when opportunity for volitional behaviour such as returning upstream or rapidly accelerating through the electric field is reduced.

Opening the pedal valves at Willem I and Overtoom could contribute to silver eel migration, while the fish passage facility at Kadoelen and the pedal valves at IJmuiden did not seem to enhance silver eel migration to a large extent. In smaller systems, the silver eels migrated through the pedal valves in the ship lock gates. At Ijmuiden, however, using the pedal valves as a fish passage facility did not contribute much, because the silver eels had multiple opportunities to migrate through the ship locks itself. Migrating silver eels tend to follow, either actively or passively, the major water flow (Kjærås et al., 2022; Lenihan et al., 2019; Økland et al., 2019; Trancart et al., 2018), which, at IJmuiden, leads to the larger ship locks and pumping station/sluice gates. However, at a fine scale, silver eels can also show avoidance and barrier-oriented behaviour, thereby choosing another route and not always following the major flow all the time. Piper et al. (2017) studied silver eel migration on the River Stour, England, and found that certain routes were consistently avoided, even when the majority of flow passed through them. The avoidance was caused by altered hydrodynamic conditions due to an increase in debris found at the site.

At small sites with less fish-friendly pumps, operating the pumps during the day and opening ship locks or pedal valves during the beginning of the night during the silver eel migration season could provide silver eels with a safe migration window to leave a polder area. Momentarily, most smaller ship locks and thereby the pedal valves are not in operation at night during the silver eel migration season, because of the lack of vessels and boats passing. Locations with low passage, such as Vinkeveen, Kortenhoef, and Kadoelen/Willem I could use the pumping stations during daytime and open the smaller ship locks or even open the pedal valves during the same night. Another option is pump replacement at Vinkeveen and Kortenhoef with a fish-friendly pump. Current pumps are not only less fish friendly but also block the passage of the silver eels.

ACKNOWLEDGMENTS

We would like to thank J. van Alphen, R. Barkhuis, R. Beentjes, X. de Boer, C. Breukers, J. Brockotter, P. Deitelzweig Senior, C. Dijkers, M. Hoexum, A. Kikkert, M. Melchers, H. Overbeek, B. Schaub, A. Stavenuiter, G. Timmermans, T. Voorhamm, M. van Wieringen, and K. Zwerver for their help with the project. We would also like to thank the local eel fishermen J. van Eeuwijk, P. Hartog, M. Hoetmer, R. Hoetmer, B. Klinkhamer, J. Last, J. Los, R. van Rhee, P. Ruijter, J. van Veen, S. van Veen, G. de Vries, A. Werkhoven, and B. van Wijk for capturing the silver eels, and Sportvisserij Nederland and VLIZ for lending their receivers. Finally, we would like to thank J. Tiano for proofreading the paper. This study was funded by Ecologische Verbindingszone Noordzeekanaal en Ommelanden: Rijkswaterstaat West-Nederland Noord and Midden Nederland, Provincie Noord-Holland, Hoogheemraadschap Hollands Noorderkwartier, Hoogheemraadschap van Rijnland, Waterschap Amstel, Gooi en Vecht, Sportvisserij Midwest Nederland, Gemeente Amsterdam, and Port of Amsterdam. All fish operation procedures were in compliance with the Dutch Animal Welfare Law.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Baker, N. J., Wright, R. M., Cowx, I. G., Murphy, L. A., & Bollanda, J. D. (2021). Downstream passage of silver European eel (*Anguilla anguilla*) at a pumping station with a gravity sluice. *Ecological Engineering*, *159*, 106069. https://doi.org/10.1016/j.ecoleng.2020.106069

Baras, E., & Jeandrain, D. (1998). Evaluation of surgery procedures for tagging eel Anguilla anguilla (L.) with biotelemetry transmitters. In J. P. Lagardère, M. L. B. Anras, G. Claireaux (Eds.), *Advances in invertebrates and fish telemetry*. Developments in hydrobiology (Vol. 130, pp. 107–111). Springer.

Bolland, J. D., Murphy, L. A., Stanford, R. J., Angelopoulos, N. V., Baker, N. J., Wright, R. M., Reeds, J. D., & 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*, 76–85. https://doi.org/10.1111/fme.12312

Brevé, N. W. P., Buijse, A. D., Kroes, M. J., Wanningen, H., & Vriese, F. T. (2014). Supporting decision-making for improving longitudinal connectivity for diadromous and potamodromous fishes in complex catchments. *Science of The Total Environment*, *496*, 206–218. https://doi.org/10.1016/j.scitotenv.2014.07.043

Buysse, D., Mouton, A. M., 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*, 13–21. https://doi.org/10.1111/fme.12046

Dębowski, P., Bernaś, R., Skóra, M., & Morzuch, J. (2020). Route selection, migration speed, and mortality of silver eel passing through two small hydroelectric facilities. *Fisheries & Aquatic Life*, *28*, 133–140. https://doi.org/10.2478/aopf-2020-0016

Dekker, W. (2000). Impact of yellow eel exploitation on spawner production in Lake IJsselmeer, the Netherlands. *Dana*, *12*, 17–32.

Deleau, M. J. C., White, P. R., Peirson, G., Leighton, T. G., & Kemp, P. S. (2020). Use of acoustics to enhance the efficiency of physical screens designed to protect downstream moving European eel (*Anguilla anguilla*). *Fisheries Management and Ecology*, *27*, 1–9. https://doi.org/10.1111/fme.12362

Drouineau, H., Durif, C., Castonguay, M., Mateo, M., Rochard, E., Verreault, G., Yokouchi, K., & Lambert, P. (2018). Freshwater eels: A symbol of the effects of global change. *Fish and Fisheries*, *19*, 903–930. https://doi.org/10.1111/faf.12300

Durif, C. M., Dufour, S., & Elie, P. (2006). Impact of silvering stage, age, body size and condition on reproductive potential of the European eel. *Marine Ecology Progress Series*, *327*, 171–181. https://doi.org/10.3354/meps327171

Durif, C. M. F., 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*, 1025–1043. https://doi.org/10.1111/j.1095-8649.2005.00662

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. https://doi.org/10.1016/j.ecoleng.2017.05.054

Elvidge, C. K., Ford, M. I., Pratt, T. C., Smokorowski, K. E., Sills, M., Patrick, P. H., & Cooke, S. J. (2018). Behavioural guidance of yellow-stage American eel *Anguilla rostrata* with a light-emitting diode device. *Endangered Species Research*, *35*, 159–168. https://doi.org/10.3354/esr00884

Gosset, C., Travade, F., Durif, C., Rives, J., & Elie, P. (2005). Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications*, *21*, 1095–1105. https://doi.org/10.1002/rra.871

Griffioen, A. B., van Keeken, O. A., & Winter, H. V. (2015). Behavioural patterns of migrating silver eel at a hydropower station on the River Meuse. In A. Don & P. Coulson (Eds.), *Eels biology, monitoring, management, culture and exploitation: Proceedings of the first international eel science symposium* (pp. 158–171). 5m Publishing.

Griffioen, A. B., van Keeken, O. A., & Winter, H. V. (2017). *Pilot studie akoestische telemetrie nabij sluiscomplex IJmuiden* (Report C060/17). Wageningen Marine Research. https://doi.org/10.18174/421903

Huisman, J., Verhelst, P., Verhelst, P., Deneudt, K., Goethals, P., Moens, T., Nagelkerke, L. A. J., Nolting, C., Reubens, J., Schollema, P. P., Winter, H. V., & Mouton, A. (2016). Heading south or north: Novel insights on European silver eel *Anguilla anguilla* migration in the North Sea. *Marine Ecology Progress Series*, *554*, 257–262. https://doi.org/10.3354/meps11797

ICES. (2021). *Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL)* (ICES Scientific Reports, 3(85)). https://doi.org/10.17895/ices.pub.8143

Kjærås, H., Baktoft, H., Silva, A. T., Gjelland, K. Ø., Økland, F., Forseth, T., Szabó-Mészáros, M., & Calles, O. (2022). Three-dimensional migratory behaviour of European silver eels (*Anguilla anguilla*) approaching a hydropower plant. *Journal of Fish Biology*, *2022*, 465–478. https://doi.org/10.1111/jfb.15278

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*, 289–295. https://doi.org/10.1016/j.ecohyd.2018.07.001

MacNamara, R. (2012). *Conservation biology of the European eel (Anguilla anguilla) on a hydropower-regulated Irish river* (Doctoral dissertation). NUI Galway. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.895.6687&rep=rep1&type=pdf

Miller, M., de Bie, J., Sharkh, S. M., & Kemp, P. S. (2021). Behavioural response of downstream migrating European eel (*Anguilla anguilla*) to electric fields under static and flowing water conditions. *Ecological Engineering*, *172*, 106397. https://doi.org/10.1016/j.ecoleng.2021.106397

Moriarty, C., & Dekker, W. (1997). Management of European eel fisheries. *Irish Fisheries Bulletin*, *15*, 1-110.

O'Briain, R. (2019). Climate change and European rivers: An eco-hydromorphological perspective. *Ecohydrology*, *12*, e2099. https://doi.org/10.1002/eco.2099

Økland, F., Havn, T. B., Thorstad, E. B., Heermann, L., Saether, S. A., Tambets, M., Teichert, M. A. K., & Borcherding, J. (2019). Mortality of downstream migrating European eel at power stations can be low when turbine mortality is eliminated by protection measures and safe bypass routes are available. *International Review of Hydrobiology*, *104*, 68–79. https://doi.org/10.1002/iroh.201801975

Palstra, A. P., Guerrero, M. A., de Laak, G., Breteler, J. P. K., & van den Thillart, G. E. (2011). Temporal progression in migratory status and sexual maturation in European silver eels during downstream migration. *Fish Physiology and Biochemistry*, *37*, 285–296. https://doi.org/10.1007/s10695-011-9496-x

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*, 87–98. https://doi.org/10.1111/eff.12257

Piper, A. T., White, P. R., Wright, R. M., Leighton, T. G., & Kemp, P. S. (2019). Response of seaward-migrating European eel (*Anguilla anguilla*) to an infrasound deterrent. *Ecological Engineering*, *127*, 480–486. https://doi.org/10.1016/j.ecoleng.2018.12.001

Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical interference for mark-recapture experiments. *Wildlife Monographs*, *107*, 1–97.

R Core Team. (2021). *R: A language and environment for statistical computing*. RStudio, PBC. Retrieved from https://www.R-project.org

Reubens, J., Verhelst, P., van der Knaap, I., Wydooghe, B., Milotic, T., Deneudt, K., Hernandez, F., & Pauwels, I. (2019). The need for aquatic tracking networks: The Permanent Belgian Acoustic Receiver Network. *Animal Biotelemetry*, *7*, 1–6. https://doi.org/10.1186/s40317-019-0164-8

Ricker, W. E. (1975). *Computation and interpretation of biological statistics of fish populations* (Vol. 191, p. 382). Bulletin of the Fisheries Research Board of Canada.

Sand, O., Enger, P. S., Karlsen, H. E., Knudsen, F., & Kvernstuen, T. (2000). Avoidance responses to infrasound in downstream migrating European silver eels, *Anguilla anguilla*. *Environmental Biology of Fishes*, *57*, 327–336. https://doi.org/10.1023/A:1007575426155

SAS Institute Inc. (2011). *SAS/QC 9.3 User's guide*. SAS Institute Inc.

Seber, G. A. F. (1970). *The estimation of animal abundance and related parameters* (2nd ed., p. 654). MacMillan.

Tambets, M., Kärgenberg, E., Järvalt, A., Økland, F., Kristensen, M. L., Koed, A., & Bernotas, P. (2021). Migrating silver eels return from the sea to the river of origin after a false start. *Biology Letters*, *17*, 20210346. https://doi.org/10.1098/rsbl.2021.0346

Trancart, T., Tétard, S., Acou, A., Feunteun, E., Schaeffer, F., & De Oliveira, E. (2018). Silver eel downstream migration in the River Rhine, route choice, and its impacts on escapement: A 6-year telemetry study in a highly anthroposized system. *Ecological Engineering*, *123*, 202–211. https://doi.org/10.1016/j.ecoleng.2018.09.002

Travade, F., Larinier, M., Subra, S., Gomes, P., & De-Oliveira, E. (2010). Behaviour and passage of European silver eels (*Anguilla anguilla*) at a small hydropower plant during their downstream migration. *Knowledge and Management of Aquatic Ecosystems*, *398*, 1–19. https://doi.org/10.1051/kmae/2010022

van der Hammen, T., Soudijn, F., Volwater, J., van Rijssel, J. C., Griffioen, A. B., Chen C., & Winter, H. V. (2021). *European Eel (Anguilla anguilla) stock size, anthropogenic mortality and silver eel escapement in the Netherlands 2006-2020* (CVO report 21.023). Centre for Fisheries Research. https://doi.org/10.18174/556153

Van der Baan, J., van der Heijden, S. & van Reen, M. (2023). *Kennisprogramma Zeespiegelstijging, spoor II. Systeemanalyses zoetwater regio Amsterdam-Rijnkanaal - Noordzeekanaal (report 30101791.3.ANL). Arcadis/Hydrologic*.

van Keeken, O. A., van Hal, R., Winter, H. V., 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*, 464–471. https://doi.org/10.1111/fme.12427

van Keeken, O. A., van Hal, R., Winter, H. V., Wilkes, T., & Griffioen, A. B. (2020). Migration of silver eel, *Anguilla anguilla*, through three water pumping stations in the Netherlands. *Fisheries Management and Ecology*, *28*, 76–90. https://doi.org/10.1111/fme.12457

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*, 395–403. https://doi.org/10.1111/j.1600-0633.2012.00559.x

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*, 73–87. https://doi.org/10.1111/eff.12565

Verhelst, P., Baeyens, R., Reubens, J., Benitez, J. P., Coeck, J., Goethals, P., Ovidio, M., Vergeynst, J., Moens, T., & Mouton, A. (2018). European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal. *Fisheries Research*, *206*, 176–184. https://doi.org/10.1016/j.fishres.2018.05.013

Verhelst, P., Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., Goethals, P., Coeck, J., Moens, T., & Mouton, A. (2018). Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management. *Fisheries Research*, *199*, 176–184. https://doi.org/10.1016/j.fishres.2017.10.018

Verhelst, P., Reubens, J., Coeck, J., Moens, T., Simon, J., Van Wichelen, J., Westerberg, H., Wysujack, K., & Righton, D. (2022). Mapping silver eel migration routes in the North Sea. *Nature Scientific Reports*, *12*, 318. https://doi.org/10.1038/s41598-021-04052-7

Vousdoukas, M. I., Mentaschi, L., Voukouvalas, E., Verlaan, M., & Feyen, L. (2017). Extreme sea levels on the rise along Europe's coasts. *Earth's Future*, *5*, 304–323. https://doi.org/10.1002/2016EF000505

Vowles, A. S., & Kemp, P. S. (2021). Artificial light at night (ALAN) affects the downstream movement behaviour of the critically endangered European eel, *Anguilla anguilla*. *Environmental Pollution*, *274*, 116585. https://doi.org/10.1016/j.envpol.2021.116585

Westerberg, H., Miller, M. J., Wysujack, K., Marohn, L., Freese, M., Pohlmann, J. D., Watanabe, S., Tsukamoto, K., & Hanel, R. (2018). Larval abundance across the European eel spawning area: An analysis of recent and historic data. *Fish and Fisheries*, *19*, 890–902. https://doi.org/10.1111/faf.12298

Winter, H. V., Griffioen, A. B., & de Bruijn, P. (2020). *Evaluatie trekvisonderzoeken Noordzeekanaal en ommelanden* (Report C015.20). Wageningen Marine Research. https://doi.org/10.18174/514957

Winter, H. V., Jansen, H. M., & Breukelaar, A. W. (2007). Silver eel mortality during downstream migration in the River Meuse, a population perspective. *ICES Journal of Marine Science*, *64*, 1444–1449. https://doi.org/10.1093/icesjms/fsm128

Winter, H. V., Jansen, H. M., & Bruijs, M. C. M. (2006). Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. *Ecology of Freshwater Fish*, *15*, 221–228. https://doi.org/10.1111/j.1600-0633.2006.00154.x

Winter, H. V., van Keeken, O. A., Kleissen, F., & Foekema, E. M. (2023). Wastewater plumes can act as non-physical barriers for migrating silver eel. *PLos ONE*, *18*(6), e0287189. https://doi.org/10.1371/journal.pone.0287189

How to cite this article: van Keeken, O. A., Griffioen, A. B., Tien, N. S. H., & Winter, H. V. (2023). Assessing migratory bottlenecks and escapement of silver eel (*Anguilla anguilla*) in the highly urbanized North Sea Canal basin, the Netherlands. *River Research and Applications*, *39*(10), 1972–1993. https://doi.org/10.1002/rra.4206

APPENDIX A

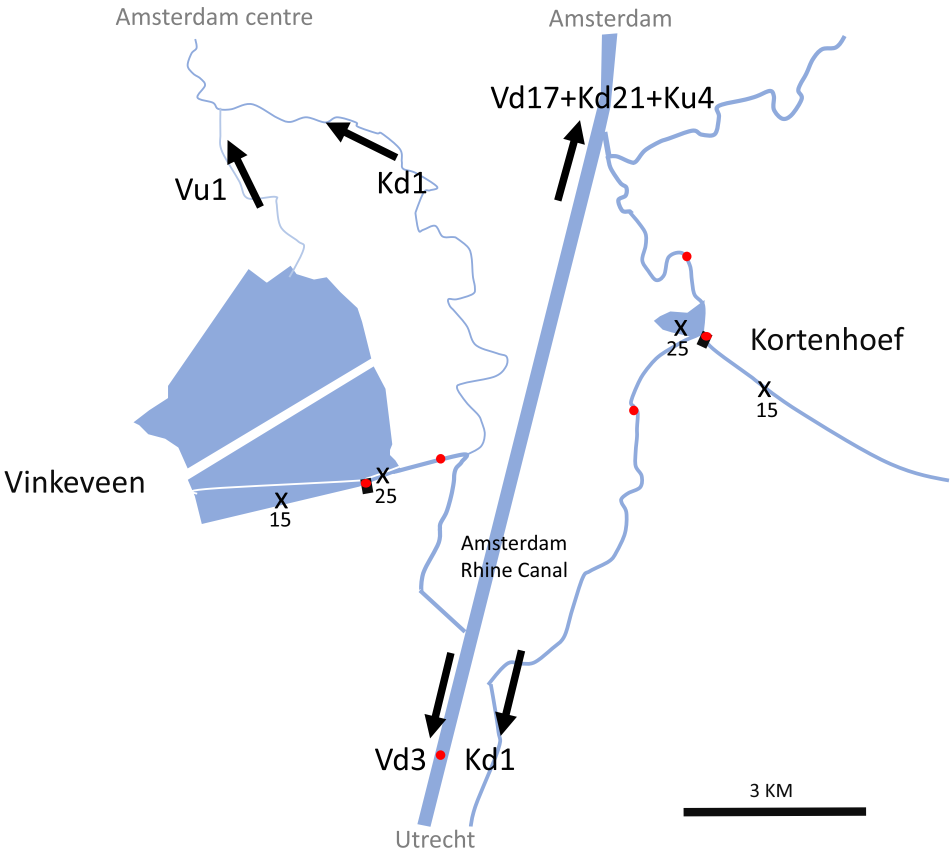


FIGURE A1 Vinkeveen and Kortenhoef. [Color figure can be viewed at wileyonlinelibrary.com]

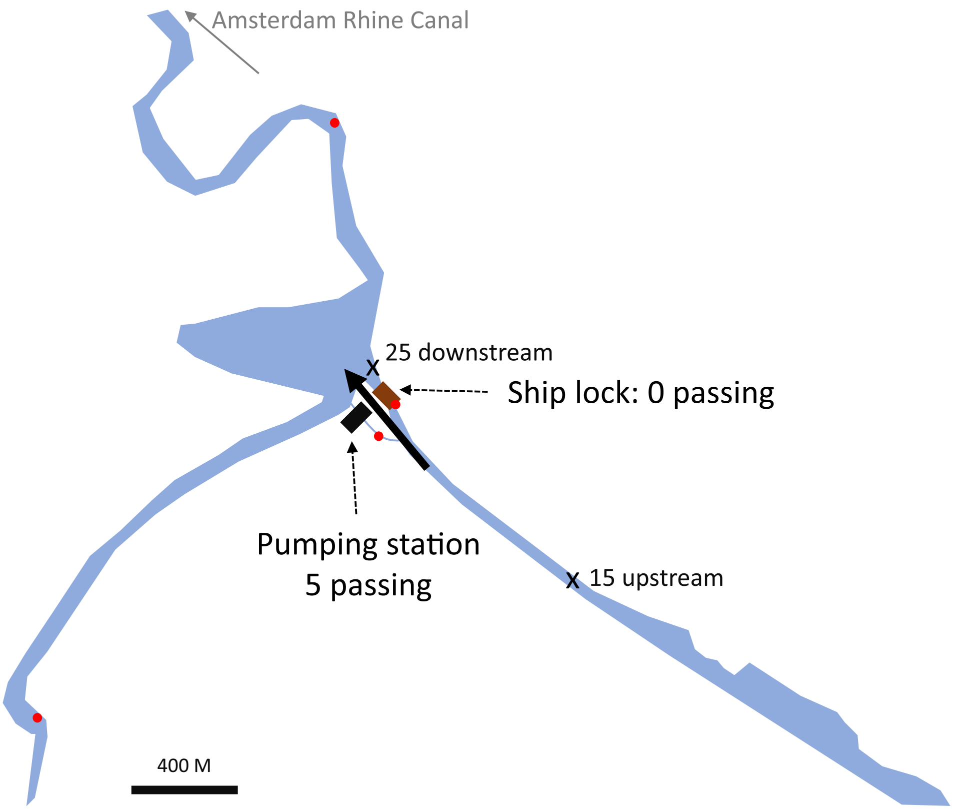
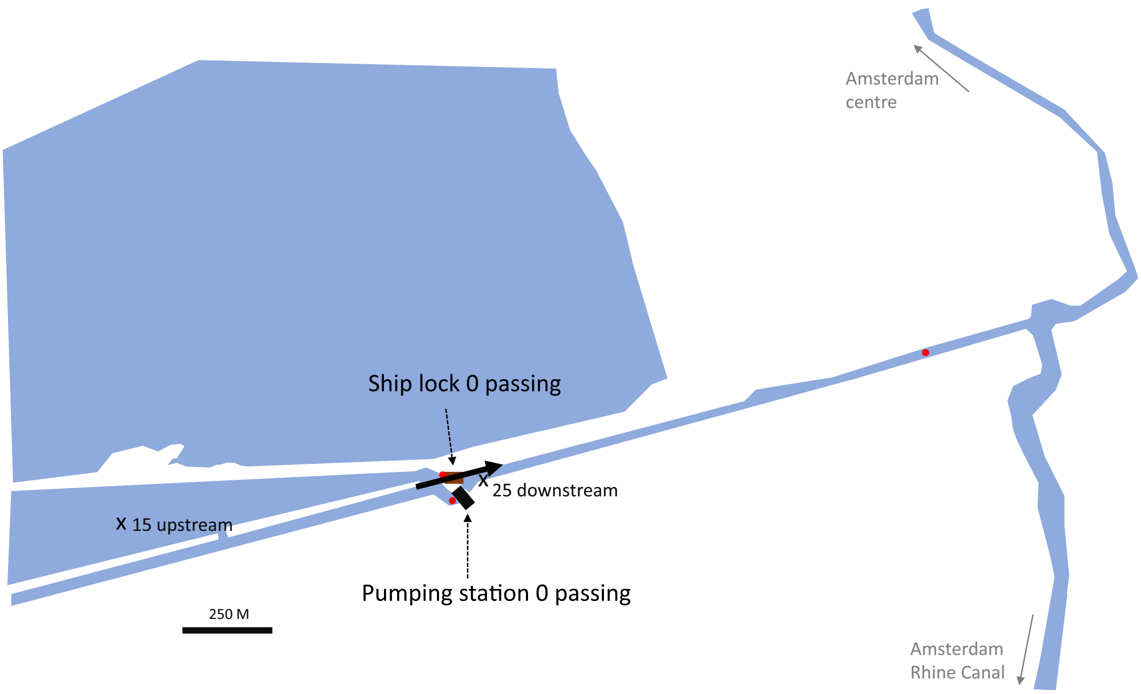


FIGURE A2 Kortenhoef. [Color figure can be viewed at wileyonlinelibrary.com]



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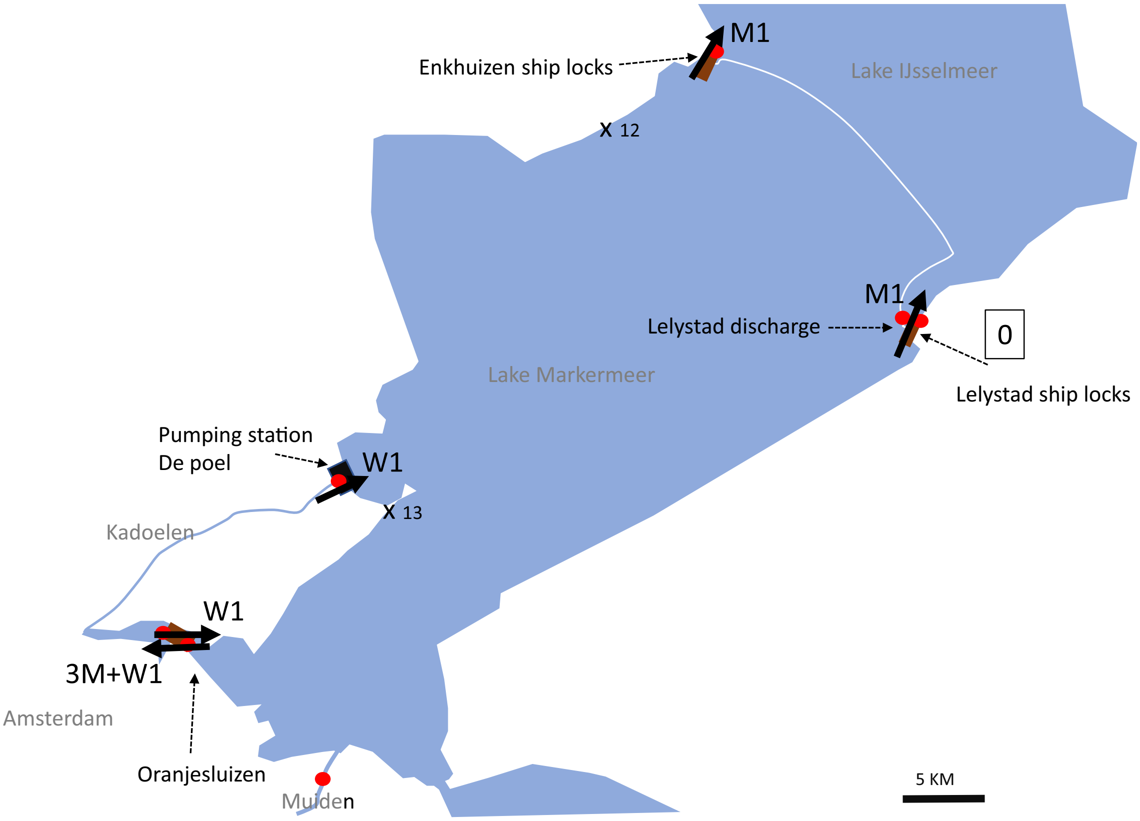

FIGURE A4 Lake Markermeer. [Color figure can be viewed at wileyonlinelibrary.com]

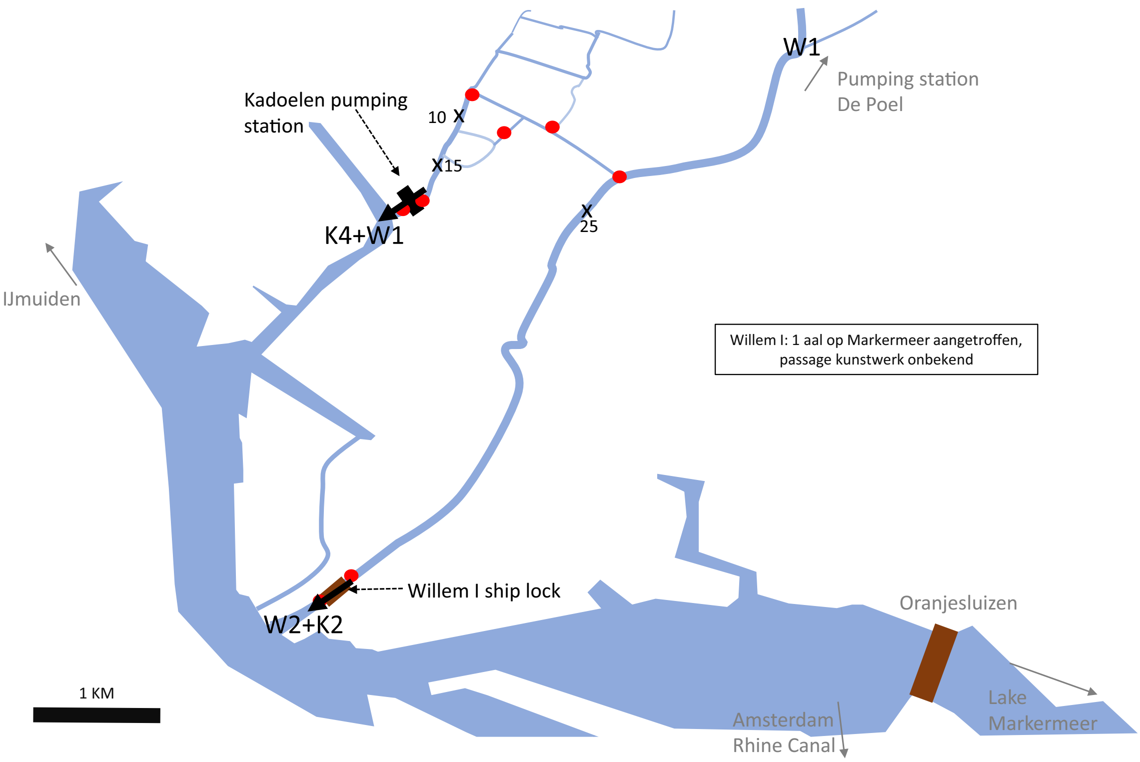

FIGURE A5 Kadoelen and Willem I. [Color figure can be viewed at wileyonlinelibrary.com]

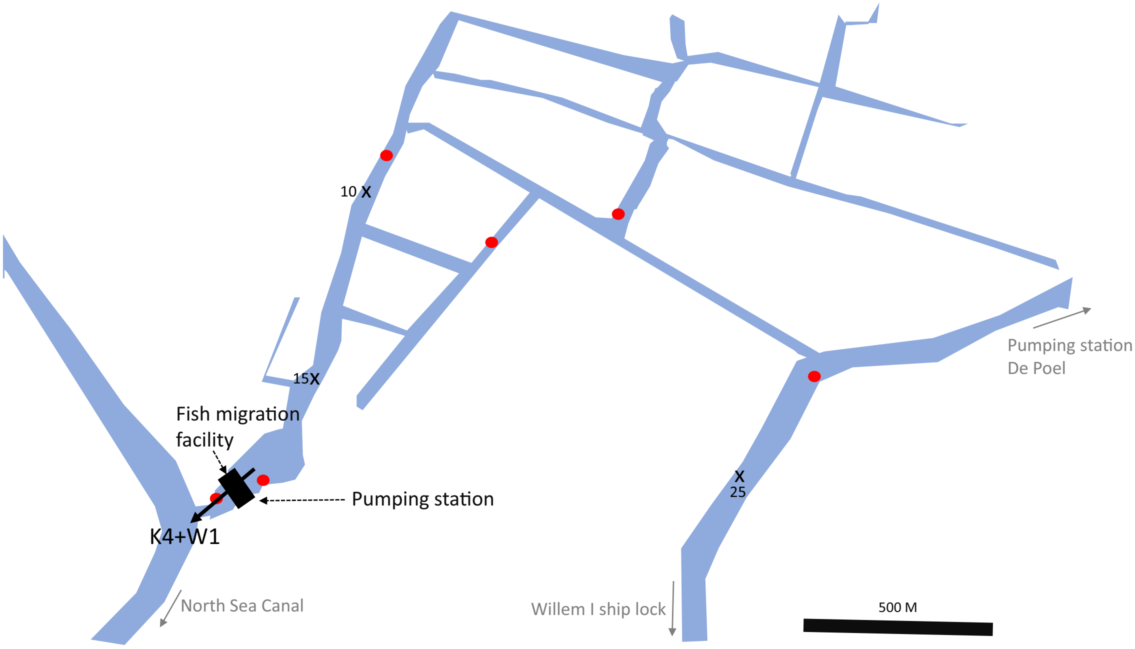

FIGURE A6 Kadoelen. [Color figure can be viewed at wileyonlinelibrary.com]

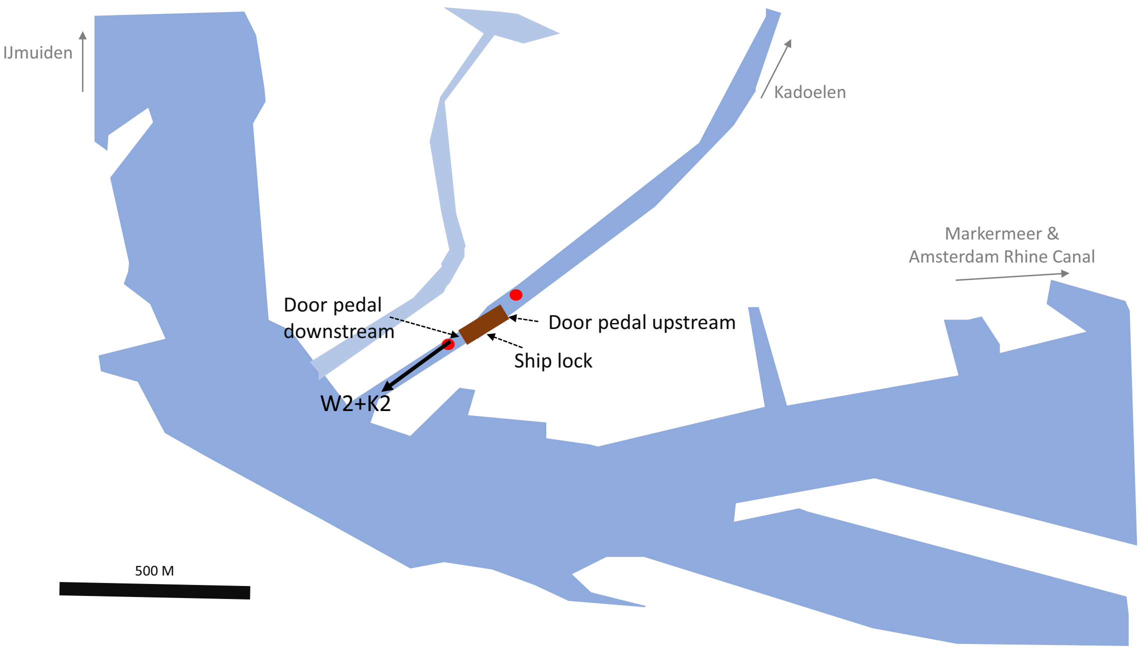

FIGURE A7 Willem I. [Color figure can be viewed at wileyonlinelibrary.com]

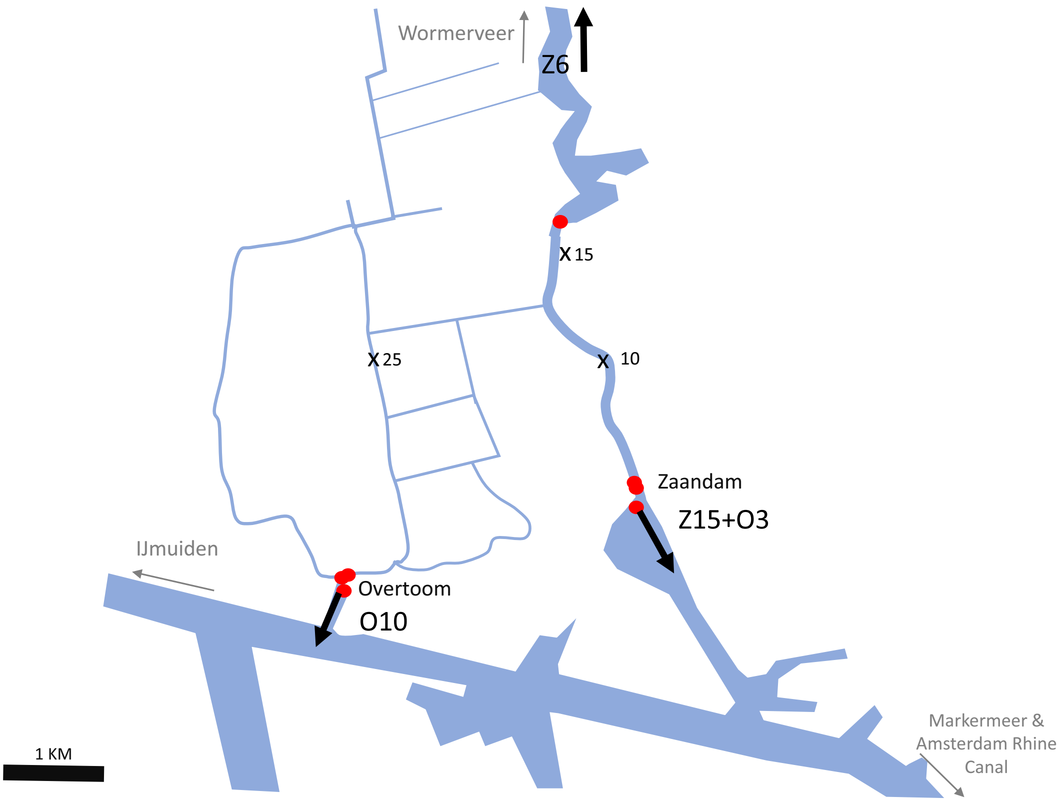

FIGURE A8 Overtoom and Zaandam. [Color figure can be viewed at wileyonlinelibrary.com]

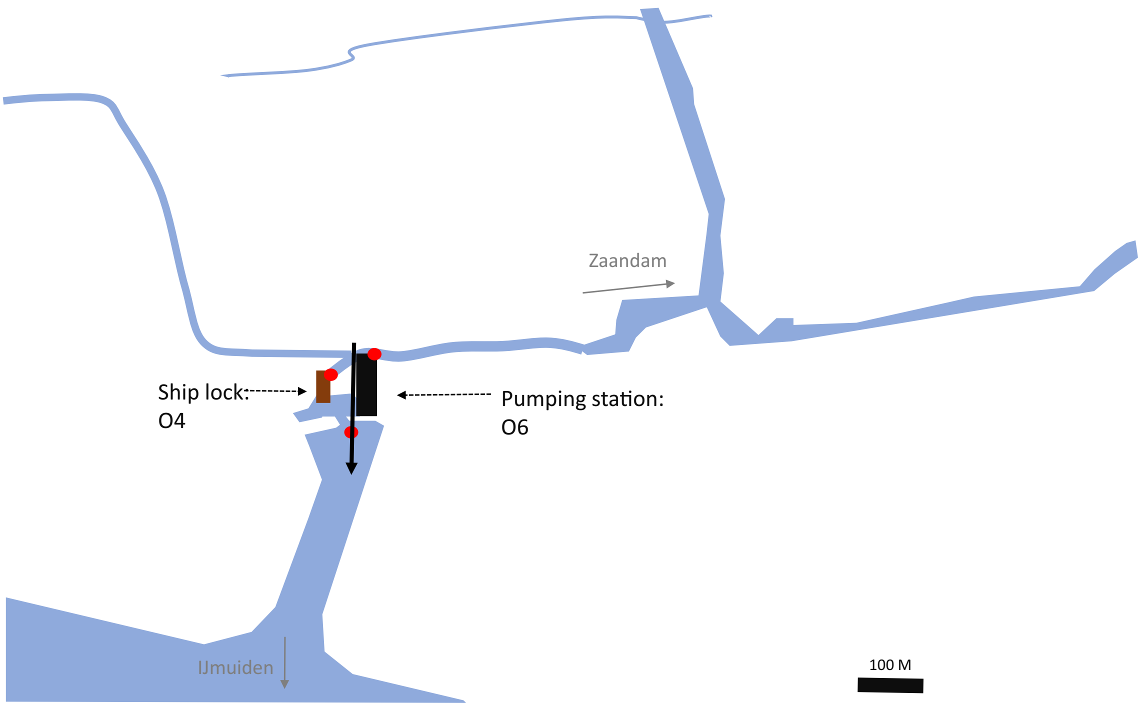

FIGURE A9 Overtoom. [Color figure can be viewed at wileyonlinelibrary.com]

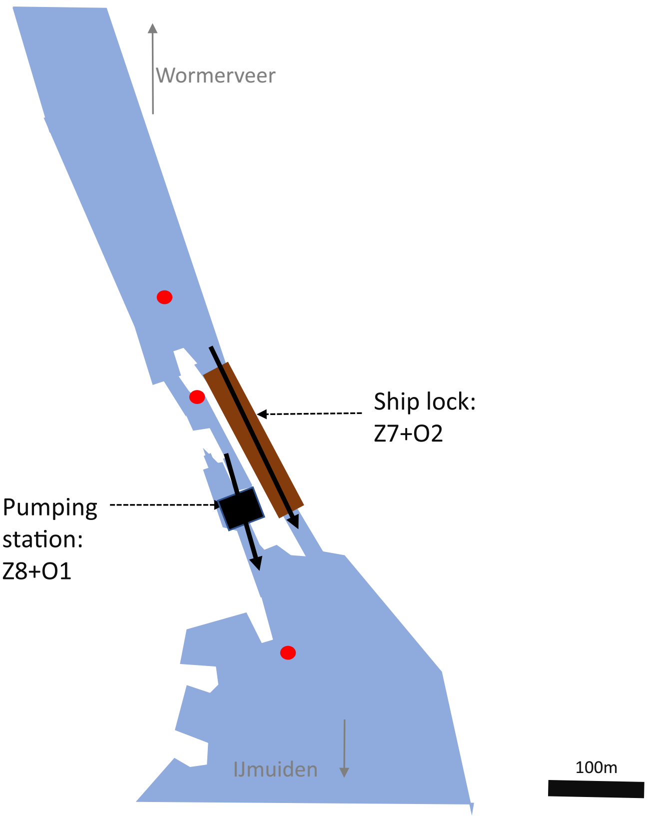

FIGURE A10 Zaandam. [Color figure can be viewed at wileyonlinelibrary.com]

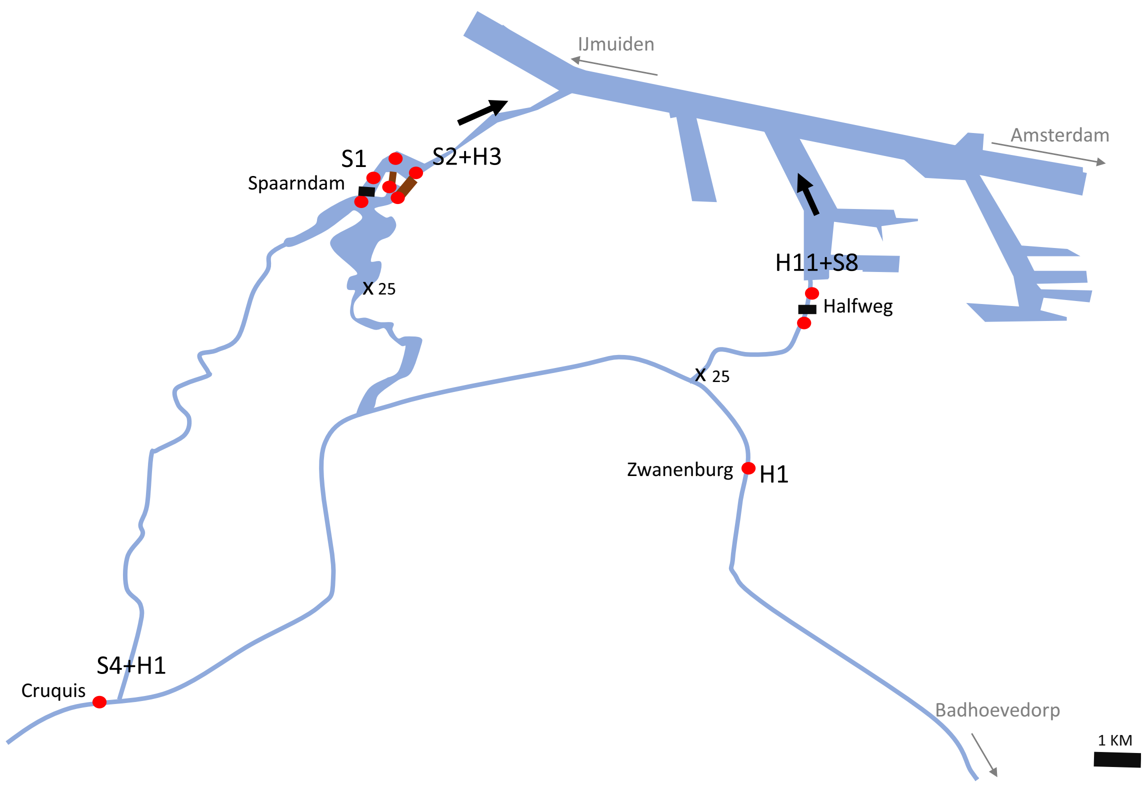

FIGURE A11 Spaarndam and Halfweg. [Color figure can be viewed at wileyonlinelibrary.com]

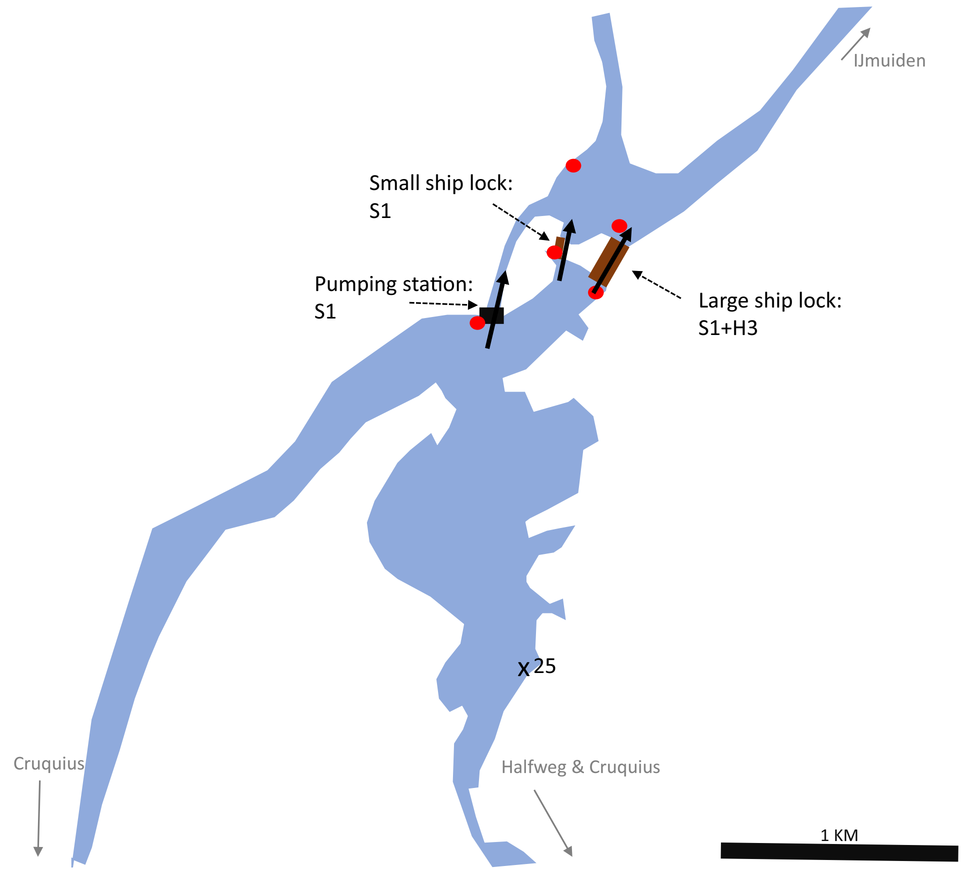

FIGURE A12 Spaarndam. [Color figure can be viewed at wileyonlinelibrary.com]

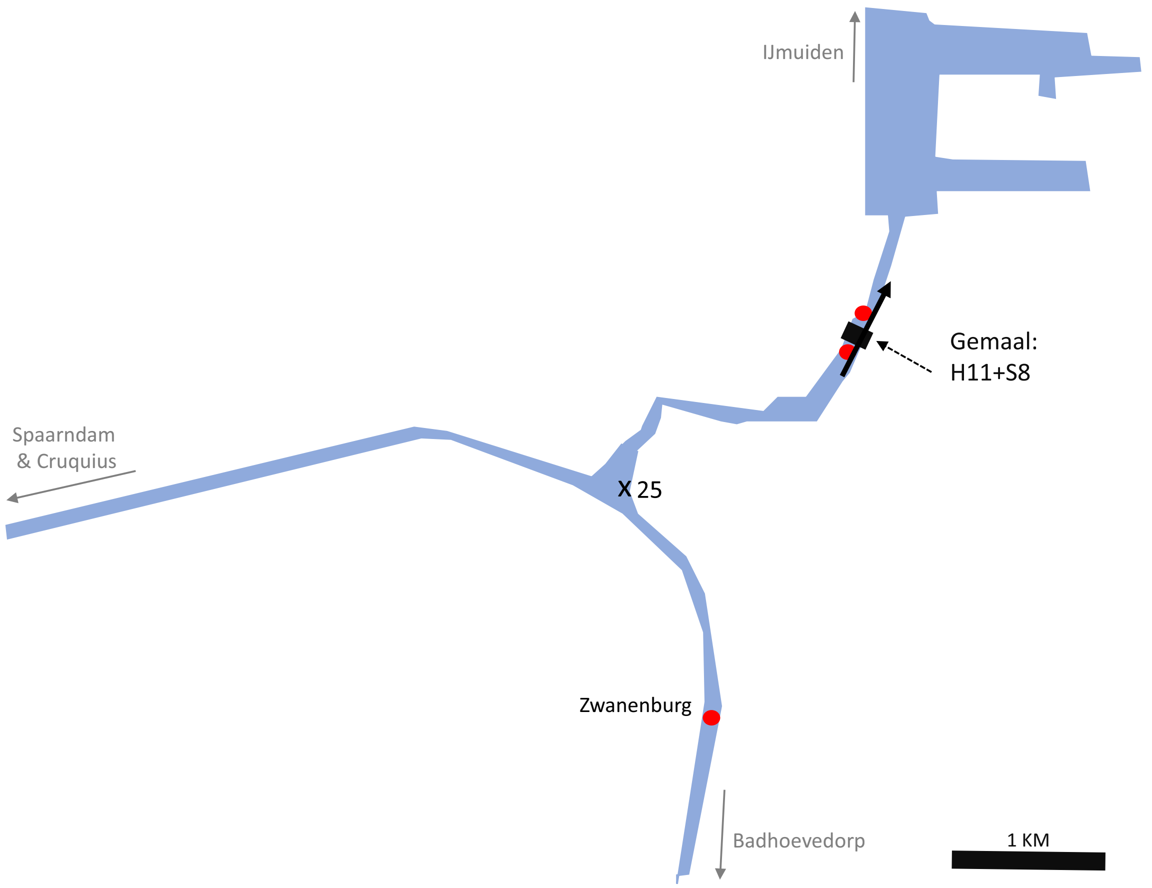

FIGURE A13 Halfweg. [Color figure can be viewed at wileyonlinelibrary.com]