Migratory windows and passage behaviour of silver eel at migration barriers in a highly regulated water system

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Abstract
Due to a variety of factors, European eel (*Anguilla anguilla*) populations have drastically decreased since the 1970s. One of these factors is the presence of migration barriers, that can delay or block the migration of European eel. In this data analysis study the effects of several, different types of migration barriers situated in a highly regulated water system on the behaviour of migrating silver eels are investigated. Using acoustic telemetry data of 165 silver eels tagged with acoustic transmitters tracked from from September 2017 till May 2018 and 11 man-made structures covered with acoustic receivers in the North Sea Canal region in the Netherlands, an analysis was conducted to study different man-made structures affect the migratory behaviour of silver eels. This study was conducted using the R programming language combining datasets concerning activity hours of the pumping stations in the North Sea Canal region, data concerning the hours of the circadian phases during the study period, and acoustic telemetry data. 8 out of 10 pumping stations pumped primarily at night and 68% of all detections were at night, as were most successfully utilized migratory windows. The migration barriers in the North Sea Canal region varied significantly in terms of passage success rates and migratory delay for the tagged silver eels, with delays ranging from a few minutes to months and passage success rates ranging from 98% to 0%. This shows there can still be measures taken to improve the facilitation of silver eel migration in this highly regulated water system, like the improvement of attractiveness for silver eels and the replacement of fish-unfriendly pumps in pumping stations without alternative routes like shipping locks.

**Keywords:** acoustic telemetry, European eel (*Anguilla anguilla*), migration barriers, silver eel, water regulation
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1. Introduction

1.1 Background

The European eel (Anguilla anguilla) is categorised as critically endangered by the International Union for Conservation of Nature (IUCN) (Jacoby & Gollock, 2014). Its recruitment has declined since the 1980s to less than 10 percent of what the recruitment was during the 1970s (Wirth & Bernatchez, 2003; Dekker, 2008; Belpaire et al., 2009). Various factors attributed to this decline of European eel, such as habitat deterioration, pollution, fisheries, the introduction of exotic parasites, climate change affecting the Gulf Stream, and habitat fragmentation by migration barriers (Køie, 1991; Feunteun, 2002; Winter et al., 2006; Jansen et al., 2007a; Buysse et al., 2014a; Dekker, 2016; Miller & Tsukamoto, 2017). The European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007) to aid the conservation and recovery of European eel stocks (European Council, 2007). This regulation imposes a management system that ensures 40 percent escapement of the spawning stock biomass, which is the number of fish that is allowed to escape from freshwater to spawn, defined as the best estimate of the theoretical escapement rate where the stock is completely free of anthropogenic influences (European Council, 2007).

The European eel is a catadromous species, meaning that it spawns in saltwater and after hatching, migrates upriver to spend most of their lives in freshwater and migrate back downriver into saltwater to reproduce (Myers, 1949; Mcdowall, 2013; Bloom & Lovejoy, 2014) (Figure 1). European eel are facultatively catadromous, because some individuals remain in the coastal areas and estuaries to mature instead of migrating upriver (Tsukamoto et al., 1998). European eels spawn in the Sargasso Sea, which is an area situated in the Northern Atlantic Subtropical Gyre (Miller et al., 2019). In the sedentary yellow eel life phase, the eels grow for three to over twenty years to accumulate energy reserves. During their development into silver eels, eels develop larger eyes and pectoral fins, and their alimentary tract degenerates, which causes the silver eels to stop feeding (Pankhurst & Sorensen, 1984; Dufour & van den Thillart, 2009). Hence, they are reliant on accumulated energy reserves for gonad development and completing their migration back to the Sargasso Sea for spawning (Tesch et al., 2003; Dufour & van den Thillart, 2009). Female silver eels grow twice as large as male silver eels (Dekker, 2008). Most silver eels migrate in autumn, but some migrate in spring (Tesch et al., 2003; Winter et al., 2006; Aarestrup et al., 2008). Water temperature, water discharge, photoperiod and light intensity influence the migratory behaviour of silver eels (Vøllestad et al., 1986).

![Figure 1: Lifecycle of the European eel](Dekker, 2008)
1.2 Migration barriers

Water levels of freshwater systems all over the world are controlled by dams, pumping stations, weirs, shipping locks and discharge sluices. These man-made structures provide water regulation, flood defence, and saltwater intrusion limitation, but also have the unintended property to act as barriers for the migration of migratory fish species (Buysse et al., 2014b). Most studies of the effects of man-made structures on silver eel migration cover overall migration routes and mortality after passing through (Jansen et al., 2007b; Winter et al., 2007; Calles et al., 2010; Buysse et al., 2014b; Økland et al., 2019). Migration barriers can cause direct mortality to eels passing through them as a result of lethal injuries caused by high water pressures and moving parts hitting the eels when the turbines are not designed in fish-friendly manner (e.g. by pumping stations, turbine stations and hydropower plants) (Feunteun et al., 2000; Winter et al., 2006; Buysse et al., 2014b).

Delays and migration stops caused by migration barriers contribute indirectly to the decline of eel stocks through a reduced fitness caused by stress, additional energy loss, and a higher predation risk (Marmulla, 2001). Some silver eel even regain yellow eel traits after an unsuccessful migration attempt and stay another year in catchment to migrate again after their migration stop (Feunteun et al., 2000). Searching behaviour for route selection results in delays in the eels migration (Piper et al., 2015). Eels are known to change their normal migration behaviour and routes when disturbing factors are encountered, such as hesitation to pass through pumping stations (Piper et al., 2017). Through olfactory, visual, and tactile cues eels perceive changes in their environment which cause changes in their behavioural response (Keefer et al., 2013). Cues such as underwater sounds emitted and changes in velocity and direction of water flows generated by pumping stations can cause approaching eel to change their behaviour over large distances, while cues like visual detection and physical encounters can cause eels close to the migration barrier to flee (Behrmann-Godel & Eckmann, 2003; Jansen et al., 2007b; Piper et al., 2015; van Keeken et al., 2020a).

To minimize delays, migration stops, and direct mortality caused by migration barriers in highly regulated water systems, more knowledge on the passage behaviour of eels at migration barriers is required (Verhelst et al., 2018b). The hours at which sluices, pumping stations, weirs and other man-made structures are operated need to be managed to correspond with the eels behaviour in order to improve the success rate of the migration of eels and route selection (Breukelaar et al., 2009). Knowledge concerning which migratory windows to pass migration barriers are utilized is needed to improve the escapement of silver eels and thus the recruitment of new eels.

This study focuses on the effect that potential migration barriers have on the migration of European silver eels in the North Sea Canal region.

1.3 Specific Aims and Scope

To investigate the migratory windows and passage behaviour of silver eels in the North Sea Canal region, the following research questions were assessed:

- How do European silver eels (*Anguilla anguilla*) behave when encountering migration barriers on their migratory route in a highly regulated water system?
  - Do silver eels show searching behaviour in the vicinity of migration barriers?
  - What diurnal pattern is present in the migratory behaviour of silver eels?

- Which migratory windows are present in time for passing migration barriers and which are utilized by silver eels?
  - During which circadian phase are pumping stations in the North Sea Canal region most active?
  - To what degree do the different migration barriers hamper silver eels in their migration in terms of passage success and delay?
2. Material and Methods

2.1 Data analysis

This study was a data analysis research conducted with a large, existing dataset on eel migration from an acoustic telemetry study in the North Sea Canal area performed by Wageningen Marine Research (WMR) from September 2017 to May 2018 (Winter et al., 2018). Datasets containing the operation hours of potential migration barriers over this period, provided as flowrate in m³/s for every 10 minutes, were provided by different water boards; Rijkswaterstaat (Ministry of Infrastructure and Water Management), the Province of Noord-Holland, Hooghuisraadsschap Hollands Noorderkwartier, Rijnland, and Waternet. The dataset of pumping station Zaangemaal contained 145 bins without value within the column containing flow rate, which were filtered using (R Core Team, 2019). In this study, each bin of 10 minutes in which a pumping station or sluice was active was considered to be a window of opportunity for the silver eels to utilize to get passed the structure.

The previously mentioned water boards also provided datasets of shipping lock operation activity of the potential migration barriers over this period, which were provided as the number of shipping lock operations per month. This resolution was not precise enough to determine the migratory windows for eels to pass shipping locks. To determine the migratory windows for eels to pass shipping locks, shipping lock operations data should provide the exact hours at which the shipping lock was operated for each operation, preferably in bins of 10 minutes. This is why shipping lock activity was not tested for migratory windows in this study.

To match timing of passage in relation to use of migratory windows, only eels successfully passing a migration barriers were used. In analysis that encompass success rate per location, all eels that appeared at locations were taken into account. This data was filtered to only contain observations between the first moment of detection at the migration barrier and the first observation on the other side of the migration barrier. The data was binned in bins of 10 minutes, to fit the biggest resolution of the flow rate data was provided in bins of 10 minutes. If the moment of an observation fits in a bin, the eel is assumed to be there for the duration of the entire bin. Individuals that were mortally wounded after passing through pumping station were also counted as successful passages in this study, even though it would not lead to a successful ending of the individuals migration attempt. The study of (Winter et al., 2018) indicates high mortality rates after passage at pumping station IJmuiden and Kortenhoef and the possibility that some successful passages could have occurred at pumping station De Ruiter. Passage through pumping station De Ruiter results in high mortality rates, as this pumping station is deemed to be fish unfriendly (Table 1). The receiver behind pumping station De Ruiter is situated at a distance from the pumping station, what could lead to that mortally wounded eels will probably not be detected by this receiver.

To investigate the diurnal pattern, data for the times of sunrise, sunset, civil dawn, and civil dusk for each day of the period of September 2017 to May 2018 was retrieved from the website https://dateandtime.info. During civil dawn and civil dusk, the geometric centre of the Sun’s disk is at most 6 degrees below the horizon. Sunrise and sunset are the moments when the Sun’s edge touches the horizon. These times provided by these websites were Central European Time (CET) and Central European Summer Time (CEST). Because the timeseries data of acoustic telemetry were in CET, the times of sunrise, sunset, civil dawn, and civil dusk were converted to CET.

Plots were made to create a visual picture of the data for each migration barrier. These plots included data concerning civil twilight, day and night time for the duration of the study, to display the effects of the diurnal pattern of silver eels. To produce plots, the R packages tidyverse and lubridate were used (Grolemund & Wickham, 2011; R Core Team, 2019; Wickham et al., 2019). To test for significant differences between the locations for the length of the intervals of the individuals that passed through the structures at these locations, one outlier of 7353 hours at Kadoeleen was removed and a Kruskal-Wallis test was performed (R Core Team, 2019). To test for significant differences between the locations and the proportions of day and night, pairwise comparisons using Fisher’s exact test and Chi-Square tests were performed (R Core Team, 2019; Hervé, 2020).
The assumption that the moment of first detection passed a structure is more or less equal to the moment of passing through might not be correct for all situations. This hypothesis was tested by checking how many bins were present between the last detection in front of the structure and the first detection behind the structure for each individual at each location (Figure 2). In most cases this hypothesis seems to be correct, but for five individual cases this does not seem to apply. The individuals where this did not apply for appeared as if they had been going back and forth between the receiver in front and behind of the structure. This is most likely the result of the signal from the transmitter being received through the structure by the receiver on the other side. Nevertheless, the very first detections behind the structures were used in this study as the moment at which the eels passed the structure.

![Figure 2: First behind - last in front interval length in 10 minute bins. Number of individuals that successfully passed each location is given as n=. Negative numbers are the result of detections in front of the structure after being detected behind the structure. This happens at IJmuiden, Overtoom, Zaangemaal, and Katwijk. Positive numbers higher than 1 are the result of a lack of detections between first detection behind the structure and the last detection in front of the structure.](image-url)
2.2 Study area

The study area where this research was performed was located in the Netherlands in the North Sea Canal region including the polder waters that discharge in the North Sea Canal. (Figure 3). The North Sea Canal connects Lake Marker, via the lock complex Oranjesluizen in the East, with the North Sea, via the lock complex IJmuiden in the West, and is an important waterway and a discharge canal for approximately 4,000 km² of hinterlands connected via 10 side canals. It is 25 kilometres long and on average 270 metres wide and 16 metres deep, with the shallowest and widest parts situated in the East. Because of the large difference in salinity at each side of the lock complex in IJmuiden, each time the shipping locks are operated the complete volume of salt water is exchanged with brackish water from the canal. This results in a strong gradient is present from fresh to salt water at a depth between 6 and 16 meter. The upper layer of 6 meters consists of relatively fresh water and is continuously mixed by shipping activity. Because of the discharging of the hinterlands through the North Sea Canal, the lock complex at IJmuiden is an important connection in the migratory route of silver eels from the polder waters in these hinterlands. Silver eel migrating through this highly regulated, fragmented water system are confronted with large, unnatural dynamics in space and time of water currents and salinity gradients. These dynamics result in a periodical availability, migratory windows, for eels to get passed the man-made structures situated in the region (Winter, 2011).
2.3 Acoustic Telemetry

In the study performed by WMR, Vemco receivers and transmitters (Figure 4) were used (Winter et al., 2018). For this study a total of 330 silver eels, all females ranging from 54 to 113 cm in length, were tagged with V9-2L acoustic transmitters (Canada, http://www.vemco.com). The acoustic transmitters were surgically administered in the abdomen of the silver eels (Winter et al., 2006). The eels were released, distributed into 13 groups. Receivers were placed near the bottom with two weights and one floater on a short rope or attached to an already existing structure, like a pole (Figure 5). The exact location of each receiver was measured after deployment with a GPS device and recorded. The receivers were placed between 14 and 28 September 2017. All receivers were in use at least until 19 March 2018. This period covers most of the period in which silver eels migrate (Tesch et al., 2003). The receivers at both ends of the North Sea Canal, at the lock complexes IJmuiden and the Oranjesluizen, were retrieved three months later, in June 2018 to ensure that also individuals that were late to start their migration were detected.

Figure 4: Vemco VR2W receiver (left) and Vemco V9-2L (circled) acoustic transmitter (right) (Winter et al., 2018)

Figure 5: Vemco VR2W receiver with two weights and one floater on a short rope (Winter et al., 2018)
A total of 64 acoustic receivers were distributed over 21 locations and read out. The locations for the acoustic receivers were picked to cover all possible routes the released silver eels could use to pass migration barriers and most of the possible escape routes the released silver eel could use to reach the sea or the hinterlands in the polders. For my study, only locations where both sides of the migration barriers were covered by acoustic receivers were selected to have the best estimates of the moments the eels successfully passed through the structures. These were 11 out of the 21 locations (Table 1 & Figure 6).

In the North Sea Canal the lock complex near IJmuiden was covered with receivers in such a way that all routes via the pumping stations, sluice and different shipping locks could be distinguished from each other. The lock complex Oranjesluizen was not covered in such a way, so no distinction could be made for which route through the complex was taken. Therefore, a complete coverage to both the side of the North Sea Canal and the side of Lake Marker was used to detect individuals moving in both directions.

All locations that were used in this study had a receiver on the side of the structure were the eels first arrive and a receiver on the other side, to detect when they passed through. These locations were Kadoelen (Figure 7), Overtoom (Figure 8), Willem I (Figure 9), Zaangemaal (Figure 10), Halfweg (Figure 11), Katwijk (Figure 12), Spaarndam (Figure 13), Oranjesluizen (Figure 14), Kortenhoef (Figure 15), De Ruiter (Figure 16), and IJmuiden (Figure 17) (Table 1).

At least 144 eels out of 330 (43.6%) succeeded to leave the North Sea Canal region into the North Sea through the sluice-complex at IJmuiden and pumping station at Katwijk. At the shipping lock complex Oranjesluizen, 43 eels were detected at the receivers in the North Sea Canal and 4 at the receivers in Lake Marker. One individual (2%) successfully passed through from the North Sea Canal into Lake Marker and 4 (100%) into the opposite direction. Out of 159 individuals in the North Sea Canal, 127 (80%) were detected at the lock complex in IJmuiden. 75 (60%) successfully passed the structure through the shipping lock and 50 (39%) successfully passed the structure through the pumping station or sluice, making 125 (98%) in total (Table 2 & Figure 18).

**Table 1: Overview Types of PS in study area.** PS = Pumping Station, SL = Shipping Lock, FP = Fish Passage, N/A= not applicable. Structures with N/A have no PS. ++ = very fish friendly, + = fish friendly, - = fish unfriendly, -- = very fish unfriendly.

<table>
<thead>
<tr>
<th>Structure</th>
<th>Barrier type</th>
<th>Fish friendly PS</th>
<th>Type PS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kortenhoef</td>
<td>PS &amp; SL</td>
<td>++</td>
<td>pipe auger</td>
</tr>
<tr>
<td>De Ruiter</td>
<td>PS &amp; SL</td>
<td>-</td>
<td>centrifugal pump</td>
</tr>
<tr>
<td>Kadoelen</td>
<td>PS &amp; FP</td>
<td>+</td>
<td>auger</td>
</tr>
<tr>
<td>Overtoom</td>
<td>PS &amp; SL</td>
<td>+</td>
<td>auger</td>
</tr>
<tr>
<td>Willem I</td>
<td>SL &amp; FP</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Zaangemaal</td>
<td>PS &amp; SL</td>
<td>+</td>
<td>horizontal screw</td>
</tr>
<tr>
<td>Halfweg</td>
<td>PS</td>
<td>+</td>
<td>auger/pipe auger</td>
</tr>
<tr>
<td>Katwijk</td>
<td>PS</td>
<td>++</td>
<td>centrifugal pump</td>
</tr>
<tr>
<td>Spaarndam</td>
<td>PS &amp; 2 SL</td>
<td>+</td>
<td>paddle wheel</td>
</tr>
<tr>
<td>Oranjesluizen</td>
<td>4 SL</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>IJmuiden</td>
<td>PS, Sluice, FP, &amp; 3 SL</td>
<td>--</td>
<td>bulb pump</td>
</tr>
</tbody>
</table>
Figure 6: Study area; Release locations of tagged silver eel (white pins) & the locations of the different migration barriers (red arrows). Katwijk is situated in the South-West, the North Sea Canal in the North, Lake Markermeer in the North-East, and the Vinkeveense Plassen (De Ruiter) and the Loosdrechtse Plassen (Kortenhoef) in the South-East of the study area. (Winter et al., 2018)

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<table>
<thead>
<tr>
<th>Structure</th>
<th>N</th>
<th>Detected N</th>
<th>Detected %</th>
<th>Passed PS N</th>
<th>Passed PS %</th>
<th>Passed SL N</th>
<th>Passed SL %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kortenhoef</td>
<td>15</td>
<td>6</td>
<td>40</td>
<td>5</td>
<td>83</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>De Ruiter</td>
<td>15</td>
<td>15</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Kadoelen</td>
<td>50</td>
<td>19</td>
<td>38</td>
<td>5</td>
<td>26</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Overtoom</td>
<td>25</td>
<td>17</td>
<td>68</td>
<td>6</td>
<td>35</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>Willem I</td>
<td>50</td>
<td>27</td>
<td>54</td>
<td>N/A</td>
<td>N/A</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>Zaangemaal</td>
<td>50</td>
<td>21</td>
<td>42</td>
<td>7</td>
<td>33</td>
<td>10</td>
<td>48</td>
</tr>
<tr>
<td>Halfweg</td>
<td>50</td>
<td>31</td>
<td>62</td>
<td>19</td>
<td>61</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Katwijk</td>
<td>25</td>
<td>25</td>
<td>100</td>
<td>19</td>
<td>76</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Spaarndam</td>
<td>50</td>
<td>33</td>
<td>66</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>15</td>
</tr>
<tr>
<td>IJmuiden</td>
<td>159</td>
<td>127</td>
<td>80</td>
<td>50</td>
<td>39</td>
<td>75</td>
<td>59</td>
</tr>
</tbody>
</table>
3. Results

3.1 Migratory opportunities

During the period of October, November, and December 2017, 57% of the time was night time. During this period, most of the pumping stations in the study area pumped most of the time during night time. A chi-square test of independence showed there was a significant association between locations and the proportion of pumping activity in each circadian phase, $X^2(30 \text{ df})=49.011 \ p<.016$ (Figure 19).

Some only because the night lasted longer than the day during this period, so evenly spread over 24 hours, others significantly more during dark than during light hours. The only exception being the pumping station at Spaarndam, which was most active during day time, with only 35% of the pumping activity during the night and significantly different than all other locations, $p<.05$ (Table 3). This was tested using pairwise comparisons using Fisher’s exact test for each location. Of all the pumping stations in the study area, De Ruiter had most night time activity (75%) and was significantly different than Halfweg (56%, $p<.05$).

![Figure 19: Pumping activity in hours per circadian phase per location over the period of October, November & December 2017. Percentages show fraction of total activity during the respective circadian phase for each location. The location “Control” shows the total amount of hours per circadian phase for the period October, November & December 2017.](image-url)
Table 3: Pairwise comparisons using Fisher’s exact test between locations and control for relative day-night ratio of pumping activity. Green = significant difference in day-night ratio for pumping activity between location and the actual day-night ratio of the period October, November, & December 2017.

<table>
<thead>
<tr>
<th>Location</th>
<th>Control</th>
<th>Spaarndam</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kadoelen</td>
<td>0.232</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Overtoom</td>
<td>0.400</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>De Poel</td>
<td>0.365</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Zaangemaal</td>
<td>0.400</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Halfweg</td>
<td>1.000</td>
<td>0.014</td>
</tr>
<tr>
<td>Katwijk</td>
<td>0.849</td>
<td>0.002</td>
</tr>
<tr>
<td>Spaarndam</td>
<td>0.011</td>
<td>0.014</td>
</tr>
<tr>
<td>Kortenhoef</td>
<td>0.903</td>
<td>0.002</td>
</tr>
<tr>
<td>De Ruiter</td>
<td>0.067</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>IJmuiden</td>
<td>0.903</td>
<td>0.002</td>
</tr>
</tbody>
</table>

3.2 Individual migration and route patterns per location

During this study, graphs were made for every individual tagged silver eel that passed one of the studied migration barrier in the North Sea Canal region. These graphs can be found in the Appendix of this report. Three out of 340 graphs were selected to illustrate the searching behaviour observed among silver eels during this study in this chapter. The gold lines in the graph represents the hours of sunrise and sunset, while area between the gold and the dark gold lines represent the hours of which it was civil dawn and civil dusk. The black dot represents the moment the eels were released at the location mentioned in the legend of the graph. The coloured circles are the distinct binned detections, in which the location of the receiver is represented by the colour of the circle. The blue background represents the flow rate at each time bin for the given pumping station, with dark to light blue representing low to high flow rates.

Evident in the data from tag 3052 at Overtoom is the lack of detections during the day, illustrating this silver eel visited the structure only at night, showing up twenty consecutive nights before making a successful attempt to pass through the pumping station. The fact that the eel was detected by both receivers in front of the building with almost no gaps in between can be attributed to the relatively short distance between both receivers, making it difficult to assign to searching behaviour (Figure 8 & Figure 20).

The data from tag 3099 at Spaarndam showed the silver eel was present at the structure during the night in contrast to the pumping station there, which had most activity during the day. It clearly showed searching behaviour, as it was detected by receivers that were separated by some distance from each other, going back and forth between the pumping station, the small shipping lock, and the bigger shipping lock to successfully pass through the bigger shipping lock (Figure 13 & Figure 21).

At IJmuiden, the silver eel with tag 1742 showed clear nocturnal searching behaviour, as it was detected by receivers that were separated by relative big distances from each other, going back and forth between the sluice, the North Sea Canal, and the shipping locks primarily at night. Gaps between detections can be attributed to the distances between receivers and the shipping intensity interfering with the signals transmitted. After approximately one month time it successfully passed through the Northern shipping lock. (Figure 17 & Figure 22)
Figure 20: Eel with tag 3052 at the Overtoom-complex.

Figure 21: Eel with tag 3099 at the Spaarndam-complex.
Figure 22: Eel with tag 1742 at the IJmuiden-complex.
3.3 Diurnal patterns in migratory windows and eel behaviour

68% of the detections, during the length of this study, were during the night (Figure 23). A chi-square test of independence showed there was a significant association between circadian phase and the number of eels detected, $X^2(3 \text{ df})=59422 \ p<.05$. There was no significant association found between the locations and the proportion of eels detected during each circadian phase, $X^2(27 \text{ df})=36.782 \ p=.099$. However, when only observations during day and night were tested, a chi-square test of independence showed there was a significant association between the different locations and the proportion of eels detected during day and night, $X^2(9 \text{ df})=35.603 \ p<.05$.

Pairwise comparisons were done using Fisher’s exact test for each location. Significant differences in the proportions of eels detected during day and night were found between Kadoelen & IJmuiden ($p<.03$), Oranjesluizen & Overtoom ($p<.02$), Zaangemaal ($p<.02$), Spaarndam ($p<.0002$), and IJmuiden ($p<.001$) and, Spaarndam & Kadoelen ($p<.02$), Halfweg ($p<.05$), and Katwijk ($p<.02$), which are illustrated in green in Table 4. The number of detections are the result of a combination of the number of individual eels detected at each location and the time spent at each location by each of those individuals (Figure 24). Most of the first detection downstream of the different structures were also during the night, indicating more eels pass the man-made structures at night. The height of the bars is explained by the number of individuals to successfully pass each structure (Figure 25).
Figure 24: Overview of the number of binned detections per circadian phase per location. Percentages show fractions of total observations during respective circadian phase for each location.

Table 4: Pairwise comparisons using Fisher’s exact test for each location. Red = N/A Green = significant differences in day-night ratio between locations.
Figure 25: Overview of the first detection downstream of the man-made structures per circadian phase per location. Percentages show fractions of total observations during respective circadian phase for each location.

3.4 Migratory delay
To determine how much migrating silver eel at each different structure in the study area were delayed, the interval between the first detection in front of the structure and the first detection behind the structure for each individual was investigated. The coverage of the interval between the first detection in front of the structure and the first detection behind the structure by detections of each individual that passed through the structures was investigated (Figure 26). Most intervals were less than 2000 hours, with two exceptions, being one individual at Overtoom and one individual at Kadoelen (Figure 27).
Figure 26: Presence between first detection in front of structure and first detection behind structure. Numbers in graph represent the medians of the fraction of interval coverage by detections per location.

Figure 27: Length of interval between first detection in front of structure and first detection behind structure in hours per location. Numbers in graph represent the medians of the length of the interval in hours per location. One outlier of 7353 hours at Kadoelen was removed from this plot.
To test differences between the locations for the length of the intervals of the individuals that passed through the structures at these locations for significance, a Kruskal-Wallis test was performed. The result confirms significant differences between the locations and the length of the intervals of the individuals that passed through the structures at these locations, Kruskal-Wallis $\chi^2(9\, df) = 35.2\, p<.0001$. The man-made structures at Overtoom, Willem I, and Kortenhoef were found to have the most delaying effect, leading to 4 to 5 weeks of migratory delay on average.

### 3.5 Integration of migratory windows, environment and behaviour

The pumping activity of each pumping station at the moment an individual was detected for the first time behind it was investigated looking only at individuals that were considered to have passed through that particular structure via the pumping station (Figure 28). At IJmuiden Sluice it does not show the pumping activity, but sluicing activity. The presence of flowing water over the top of the sluice would have provided migratory windows for silver eels to utilize the sluice to get passed the complex at IJmuiden. The height of the bars shows the numbers of individuals passed through the structures. Note that some individuals passed through the pumping station when these were inactive (Figure 28).

![Figure 28: Pumping activity at the moment of first detection behind structure of individuals that passed through pumping stations per location. Percentages show fraction of total detection during the respective pumping activity for each location.](image_url)
Table 5: Attractiveness, passage success rate, and average delay. There was no average delay calculated for De Ruiter as this structure blocked all eels that attempted to get passed.

<table>
<thead>
<tr>
<th>Structure</th>
<th>Detected %</th>
<th>Passed %</th>
<th>Average Delay (hours)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kortenhoef</td>
<td>40</td>
<td>83</td>
<td>601</td>
</tr>
<tr>
<td>De Ruiter</td>
<td>100</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Oranjesluizen</td>
<td>-</td>
<td>-</td>
<td>154</td>
</tr>
<tr>
<td>Kadoelen</td>
<td>38</td>
<td>26</td>
<td>583</td>
</tr>
<tr>
<td>Overtoom</td>
<td>68</td>
<td>59</td>
<td>930</td>
</tr>
<tr>
<td>Willem I</td>
<td>54</td>
<td>15</td>
<td>674</td>
</tr>
<tr>
<td>Zaangemaal</td>
<td>42</td>
<td>81</td>
<td>271</td>
</tr>
<tr>
<td>Halfweg</td>
<td>62</td>
<td>61</td>
<td>616</td>
</tr>
<tr>
<td>Katwijk</td>
<td>100</td>
<td>76</td>
<td>354</td>
</tr>
<tr>
<td>Spaarndam</td>
<td>66</td>
<td>18</td>
<td>361</td>
</tr>
<tr>
<td>IJmuiden</td>
<td>80</td>
<td>98</td>
<td>129</td>
</tr>
</tbody>
</table>

The number of migratory windows in the interval between the first detection in front of the structure and the first detection behind the structure was investigated for each individual that got passed a structure (Figure 29). Overtoom, Willem I, Halfweg, Kortenhoef, and Kadoelen were found to have delaying effects with averages ranging between 24 and 39 days, while IJmuiden had the lowest delaying effect of 5 days on average (Table 5).

The original study showed clear differences between the structures in the study area in terms of attractiveness and passage success rate (Winter et al., 2018). Kadoelen (38%), Kortenhoef (40%), and Zaangemaal (42%) were least attractive, while De Ruiter (100%), Katwijk (100%), and IJmuiden (80%) were most attractive. High passage rates were observed at IJmuiden (98%), Kortenhoef (83%), and Zaangemaal (82%). The lowest passage rates were observed at De Ruiter (0%), Willem I (15%), and Spaarndam (18%). Even though pumping station Kortenhoef had a high passage rate, low attractiveness to the structure resulted in low numbers of eels to attempt passing through. For De Ruiter, it was the opposite true, as high attractiveness leads to high numbers of eels showing searching behaviour near the structure without making successful attempts to pass through. The coverage of the interval between the first detection in front of the structure and the first detection behind the structure by migratory windows was investigated for each individual that passed through the structures (Figure 30). A chi-square test of independence showed there was a significant association between pumping activity and the number of eels detected at each location, $X^2(7 \text{ df})=82.278 \ p<.05$. 
Figure 29: Number of migratory windows between first detection in front of structure and first detection behind structure per individual per location. Numbers in graph represent the medians of the amount of migratory windows per location. One outlier of 11,570 windows at Kadoelen was removed from this plot.

Figure 30: Window of opportunity coverage of interval between first detection in front of structure and first detection behind structure per individual per location. Numbers in graph represent the medians of the fraction of migratory windows coverage per location.
4. Discussion

The focus of this study was on the migratory behaviour and migratory windows of silver eels at migration barriers in a highly regulated water system. In this study, nocturnal activity in silver eel is confirmed, as most of the detections and successful passages occurred during the night. Searching behaviour was also observed in some eels, as they were detected by multiple receivers before successfully passing the migration barriers. During this study, significant variation between the different man-made structures in the North Sea Canal region in terms of passage rate and delaying effect for migrating silver eels was observed.

Concerning the daily pattern of silver eels, the difference between activity and presence should be mentioned. Because of the fact that eels being detected are not always active, but could also be passively within range of the receiver. This could lead to the false conclusion of activity during moments of passiveness. The moments of first detection behind each of the structures were in 88% of the cases during the night, which confirms nocturnal activity in migrating silver eel as eels have to actively swim to pass the man-made structures. The delaying effect at IJmuiden, Overtoom, Zaangemaal, and Katwijk could have been underestimated as for each of these locations one individual was detected in front of the migration barriers after already being detected behind the migration barriers. This may have caused the moment of passage to be assumed to have happened earlier than it in reality might have been. In addition, some individuals seem to have passed the pumping station when these were not actively pumping (Figure 28). An explanation for this could be the existence of alternative routes through the structure without passing through the pump itself, or that eels got through the pumping station and it stopped pumping at the same moment the eel was detected.

Two plausible explanations for the nocturnal behaviour of European eels are suggested by (Verhelst et al., 2018c): to avoid predators and for foraging. The most likely predators in the North Sea Canal region to feed on eels are the northern pike (Esox Lucius L.), great cormorant (Phalacrocorax carbo L.), and grey heron (Ardea cinereal L.), which forage primarily during the day (Ibbotson et al., 2006). The fact that a lot of invertebrates avoid predation by emerging at night and low light conditions is beneficial for ambushig fish, which may explain why eels forage at night (Learner et al., 1990). Having a diurnal pattern with reduced activity during the day is suggested to be beneficial for eels, as periods of reduced activity allow eels to meet the energetic costs of feeding (Owen, 2001). Eels are known to hide inside the bottom substrate, under objects, and in crevices during the day ((Baras et al., 1998; Verhelst et al., 2018c).

Concerning passage success, the passage success at the shipping locks at IJmuiden was significantly higher than those of the shipping locks in the hinterlands. This could be explained by the fact that shipping locks at IJmuiden are operated around the clock, move larger volumes of water and are situated on border between fresh- and saltwater (Winter et al., 2018).

It is recommended that in future studies also environmental migration windows are analysed, as these might have a moderated the delaying effects seen in this study. In other telemetric studies, active downstream migration was periodically, and during environmental migratory windows, related to higher water discharge (Vøllestad et al., 1986; Winter et al., 2006; Jansen et al., 2007b; Verhelst et al., 2018a; van Keeken et al., 2020b).

Future studies concerning daily patterns in the behaviour of silver eels could investigate whether the detections during the day happened during periods of higher turbidity or during overcast weather (LaBar et al., 1987; Baras et al., 1998). It is recommended that these detections that cause this uncertainty are identified and if needed removed during future studies using this dataset. This also applies to detections of eels that appear to go through pumping stations at moments of inactivity of the pumping stations.

The datasets containing the operation activity of the shipping locks contained the number of times the shipping lock was active per month. For future studies it would be recommended that the exact times of the day at which the shipping locks in the study area were operated are documented, to determine which migratory windows provided by shipping locks are utilized by eels to get passed migration barriers.
Implications for management
In the preceding study, it was recommended that at Kadoelen and Willem I the fish migration facilities should be made more attractive, as this would most likely greatly decrease the barrier effect at these locations. It was also recommended that the shipping locks at De Ruiter and Kortenhoef provide “loze schuttingen”, which is Dutch for operations of a shipping lock without vessels going through, in the first part of the night to facilitate the migration of silver eels in the Loosdrechtse plassen and the Vinkeveense plassen and to provide an alternative to the highly dangerous pumping stations located there. Pumping activity during the day followed by loze schuttingen during the first part of the night was suggested to increase the attractiveness of the shipping locks for silver eels. Another recommendation was that the fish unfriendly pumps at Kortenhoef, IJmuiden, and De Ruiter should be replaced by fish friendly pumps. On top of this, fish detering devices at locations with both a pumping station and alternative routes were recommended (Winter et al., 2018). The stimulation of gravitational flow during windows at night. During periods of high discharge was recommended for pumping stations where fish-friendly adaptations are absent (Verhelst et al., 2018a).

5. Conclusions
In conclusion, silver eels express searching behaviour in the vicinity of migration barriers, primarily during the night. Even though some silver eels were detected during the day, most silver eels utilized migratory windows at night. 8 out of the 10 pumping stations in the North Sea Canal region had most of their pumping activity during the night, at which silver eels were most actively migrating. Passage success and migratory delay was observed to vary significantly amongst migration barriers in the North Sea Canal region. This shows there are opportunities present to improve the facilitation of silver eel migration in this highly regulated water system.

Acknowledgements
I would like to thank to my supervisors Dr. Ir. Leo Nagelkerke and Dr. Ir. Erwin Winter for their feedback and supervision during my thesis. I would also like to thank Wageningen Marine Research and the water boards Rijkswaterstaat (Ministry of Infrastructure and Water Management), the Province of Noord-Holland, Hoogheemraadschap Hollands Noorderkwartier, Rijnland, and Waternet. Their datasets made this thesis possible. I would like to thank Olvin van Keeken for his explanations of the acoustic telemetry dataset and for taking me with him to show the process of tagging fish with acoustic transmitters and the placement of acoustic receivers.
References


Appendix

Kadoelen 3004

Group
- Willem I sluis

Flow rate (m³/s)
- 9
- 6
- 3
- 0

Location
- Kadoelen Pumpingstation Outside
- Kadoelen Pumpingstation Inside

Kadoelen 3023

Group
- Kadoelen

Flow rate (m³/s)
- 9
- 6
- 3
- 0

Location
- Kadoelen Pumpingstation Outside
- Kadoelen Pumpingstation Inside

Date
- okt 09
- okt 16
- okt 23
- okt 30
- nov 06
Katwijk 3139

Flow rate (m³/s)
30
20
10
0

Group
Katwijk

Location
Katwijk Pumpingstation North Sea
Katwijk Pumpingstation Inside

Katwijk 3140

Flow rate (m³/s)
75
50
25
0

Group
Katwijk

Location
Katwijk Pumpingstation North Sea
Katwijk Pumpingstation Inside
IJmuiden 1719

Group
- Noordzeekanaal

Location
- Northern Shippingboek North Sea
- Northern Shippingboek NZK
- Noordzeekanaal

Flow rate (m³/s)
- 200
- 150
- 100
- 50
- 0

IJmuiden 1720

Group
- Noordzeekanaal

Location
- Middle Shippingboek NZK
- Northern Shippingboek North Sea
- Northern Shippingboek NZK
- Noordzeekanaal
- Sluice NZK

Flow rate (m³/s)
- 200
- 150
- 100
- 50
- 0