Received: 18 January 2021 | Revised: 3 March 2022 | Accepted: 12 March 2022

DOI: 10.1002/rra.3967

RESEARCH ARTICLE

WILEY

Passage efficiency and behaviour of sea lampreys (*Petromyzon marinus*, Linnaeus 1758) at a large marine–freshwater barrier

Arie Benjamin Griffioen[1] | Olvin Alior van Keeken[1] | Alicia Lianne Hamer[1] | Hendrik Volken Winter[1,2]

[1]Wageningen Marine Research, IJmuiden, The Netherlands

[2]Aquaculture and Fisheries group, Wageningen University & Research, Wageningen, The Netherlands

Correspondence
Arie Benjamin Griffioen, Wageningen Marine Research, Haringkade 1, 1976 CP IJmuiden, The Netherlands.
Email: ben.griffioen@wur.nl

Funding information
Dutch Ministry of Agriculture, Nature and Food Quality, Grant/Award Number: BO-11-015-040

Abstract

Passage success of sea lampreys *Petromyzon marinus* and behaviour in the vicinity of man-made structures such as marine–freshwater barriers are poorly understood. To mitigate these migratory problems, a better understanding of passage behaviour is needed. To investigate this, 25 sea lampreys were tagged with V7 VEMCO acoustic transmitters at a large marine-freshwater barrier, consisting of ten sluice gates and a ship lock complex in the Netherlands. Overall passage success was assessed to be 16%, with four sea lampreys passing the sluice gates, while none passed the ship locks. Successful passage through the barrier occurred either at the beginning or at the end of a discharge period, when water level differences between sea and lake and thus water velocities were relatively low. Most sea lamprey showed exploratory searching behaviour but only for a short duration, before leaving the area again when unsuccessful. Low passage success and search duration were likely related to the unnatural infrequent occurrence of flow and only short lasting windows with suitable conditions for passage at the sluice gates. To mitigate the poor migration success of sea lampreys at the marine-freshwater barrier with the current adapted sluice management, a fish passage facility with lower water velocities and longer or continuous passage opportunities is needed.

KEYWORDS
conservation, fish migration, lamprey, telemetry

1 | INTRODUCTION

Diadromous fish species migrate between marine and freshwater habitats to complete their life cycle (McDowall, 1988). They require a sequence of different habitats with good connectivity, and are vulnerable to factors such as habitat loss, habitat fragmentation and migration barriers, climate change and fisheries (Belletti et al., 2020; B. Clemens, Mesa, Magie, Young, & Schreck, 2012; Duarte et al., 2020; Lassalle, Crouzet, & Rochard, 2009; Merg et al., 2020). As a result diadromous fish populations in Western Europe have strongly declined (de Groot, 2002; Limburg & Waldman, 2009; Merg et al., 2020). Diadromous fish that migrate long distances in heavily regulated freshwater systems are intrinsically the most vulnerable to migration blockage, since series of consecutive barriers have to be passed (Merg et al., 2020). One of these diadromous fish is the sea lamprey (*Petromyzon marinus*, Linnaeus 1758), which is an anadromous fish species. It lives as a parasitic fish in the adult phase at sea and migrates upstream during spring to spawn in freshwater. The sea lamprey population has been declining strongly due to hampered migration (B. J. Clemens et al., 2020; Legrand et al., 2020; Mota, Rochard, &

Antunes, 2016) and thus is listed in Annex II of the EU (European Union) Habitats Directive which requires designation of Special Areas of Conservation in EU member states (EEC, 1992). Passing through turbulent and high velocity areas, such as tide- or sluice- gates at marine-freshwater barriers, can be particularly challenging for upstream migrating sea lamprey, as they lack pectoral fins for stabilization (Kemp, Russon, Vowles, & Lucas, 2011; Liao, 2007).

The influence of marine-freshwater barriers and tidal gates on fish migration (e.g., Piper, Wright, Walker, & Kemp, 2013; Wright, Wright, & Kemp, 2014, 2015) has received less attention in Europe than barriers in rivers, such as hydropower dams, weirs or large pumping stations (e.g., Duarte et al., 2020; Harrison et al., 2019; Van Keeken, van Hal, Volken Winter, Tulp, & Griffioen, 2020). Sluice gates at marine-freshwater barriers or tidal gates are often associated with accelerating flow velocities and high turbulence (Kolvoort & Butijn, 1990; Russon & Kemp, 2011) and therefore may hamper fish migration when opened. Upstream migrating fish are attracted by discharged freshwater flows (Kroes, Van Loon, Goverse, Schiphouwer, & Van der Geest, 2020; Wright, Wright, Bendall, & Kemp, 2016), but passage at the gates is limited to short-lasting windows during discharge events accompanied with strong currents. Accumulation due to delay may result in higher predation risk (Boulêtreau et al., 2020).

In 1932, a large marine-freshwater barrier, the Afsluitdijk, closed off a large natural estuary, the Zuiderzee, and formed a new large freshwater Lake Ijsselmeer in the Netherlands. The 32 km long barrier has two sluice gate complexes including ship locks, one at either end of the barrier. At these sluice gates high water velocities, up to 4.5 ms^{-1}, may occur during the discharge of freshwater (Kolvoort & Butijn, 1990; Vlag, 1999). Small diadromous fish, such as smelt (*Osmerus eperlanus* Linnaeus 1758), are hampered by this barrier (Tulp et al., 2013). Previous analysis of 111 individual Sr/Ba otolith profiles showed no evidence of the migration of smelt from the Wadden Sea to Lake IJsselmeer (Phung et al., 2015). Additionally the contribution from the diadromous population to the spawning stock of the landlocked population was found to be limited (Tulp et al., 2013). High accumulations of glass eel at the sea side of the sluice gates were observed, in a previous study, suggesting a migratory delay of several weeks (Dekker & van Willigen, 1997). Contrary to small diadromous fish, studies on North Sea houting (*Coregonus oxyrinchus*, Linnaeus 1758) and sea trout (*Salmo trutta*, Linnaeus 1758) showed evidence that these species were able to pass the Afsluitdijk (Bij de Vaate, Breukelaar, Vriese, De Laak, & Dijkers, 2003; Borcherding, Breukelaar, Winter, & König, 2014). Behaviour and passage success of sea lamprey at this barrier is still unknown.

In this study, behaviour and passage success of sea lampreys at a large marine - freshwater barrier, the Afsluitdijk, was determined using acoustic telemetry. Sea lampreys have known spawning sites riverine spawning sites in the Rhine catchment area (e.g., Baer, Hartmann, & Brinker, 2018) which can be reached by passing the Afsluitdijk. The aims of this study are: (1) to estimate the passage success rate at the entire barrier complex; (2) to assess which migration routes within the barrier complex were used by sea lampreys, that is, the sluice gates and/or the adjacent ship locks and (3) if passage was successful, during what conditions and timing the barrier was passed.

2 | MATERIALS AND METHODS

2.1 | Study site

The Afsluitdijk has two sluice gate complexes, Den Oever and Kornwerderzand, one at either end of the barrier. Excess freshwater from Lake IJsselmeer which is fed by the river Rhine is discharged into the Wadden Sea. Freshwater can only be discharged when the water level in the Wadden Sea is 10 cm lower than that of the lake IJsselmeer. No salt water intrusion in the freshwater lake is allowed (Figure 1), but occasionally occurs during maintenance or malfunction. Water velocities at the gates can reach up to 4.5 ms^{-1} (Vlag, 1999).

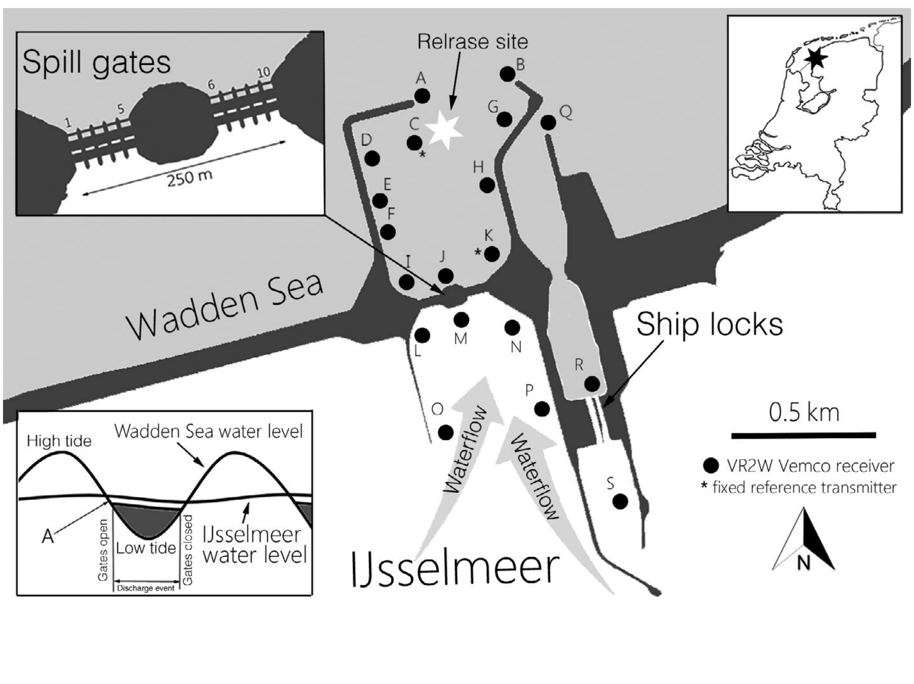

FIGURE 1 The study site of Kornwerderzand located in the north of the Netherlands. The bottom left diagram represents schematically the discharge regime: sluice gates are opened and closed when water level of the freshwater lake is 10 cm below the water level on the marine side (A). The dimensions of the spilling basin are approximately ~480 × 680 m. The deepest part in the basin is over 15–20 m deep

The Kornwerderzand study site (Figures 1, 53.074 N, 5.333 E) consists of ten sluice gates. Each gate consist of two 12 m wide doors which are 50 m apart, one door at the sea side and one at the lake side. Both doors can be raised independently from each other and function as a undershot sluice (Figure 1). The flat chamber (12 × 50 m W × L) in between the doors is made of smooth concrete. Under most conditions, the sluice gate doors are raised each low tide to discharge excess freshwater from Lake Ijsselmeer into the Wadden Sea. Depending on the weather conditions and water levels, the doors at gates 1, 5, 6 and 10 are raised only 0.5 m from the bottom to facilitate upstream fish migration: "Fish Friendly Management Regime" (FFMR). With FFMR, maximum water velocity only occurs at a small stretch directly below the partially raised door, and water velocities in the remaining part of the sluice gate are much lower, whereas with fully raised doors, maximum velocity occurs at the full stretch length of the sluice gate (ca. 50 m long). The gates are therefore expected to be more passable for fish when FFMR is applied. In this paper five categories of sluice gate events are defined (Figure 2):

1. "Closed gates": all gates are closed.
2. "FFMR + gates closed": Up to four gates are partially raised (FFMR) and the other gates are closed,
3. "FFMR + gates open": Four gates are partially raised (FFMR) and one to six gates are fully raised,
4. "Fully opened": All or multiple gates are fully raised,
5. "Atypical": Occasionally, there may also be atypical sluice gate events. During these events the gate(s) may be opened for maintenance or malfunction for a short or long period (10–20 min or longer). This may also occur during incoming tide and sea water, as opposed to protocols, may reach the lake.

Detection of lampreys was linked to the discharge data and water level differences to determine at what sluice gate events (FFMR + open/closed gates, fully opened, atypical) and timing within this migratory window the lampreys successfully passed the gates. Detailed data on water discharge through the sluice gates, at a 10 min time interval, were available from the operators of the complex. Average discharge per gate during the study period (April–June 2014) was 9.3 $m^3\ s^{-1}$ for FFMR and 139.7 $m^3\ s^{-1}$ for a full open gate. From the period May 20 to May 26 no detailed discharge data were available.

Next to the spilling basin, there is also a canal with two ship locks (Lorentzsluizen) which are intensively used for commercial and recreational shipping (Figure 1). These locks are operative continuously 24 hr a day, all year-round, with on average one shipping lock operation per hour during April–October (Weiler, 2019).

2.2 | Acoustic telemetry setup

A total of 19 VEMCO VR2W receivers were deployed, of which 13 were placed downstream of the complex on the marine side in the spilling basin and six upstream on the fresh water side (Figure 1). A VR2W receiver records the identification number and time stamp from acoustic transmitters with a frequency of 69 kHz when a tagged

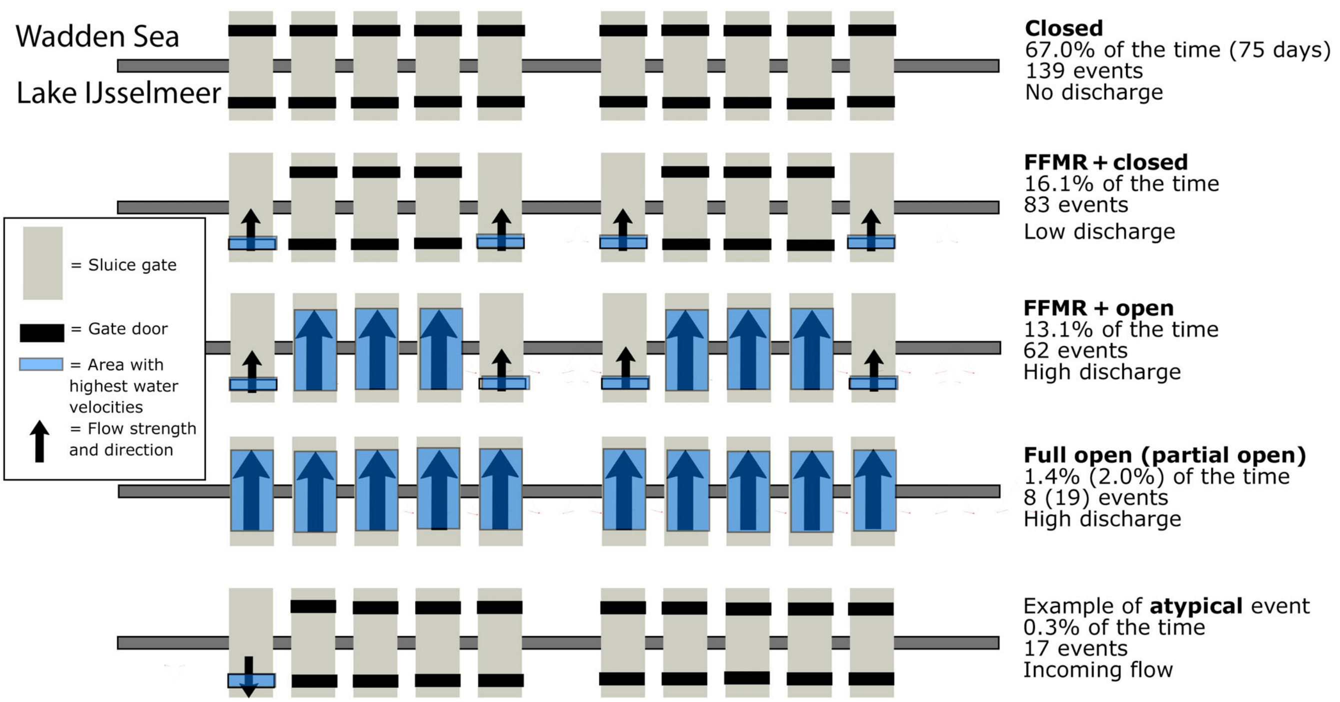

FIGURE 2 Schematic top view of the discharge sluices that shows the distinct categories of discharge events which may occur at the sluice gates at the study site of Kornwerderzand located in the north of the Netherlands. The figure also presents the number of occasions of each event during the study including the actual percentage of the time each event occurred during the study period (April 1 to June 15, 2014) [Color figure can be viewed at wileyonlinelibrary.com]

animal swims within receiver range. The VR2W consists of a hydrophone, ID detector, data logging memory and battery all housed in a submersible case. The VR2W has a battery life of approximately 15 months and can store 1 million detections. To deploy a VR2W, the receiver was attached with tie-wraps during low tide to a wooden pole, which was hammered into the ground to ensure that they were completely submersed during the complete tidal cycle at the marine side of the complex. Data from the receivers were exported to a computer through a Bluetooth connection using the VEMCO VUE software package (Canada, http://www.VEMCO.com).

For this study, the sea lampreys were tagged with V7-4L VEMCO coded transmitters that operate at 69 kHz. Each tag sends an acoustic pulse train (eight pulses in approximately 3.2 s) at pre-set time intervals. To minimise collisions between different tag pulses, the trains are sent with a random delay around an average time. Transmitters were set to send a pulse train randomly between 30 and 50 s. Each pulse train includes a specific ID number for each tag to track the individual fish. Two fixed reference transmitters were placed to determine how the detection rate was influenced by discharge events and the large hydrodynamics in the spilling basin (Figure 1, at receivers C and K). These transmitters were set to send a pulse train random between 460 and 500 s during the experiment. The detection range of a transmitter varies depending on environmental water conditions (e.g., environmental noise, reflection/refraction). In good conditions a V7 transmitter could yield a range of 300–400 m.

2.3 | Test fish and tagging procedure

A total of 25 lampreys were caught near location A, C and I (Figure 1) by professional fishermen on the marine side of the barrier using fykes in or near the spilling basin. Fykes were installed at the beginning of March and all lampreys that were caught were used in the study ($n = 25$). Total lengths of caught fish ranged between 66 and 91 cm and 16 males and 9 females were identified. The sea lampreys were temporarily housed in the ship's hold with a continuous inflow of fresh seawater and were kept for a maximum of 24 hr. However, most lampreys were tagged within hours after being caught. The lampreys were anaesthetised with 2-phenoxyethanol (0.5 ml/L) and measured to the nearest cm total length. The VEMCO transmitters were surgically implanted in the body cavity by making a mid-ventral 1–2 cm incision in the posterior quarter of the body cavity. The incision was closed with resorbable sutures (Vicryl 3/0 FS2 needle). Surgery lasted 3–5 min. The lampreys were observed in a recovery tank until normal swimming behaviour appeared and were then released in the spilling basin to continue migration. Around 23 lampreys were caught (near location A and C), tagged and released in the northern part of the spilling basin on April 10 (six individuals), April 17 (1 ind.), April 28 (9 ind.), May 16 (2 ind.), May 21 (3 ind.), June 2 (2 ind.) and June 5 (2 ind.) 2014. On May 7, two individuals were caught near location I, tagged and released at the southern part of the spilling basin. One tagged sea lamprey (ID.3) was caught in a fyke near receiver I (Figure 1) during the experiment from April 25 up to May 1. Data from this period was excluded in the data analysis. Analyses were performed using SAS (SAS institute Inc., 2011) and R (R Core Team, 2019).

2.4 | Ethical statement

The care and use of experimental animals complied with the Dutch animal welfare laws, guidelines and policies as approved by the "Central Committee Animal experiments" under permit 2014.031a.

3 | RESULTS

3.1 | Range test

The detection percentage of the two stationary reference transmitters by the two adjacent receivers was 92% with the sluice gates closed (Figure 3). With the sluice gates open, the detection percentage remained at the same value for the reference transmitter near receiver

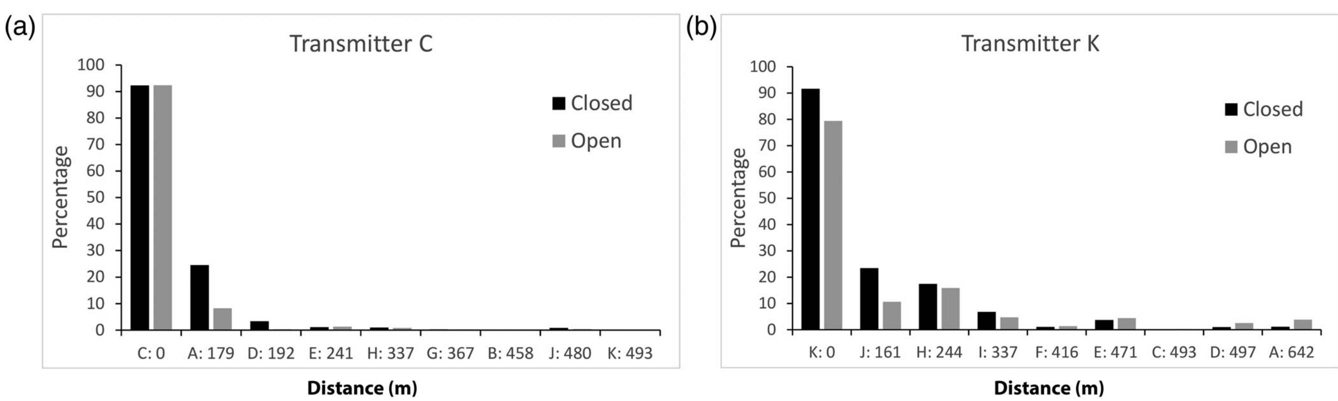

FIGURE 3 Percentage of detections of the two stationary range test transmitters adjacent to receivers C (Figure a) and K (Figure b) given by the receivers, stationed in the discharge basin of Kornwerderzand the Netherlands, during the period April 1 to June 15, 2014. For each receiver the distance to the stationary range test transmitter is given

C. However, the percentage for reference transmitter near receiver K was slightly lower, at 79%. At a distance of 160–180 m from the reference transmitters, the detection percentage was 23–24% with the sluice gates closed, and 8–11% with the sluice gates open. At a distance of 240 m the detection percentage was 1.0–1.4% for the reference transmitter near receiver C and 16–17% for the reference transmitter near receiver K, regardless of whether the sluice gates were open or closed. The detection percentage dropped further with larger distances.

3.2 | Sluice gate discharge events

In the period April 1 to June 15, 2014, 328 consecutive sluice gate events were registered of which 139 were closed (67.0% of total study period time of 75 days), 83 FFMR + closed, (16.1% of the time) 62 FFMR + open (13.1% of the time), 8 full (1.4% of the time), 19 partial open (2.0% of the time) and 17 atypical (0.3% of the time) (Figure 2). The average time the sluice gates were open was 4.5 hr (range: 10 min to 6 hr) and the average time they were closed was 8.5 hr (range: 5.5–25 hr). Of the 25 sea lampreys, 13 were detected for a short period.

3.3 | Sea lampreys movements and passage success

All lampreys were detected at least once after release in the basin (Figure 4). In total 20 lampreys were detected near the sluice gates at receiver I, J or/and K during the study. Of those, 11 lampreys (55%) spent on average 25 min near these receivers when the gates were open (12–108 min, excluding lamprey ID.3 which was trapped in a fyke). In addition, 19 out of those 20, spent on average 248 min near these receivers when the gates were closed (7–2,445 min, excluding lamprey ID.3).

Four lampreys (16% of 25 individuals) migrated successfully into Lake IJsselmeer, three of which were tagged on April 10 and one tagged on April 28 (Figure 5). The duration between first and last detection ranged from less than 1 hr up to 45 days and two lampreys stayed for consecutive days (6–7 days) in the spilling basin (lamprey ID.3 and ID.10, Figure 5a). None of the lampreys used the ship locks as a passage to Lake Ijsselmeer. Three lampreys ID.3, ID.4 and ID.22 were detected at the marine entrance of the ship locks (Figures 4 and 5a) while leaving the basin. Of those only one (ID.22) lamprey was detected directly near the doors of the ship locks and was never seen again in the basin (Figure 5a). About 13 lampreys (ID.5, 9, 11, 14–16, 18–21 and 23–25) were seen for a short period (hours) in the basin and leaving without coming back to the study site. ID.13 recurred 8 hr after release at 15:30 (UTC) and left the basin within 2 hr again. ID. All 10 lampreys (ID.1–4, 7–8, 10, 12, 13 and 17) showed recurrence behaviour after leaving the basin and were seen again in the basin (or near the entrance of the basin) after one or several days. Of those ten, three (ID 1, 2 and 12) were successful in reaching the lake

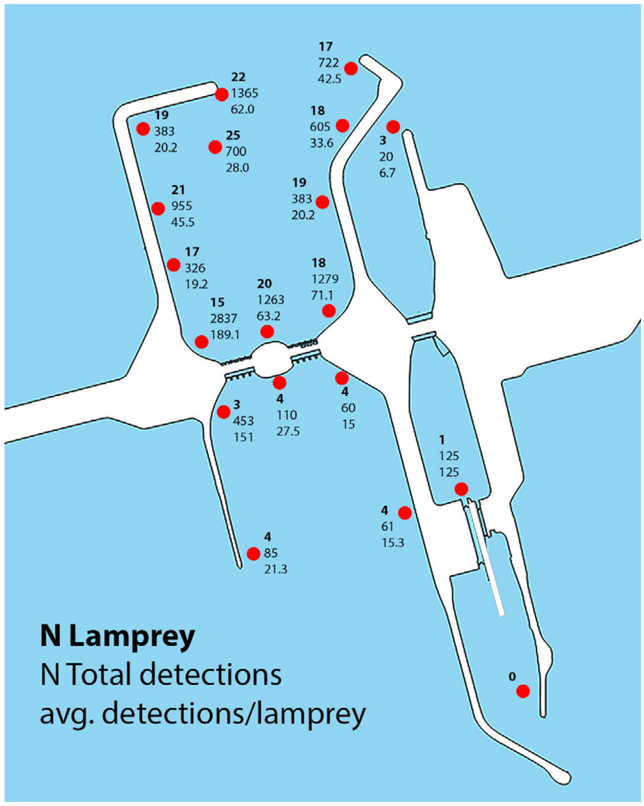

FIGURE 4 Total number (*n*) of sea lamprey (*Petromyzon marinus*) detected at each receiver during the study, in the study area: Kornwerderzand, The Netherlands. The figure represents the number of sea lamprey (*n*), the total number of detections, the average number of detections per lamprey and the corresponding receiver location at which it was first detected at the beginning of a sluice event including detections at release [Color figure can be viewed at wileyonlinelibrary.com]

during another approach. Lamprey ID.1: returned after 9 days, ID.2: returned after 9 days and ID.12: returned after 1 day. The other 7 lampreys left the basin again (Figure 5a). The duration between the first and the last detection of the successful (ID1, 2, 6, and 12) attempt was 13, 33 min and 9 hr and 13 min in the basin before passing the gates. In general, the lampreys were mostly detected in the basin when no discharge event or at the start of the end and were present throughout the diel cycle (Figure 5b). The absence of lampreys during discharge events cannot be fully explained by absence in the spilling basin. Discharge events could cause misdetections (Figure 3). However, the number of receivers in relation to the dimension of the basin 480 × 680 (WxL) and the expected detection range > 100 m suggests that the lampreys were indeed mostly absent during these events.

3.4 | Timing of successful passage

All four lampreys that passed the complex successfully used the sluice gates during discharge periods, while none used the ship locks. Two of the four lampreys (ID.1 and ID.2) passed the gates at the end of the

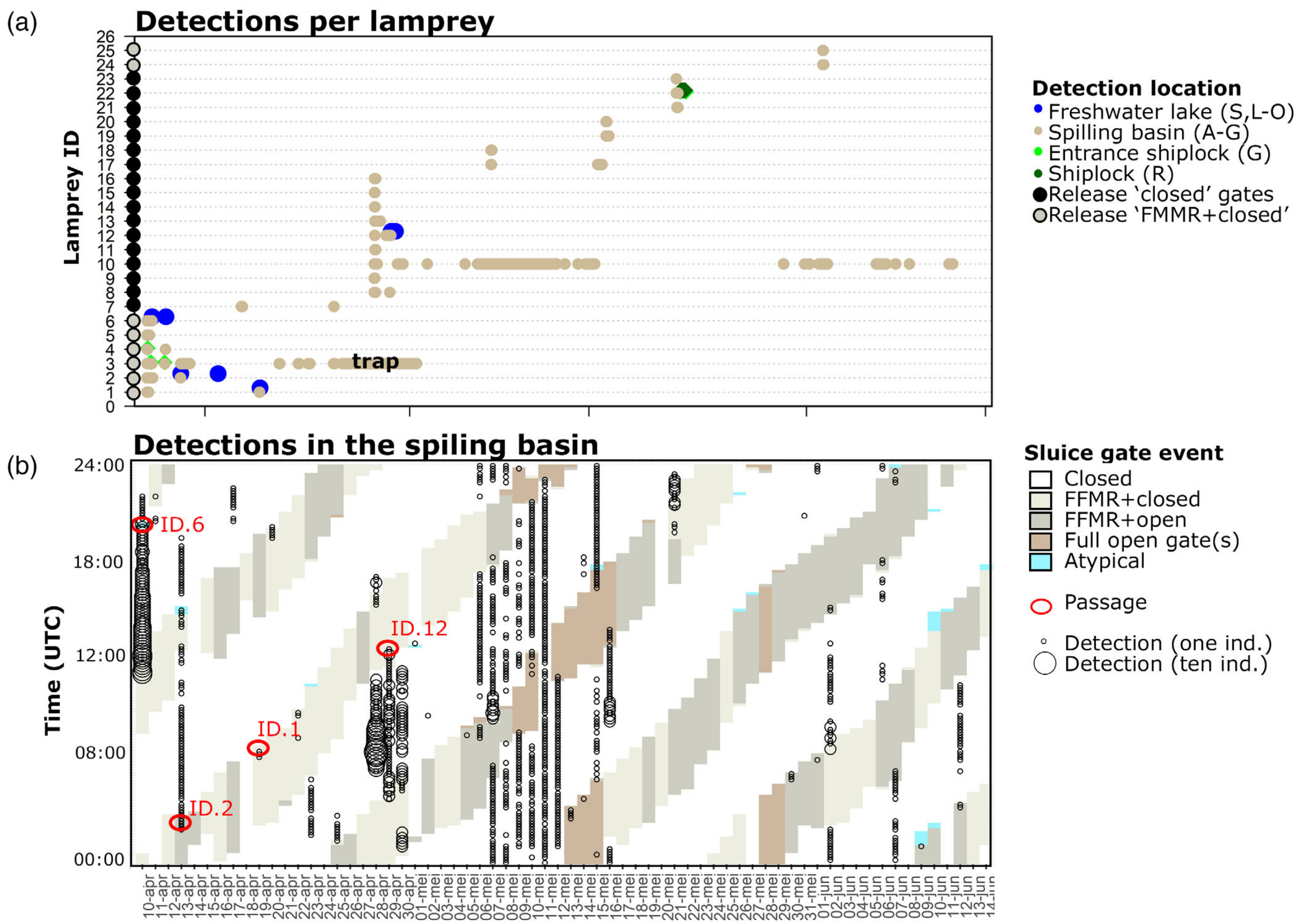

FIGURE 5 Detections of sea lampreys (*Petromyzon marinus*) during April and June 2014 in the spilling basin and ship lock area near Kornwerderzand, The Netherlands. (a) Detections are indicated with different colours for each sea lamprey separately. The first detection was also the release date in the spill gate basin. (b) The detections of the individual lampreys in the basin (receivers A–K, excluding the period in the trap for lamprey ID.3) and the distinct discharge event throughout the day. Generally, closed gates are present when water level of the Wadden Sea is lower compared to the water level at the Ijsselmeer (Figure 1) [Color figure can be viewed at wileyonlinelibrary.com]

discharge window, one (ID.12) at the beginning of the discharge window and one (ID.6) during an atypical discharge event of 20 min (Figure 6). Water level differences at which the lampreys passed the gates were below 0.6 m and on average 0.2 m, in which associated water velocity rates were assumed to be low. Lampreys ID.1 and ID.2 entered the basin at or just after the highest water level difference between the lake and the Wadden Sea (i.e., low water and rising tide) during a FFMR+closed (ID.1) or FFMR+open (ID.2) event. They both passed the gates approximately 30 min after entering the basin, while the other two spent multiple hours in the basin before reaching the lake.

The lampreys only passed within 30 min after opening or before closing of the gates. None of the lamprey passed the gates when all gates were fully opened with highest associated water velocities and turbulence in the basin and the gates. The first lamprey that reached Lake IJsselmeer on April 10 swam through the sluice gates during an atypical event of 20 min under dark conditions (time of passage = 20:21 UTC) at the west part of the complex (Figure 6). This lamprey was released on April 10 11:20 during a FFMR event which stopped 10 min after release and the lamprey stayed in the basin. After 9 hr the gates were opened for 20 min (atypical event) when the water level in Lake Ijsselmeer was almost equal to the Wadden Sea water level (difference was −0.04 m). Therefore water velocity was limited during an incoming tide. The second lamprey ID.2 entered the basin at 1:57 UTC during a discharge event and reached Lake IJsselmeer after 37 min on April 13 at the end of the discharge window of 240 min at night (time of passage = 2:30–2:35 UTC). Water level difference between Lake Ijsselmeer and Wadden Sea was 0.08–0.17 m and the water flow was directed to the Wadden Sea. Based on the data it is unclear which of the three Western gates it used. The lamprey could have used the fully opened gates or the gate with FFMR at the west of the complex. The third lamprey ID.1 entered the basin at 6:22 UTC during a discharge event and reached Lake IJsselmeer after 24 min on April 19, at the end of the discharge window, which lasted for 290 min in the morning (time of passage = 6:35–6:46 UTC) at the east of the complex. At the time four gates were not

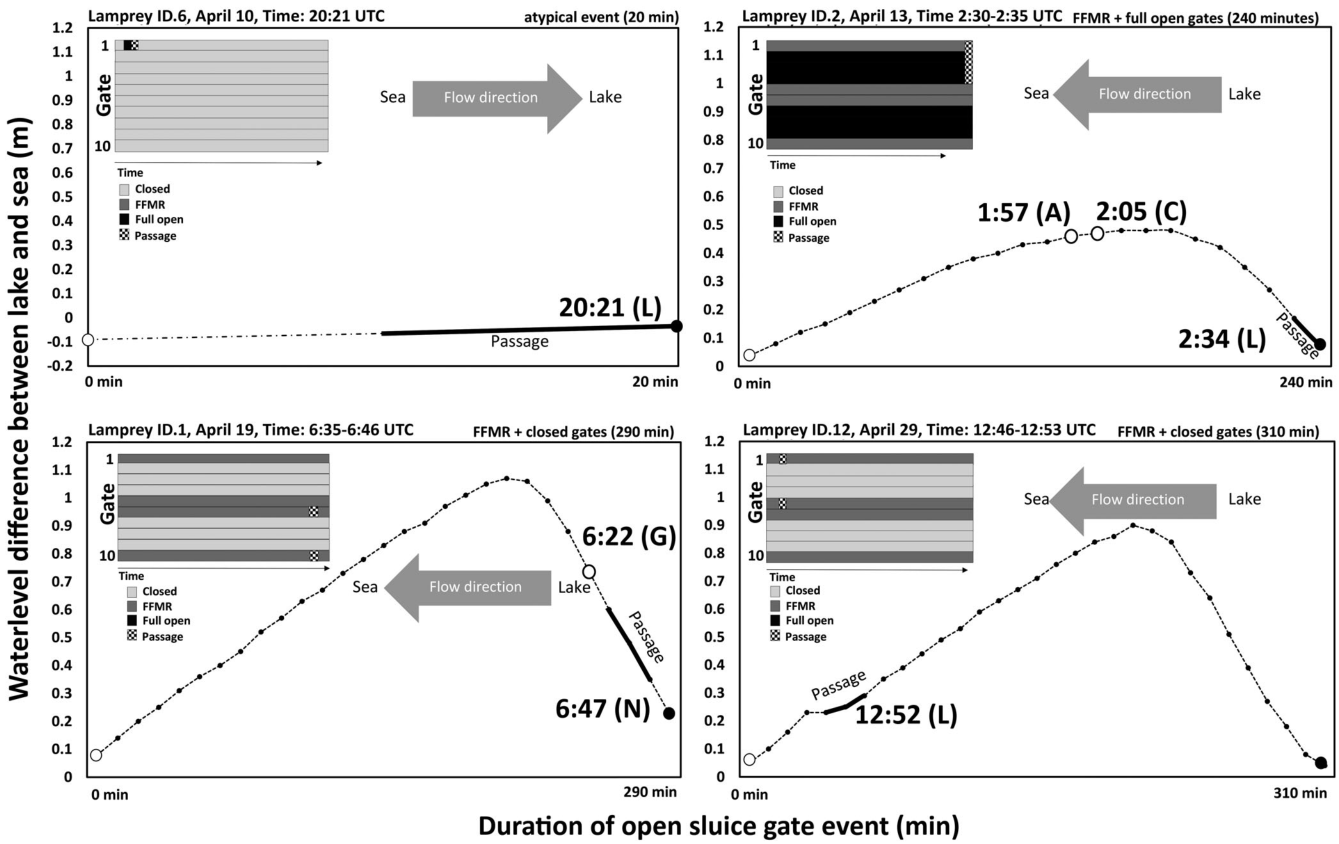

FIGURE 6 Detailed discharge conditions and timing of lamprey passage through the gates. The graphs show water level differences between Lake Ijsselmeer and the Wadden Sea, discharge conditions, flow direction and timing and position (receiver ID) in the spilling basin and the lake for each successfully passing lamprey. Water level differences are related to rising and falling tide at the Wadden Sea. In general a discharge event starts at falling tide when water level at the Wadden Sea is lower compared to the lake. If the tide rises, water level difference decreases to zero, ending the discharge event. *Top left*: Lamprey ID.6 never left the basin (release 11:20 UTC) and was first detected in the lake (receiver L) at 20:21 UTC. There was no discharge event until an atypical event at 20:10 UTC. *Top right*: Lamprey ID.2 was first detected at the entrance at 1:57 UTC and in the basin at 2:05 UTC. At 2:34 UTC it was detected in the lake (receiver L). *Bottom left*: Lamprey ID.1 was missed at receiver A or B and detected in the basin (receiver G) at 6:22 UTC and in the lake (receiver N) at 6:46 UTC. *Bottom right*: Lamprey ID.12 was detected at the entrance (receiver B) at 2:52 UTC and in the basin at 3:56 UTC (receiver G). This lamprey was detected in the lake at 12:52 UTC (receiver L)

fully opened (FFMR), there was a difference in water level between Lake Ijsselmeer (0.60 m) and the Wadden Sea (0.35) and the water flow was directed to the Wadden Sea. The fourth lamprey ID.12 entered the basin during the last 60 min of a FFMR event at 3:52, waited or searched in the basin for 8 hr and reached Lake IJsselmeer on April 29, 12:52 UTC, at the start of the discharge window of 310 min during daylight (time of passage = 12:46–12:53 UTC) at the west of the complex (FFMR).

4 | DISCUSSION

Passage success was poor with only four (16%) of the 25 tagged lampreys migrated successfully into Lake IJsselmeer using opened sluice gates, whereas none used the ship locks. If the lampreys that left the study area shortly after release and did not successfully reach Lake IJsselmeer (13 individuals) were excluded, passage success was four out of 12 lampreys (33%). The low passage success rate can be explained by different potential causes which will subsequently be discussed below.

First, the sea lampreys were not able to use or find the short-lasting windows with suitable passage conditions when at least one of the ten sluice gates was opened and water velocities were relatively low, that is, at the first or last half hour of a discharge event. Although data is limited, lampreys ID.1 and ID.2 passed the gates at the end of a discharge event and only needed 30–60 min to swim from the Northern part of the basin to the freshwater lake. Both entered the spilling basin after the highest water level difference, suggesting that lampreys are able to reach the gates when water velocity in the basin is at highest level. However, since the fully opened sluice gate events (all open) were not used, it is suggested that in order to be successful at the gates lampreys were restricted to low water velocity events using the FFMR or atypical events. Although lampreys have the ability to use their oral disc and use a strategy referred to as "burst-and-attach," especially in areas with fast water velocity (Quintella, Pova, & Almeida, 2009), this strategy is highly ineffective in terms of energy costs (Beamish, 1978). Moreover, less energy may be available for further migration or spawning itself. Possibly, the concrete walls of the gates in combination with the high water velocities cannot efficiently be used by the lampreys. In addition, having no pectoral fins that facilitate stability, turbulent environments are likely to be particularly challenging to lampreys (Liao, 2007).

Second, generally lampreys were detected in the basin for short periods (Figure 5a), suggesting that a missing continuous attraction flow, that is, unnatural occurrence of stagnant conditions during high tide, may have caused them to turn around to the Wadden Sea and they were never seen thereafter. Attraction flow seemed important since 10 lampreys swam back and forth between the Wadden Sea and the sluice gate complex, while ignoring the ship locks, where hardly any attraction flow occurs. Only one sea lamprey swam to the seaside ship lock doors (ID.22). This may suggest that lampreys were more attracted by the discontinuous, but large in volume, freshwater flow that was discharged in the Wadden Sea than by the sluice gates. Most sea lampreys however, did not appear to be willing to continue searching for passage opportunities. The ship locks open frequently for only a short duration and release only a small discharge volume that could serve as an attraction cue. Similar results were shown with river lampreys in the River Ouse (England), where lamprey preferred sluices over ship locks, probably caused by poor attraction to the lock (Silva, Lowry, Macaya-Solis, Byatt, & Lucas, 2017). In addition, shoreward orientation using bathymetry (Meckley, Gurarie, Miller, & Wagner, 2017) may lead the lampreys toward the barrier initially but the relatively deep spilling basin may cause the lampreys to turn around.

Third, the pheromone trace of ammocoetes, which can serve as an attraction cue for migration of adult sea lamprey (Buchinger, Siefkes, Zielinski, Brant, & Weiming, 2015), from upstream rivers and tributaries may be diminished in the downstream situated large unnaturally created freshwater Lake IJsselmeer. Lampreys may have been attracted by a large freshwater flow initially, but due to a lack of pheromone traces lampreys might have ceased their upstream migration attempts at this site and moved out of the area in search of other river mouths.

Fourth, predation by large predators such as seals may also cause a more rapid disappearance of sea lampreys from the spilling basin. A study conducted upstream of the tidal area of the Gironde estuary showed that 80% of tagged lampreys were eaten by European catfish (*Silurus glanis* Linnaeus 1758) within a month and 50% within 8 days (Boulêtreau et al., 2020). Such large predator fish are lacking at our study site, but harbour seals (*Phoca vitulina*, Linnaeus 1758) and grey seals (*Halichoerus grypus* Linnaeus 1758) do occur (Brasseur et al., 2015) and are known to feed on river lampreys (Keszka et al., 2020). Whether Great cormorant (*Phalacrocorax carbo*, Linnaeus 1758), abundantly present in the area, also predate on sea lamprey or whether they are too vigorous for cormorants to predate them is unknown though some consider them as potential predators (Braga et al., 2020).

And lastly methodological causes like tag expulsion, mortality due to tagging or misdetection may also have contributed to the observed low passage success. Tag expulsion and mortality due to tagging cannot be verified within this study. Given the short duration of the study, tag expulsion is unlikely. Studies using eels and similar tagging procedures however, showed no signs of tag expulsion or mortality due to tagging (van Keeken, van Hal, Winter, Wilkes, & Griffioen, 2021). All lampreys were last detected at either stations bordering the sea, or stations bordering the inside lake, and no signs of mortality, such as continuous detections at a single station, within the study area was apparent (Klinard & Matley, 2020). Therefore, there is no reason to assume that this study was influenced disproportionally by tag expulsion or mortality. The receiver set up within this study took into account misdetection changes due to turbulence during discharge events. The reference tags in the spilling basin showed that the detection range dropped during the open sluice gate events and associated turbulence. At the positions of the receivers at lake side however, no turbulence is present during open sluice gate events and two rows of receivers (L,M,N and O,P) rule out low passage success due to misdetection.

Although numbers are relatively low, this study suggests that sea lampreys are restricted to low velocity conditions to pass the tidal gates. All lampreys passed in the first or last 30 min of a migration window. During the first or last 30 min, water velocity of a typical discharge event is below 2 ms^{-1} according to Kolvoort and Butijn (1990) and Vlag (1999). All sea lampreys ignored the periods of water velocities above 2 ms^{-1} independent of the various discharge conditions. Migration of lampreys in conditions with water velocities up to approximately 2 ms^{-1} is supported by various other studies. Quintella et al. (2009) found that at slow-flow stretches, sea lampreys maintained a constant pattern of activity, attaining an average ground speed of 0.69 ms^{-1}. When they encountered rapid flow reaches they alternated between short movements (c. 67 s) and periods of rest (c. 99 s). In each swim bout they progressed approximately 14 m (Quintella et al., 2009). Quintella et al. (2009) also found that in more difficult situations they increased burst movements instead of more violent swimming events. For pacific lamprey (*Lampetra tridentate*), experiments of Johnson et al. (2012) showed that adults preferred reduced water velocity of 1.20 ms^{-1} instead of 1.98 ms^{-1}. Keefer et al. (2010) conducted experiments with Pacific lamprey and their results consistently indicated that the structural challenges reduced passage efficiency and lengthened passage times. Very few lampreys passed weirs when maximum velocities reached $\sim$2.7 ms^{-1}. They suggest that Pacific lamprey may be facilitated by removing or modifying vertical steps and other sharp-edged corners and by providing adequate attachment surfaces. Furthermore they state that such accommodations should be especially beneficial in areas with high water velocity.

This study was conducted during the sea lamprey spawning season, at a freshwater outlet site away from marine feeding areas and en route to known riverine spawning sites in the Rhine catchment area (e.g., Baer et al., 2018). Therefore each caught adult sea lamprey could be assumed to be highly motivated to migrate upstream into the lake and subsequent rivers. However, the majority of the tagged lampreys ($n = 21$, 84%) did not eventually migrate into Lake

IJsselmeer at this site. Since homing behaviour is not present in lampreys (Waldman, Grunwald, & Wirgin, 2008), unsuccessful migrants might have searched for other migration opportunities elsewhere along the coast. However, this may also hamper their spawning success due to unfavourable energy costs.

In conclusion, our results show poor passage efficiency (16–33%) of sea lamprey at a large marine-freshwater barrier, consisting of ten sluice gates and a ship lock complex in the Netherlands. Successful passing only occurred through the sluice gates, while none passed the ship locks. Low passage success and search duration were possibly related to the unnatural infrequent occurrence of attraction flow and only short lasting windows with suitable conditions for passage at the sluice gates. However, given the complexity and variety of discharge events and migratory opportunities, a dataset from multiple years and more individuals are needed to statistically analyse the behaviour in relation to migratory success and environmental condition (e.g., tidal phase, seasonal and diurnal timing and local water velocities).

4.1 | Management implications

The results of the present study indicate that lamprey passage success at marine - freshwater barriers may benefit from facilitating passage with lower water velocities and incoming tidal water flows. In addition, more continuous occurrence of migratory windows may also be beneficial. In contrast to riverine systems with unidirectional water streams, sluice gates are situated in an estuarine environment including tidal currents and two-way directional water streams. Fish migration measures and fish passage design in estuarine environments have to take into account a discontinuous two-way directional flow, various salinity levels and various migration strategies from selective tidal stream transport to active swimming. Moreover, due to sea level rise (Vousdoukas, Mentaschi, Voukouvalas, Verlaan, & Feyen, 2017), and an increased number of summer droughts (O'Briain, 2019), man-made coastal (flood) protection may induce lesser and shorter lasting windows in time that enable successful passage in the future when solely relying on migration measures such as adaptive sluice management that allow only limited sea water intrusion (Mouton et al., 2014). An inclusive approach with adapted existing structures (e.g., ship locks, sluice gates) accompanied with parallel nature-like or technical fishways are needed to provide continuous migration opportunities for multiple species including lampreys. Given the salt water intrusion restrictions and maximum discharge guaranties for peak river flow to lower inland flooding risk set by the authority, additional measures to adapt the sluice gate or ship lock management regime are very limited. Moreover, this study showed that lampreys may not benefit from an adapted ship lock management regime since attraction flows will always remain discontinues and small in volume which likely attracts the lampreys less. Therefore, a fishway, designed within the authority saltwater intrusion safety restrictions, that allows two-directional water streams next to the sluices gates may restore small scaled tidal currents at this site, is planned to be built in the near future (Fish Migration River). The design is adapted to also facilitate small diadromous fish (smelt, stickleback, glass eel, flounder larvae) in addition to larger fish such as lampreys. The fishway offers alternating velocity rates in both directions with the tides and during the diel cycle. Given the intensive but short lasting searching behaviour of sea lamprey, the attraction flow of this fishway should be in the vicinity of the main water flow from the sluice gates to increase attraction efficiency. Migratory windows should be provided both day and night since present study shows that lampreys were present in the spilling basin and passed the gates during the full diel cycle. This is in accordance with the study by Keefer, Caudill, Peery, and Moser (2013) that suggests that behaviour is context-dependent and that diel activity patterns vary with the degree of effort or predation risk required for movement. in addition, water velocities must be below 2.0 ms^{-1} with sufficient substrate to increase small scale water velocity variability and allowing lampreys to rest between burst-and-attach performances and negotiating high water velocities and more difficult circumstances in terms of hydraulic situations (Johnson et al., 2012; Keefer et al., 2010; Kemp et al., 2011; Quintella et al., 2009).

ACKNOWLEDGEMENTS

We would like to thank M. and T. van Malsen, for their effort of catching the sea lampreys and their experienced insights in this study area as professional fishermen. We would also like to thank and T. and S. Wigbout for help with the receiver placement. We would like to thank Rijkswaterstaat for providing discharge data. This study was funded by the Dutch Ministry of Agriculture, Nature and Food Quality (BO-11-015-040).

CONFLICT OF INTEREST

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.

ORCID

Arie Benjamin Griffioen https://orcid.org/0000-0002-8366-0818

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How to cite this article: Griffioen, A. B., van Keeken, O. A., Hamer, A. L., & Winter, H. V. (2022). Passage efficiency and behaviour of sea lampreys (*Petromyzon marinus*, Linnaeus 1758) at a large marine–freshwater barrier. *River Research and Applications*, 1–11. https://doi.org/10.1002/rra.3967