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Efficient and timely downstream passage solutions for European silver eels at hydropower dams

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ABSTRACT

The European eel population is critically endangered due to a multitude of human-induced factors such as habitat fragmentation, parasites, fishing, and climate change. In freshwater, downstream migrating silver eels encountering hydroelectric plants often suffer substantial delays and increased mortality from trash-rack impingement and turbine-induced mortality. Downstream passage problems can be ameliorated by implementing different types of downstream passage solutions that show variable but promising results for salmonids, but their performance for silver eels remains largely unknown. To address these knowledge gaps, radio telemetry was used to monitor the downstream migration of silver eels during 2 years past a hydroelectric plant recently equipped with two new fish passage solutions, consisting of an angled bar rack with a full-depth bypass, and a nature-like fishway. No tagged eels passed through the turbines, but bypassed the dam evenly between the two passage solutions, resulting in a 95% impediment passage efficiency and a median passage time of 1 h. Movement patterns and route selection were associated with variation in discharge and most individuals approached both passage solutions before passing, resulting in route-specific efficiencies of 69% for the angled rack and bypass, and 46% for the nature-like fishway. We conclude that the combination of a new bypass, paired with an angled rack, and a large nature-like fishway provided downstream migrating silver eels with a highly effective combination of passage solutions, with high impediment passage success and relatively low passage times.

1. Introduction

The panmictic European eel (*Anguilla anguilla*) population has been severely reduced over the last century, with juvenile eel recruitment plummeting by >90% over just a few decades (Dekker and Casselman, 2014; ICES, 2016). The probable causes of this decline are myriad, affecting each part of the European eel's complex life cycle. From commercial fishing, pollutants, parasites, fragmentation of aquatic waterways used during spawning migrations, and various aspects of climate change (Friedland et al., 2007; Dekker, 2016), the panmictic European eel population is in decline. Unfortunately, no single bottleneck has been identified and countries participating in the European eel recovery plan, implemented in 2007, must attempt to address multiple sources of population suppression. The primary targets of this plan are commercial fisheries and the fragmentation of rivers by hydropower operations, and while several countries have already reduced fishing quotas or closed their eel fishery entirely, little has yet been done to reduce the impact of hydropower on eel migrations (Dekker, 2016).

As a catadromous species, mature European eels (silver eels) migrate from freshwater into the Atlantic Ocean to spawn in the Sargasso Sea. The resulting juveniles migrate back to European waters and, typically, up into freshwater river systems to grow and mature. When rivers have been fragmented by dams, however, juvenile eels are prevented from reaching their rearing grounds, thereby greatly reducing the production of silver eels. Connectivity can be reinstated between eel spawning and rearing grounds through the constructing of fish passage solutions adapted to the swimming and climbing capacity of eels, such as nature-like fishways and eel ramps, or by trapping juvenile eels in the marine environment and releasing them in rivers or lakes upstream of dams (Vowles et al., 2015; Podgorniak et al., 2016; Tamario et al., 2019). Unfortunately, many conservation programs in freshwater environments only target the upstream passage of juveniles and can even have

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negative effects on silver eel production if other survival bottlenecks, such as habitat availability or restrictions on downstream migration, are ignored (Pelicice and Agostinho, 2008; Calles and Greenberg, 2009). For this reason, hydropower poses a serious threat to migrating eels, in particular to downstream migrating silver eels which experience substantial delays and increased mortality at hydropower plants. Delays can cause increased stress and energy expenditure, as well as susceptibility to diseases, parasites and predation that may collectively lead to migration failure (Calles et al., 2010; Nyqvist et al., 2017a; Baktoft et al., 2020). The highest direct mortality for downstream migrating silver eels, however, is often caused by trash rack impingement and turbine-induced mortality, which can reach levels as high as 100% (EPRI, 2001; Carr and Whoriskey, 2008; Calles et al., 2010). Despite this, downstream fish passage solutions have historically targeted salmonids, whereas eel passage efforts have been restricted to lab studies and developing methods to estimate turbine-induced mortality (EPRI, 2002). During the last decades, however, attempts have been made to implement full-scale passage solutions for multiple species, including eels (Larinier and Travade, 2002; Calles et al., 2013).

Downstream passage solutions aim to maximize survival of migrating fish encountering a dam by guiding fish away from the turbine intakes and towards a safe passage alternative (a bypass) without substantial delay. Downstream guidance can be achieved via behavioral and/or mechanical means. Behavioral guidance relies on predictable repulsion/attraction to certain stimuli (e.g., sound, light, or hydrodynamic cues) and tends to be species-specific. Though some multisensory systems have been proposed, there are few examples of successful multi-species solutions using behavioral guidance (Coutant, 2001; Albayrak et al., 2019). A far more common approach is to use mechanical guidance solutions which physically prevent fish from passing the guiding device. Today fish guidance devices, usually a rack or screen, combine mechanical exclusion with hydrodynamic behavioral guidance and have shown promising results for multiple species (Nyqvist et al., 2017b; Albayrak et al., 2019). Racks can be oriented to either guide fish vertically towards the water's surface (inclined or α-racks) or laterally towards one side of the river/channel (angled or ß-racks). In either case, a slope of 30° or less is recommended to avoid impingement and maximize the sweeping velocity which guides fish along the rack to a bypass (DWA, 2005). Published evaluations of downstream passage facilities and guidance solutions show variable but promising results for juvenile Pacific salmon species (Cramer, 1997; Karchesky et al., 2008) and Atlantic salmonid smolts (Nettles and Gloss, 1986; Scruton et al., 2008; Nyqvist et al., 2018; Tomanova et al., 2021) and kelts (Nyqvist et al., 2017b), however few corresponding studies exist for eels (but see, Travade et al., 2010, Calles et al., 2013).

At the Herting hydroelectric plant (HEP) in the river Ätran, outdated fish passage solutions (FPSs) were recently replaced by best practice solutions in an attempt to improve longitudinal connectivity for migratory species in the river (Nyqvist et al., 2017b). To improve downstream passage conditions, a conventional trash rack with an ice/trash spill gate was replaced with a 30° angled bar rack and a full-depth bypass. Furthermore, upstream passage conditions were improved by replacing a Denil fishway with a large nature-like fishway that allows for a high minimum discharge. These new FPSs were found to increase passage efficiency and decrease passage time (delay) for both upstream migrating Atlantic salmon (*Salmo salar*) spawners and downstream migrating salmon kelts (Nyqvist et al., 2017b) and smolts (Nyqvist et al., 2018). How well they function with other species such as eel has not yet been assessed. A previous evaluation of the old FPS indicated a need for improvement when eel passage was considered, particularly for downstream migrating silver eels (Calles et al., 2012b).

To assess the efficiency of the new FPS at the Herting HEP with regards to European eel, radio telemetry was used to monitor the downstream migration of silver eels over two migratory seasons. Passage efficiency, passage time (delay), and passage rate were assessed in relation to the prevailing environmental conditions. By studying these new fish passage solutions in-situ and with a wild population, we hope to improve our understanding of how to best restore longitudinal connectivity along migratory paths for this endangered species and provide managers with the information they require to make informed decisions and achieve the goals of the European eel recovery plan.

2. Material and methods

The evaluation of the new FPSs for silver eels was carried out at the Herting HEP in the river Ätran over the 2014 and 2015 migratory seasons. The river Ätran catchment is 3342 km^2 with a mean annual discharge of 57 $m^3 s^{-1}$ (range 20–319 m^3s^{-1} between 1990 and 2011; Olfsson, 2013) and enters the Kattegat subbasin of the North Sea in the town of Falkenberg (56°52′55″N, 12°28′46″E; Fig. 1). Diadromous fish species migrating upriver encounter the Herting HEP after 3 km. Continuing upriver, fish can access another 24 km of the main stem before encountering the first definite obstacle, the Ätrafors HEP. Just below the Ätrafors HEP, however, migrating fish can enter a tributary to the river Ätran, the river Högvadsån, which grants access to an additional 34 km if they can successfully pass the Nydala HEP, located 5 km upstream from the confluence with the Ätran main stem. At Nydala, ascending salmonids must jump or be manually lifted over a series of semi-natural falls (total head is 3 m) that are potentially passable for juvenile eel. With its proximity to the North Sea, most spawning and rearing areas available to diadromous fish species are situated upstream of the Herting HEP. For this reason the Herting HEP is often described as "the key to the river Ätran". We refer readers to Nyqvist et al. (2017b) for further details on the river Ätran and its catchment.

2.1. Herting HEP

The Herting HEP consists of two powerhouses, Herting 1 (H1) and Herting 2 (H2, Fig. 2A), with a total intake capacity of 65 $m^3 s^{-1}$. H1 is equipped with two Kaplan turbines with a combined intake capacity of 40 $m^3 s^{-1}$ (15 + 25 $m^3 s^{-1}$) and H2 is equipped with one Kaplan turbine with an intake capacity of 25 $m^3 s^{-1}$. As mentioned above, the Herting HEP went through extensive modifications in 2013 to improve longitudinal connectivity for migratory species in the river Ätran. At the H1 powerhouse, a 40 m long angled composite rack (CompRack®, Halmstad, Sweden) with horizontal bars spaced 15 mm apart was installed immediately upstream of the turbine intake (Fig. 2B). At a 30° angle relative to the banks of the intake channel, this rack guides fish towards a full-depth bypass with an electrically controlled hydraulic gate. During normal operation, two slots in this gate, a surface slot (300 × 650 mm; W

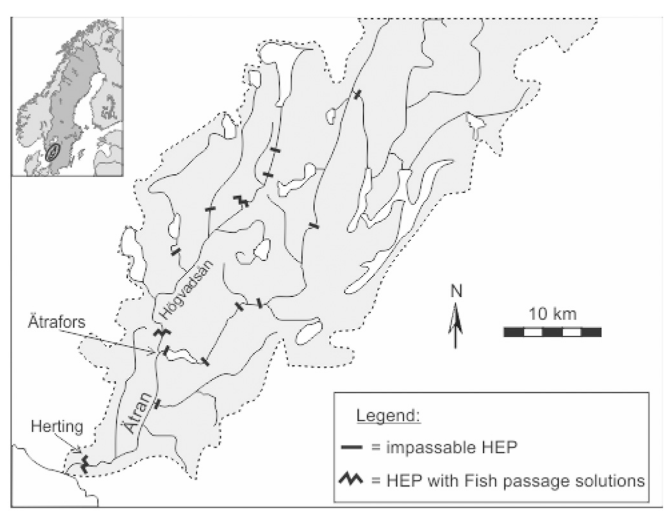

Fig. 1. Map of Sweden and the Ätran catchment including barriers with and without fish passage solutions. Figure modified from (Nyqvist et al., 2018).

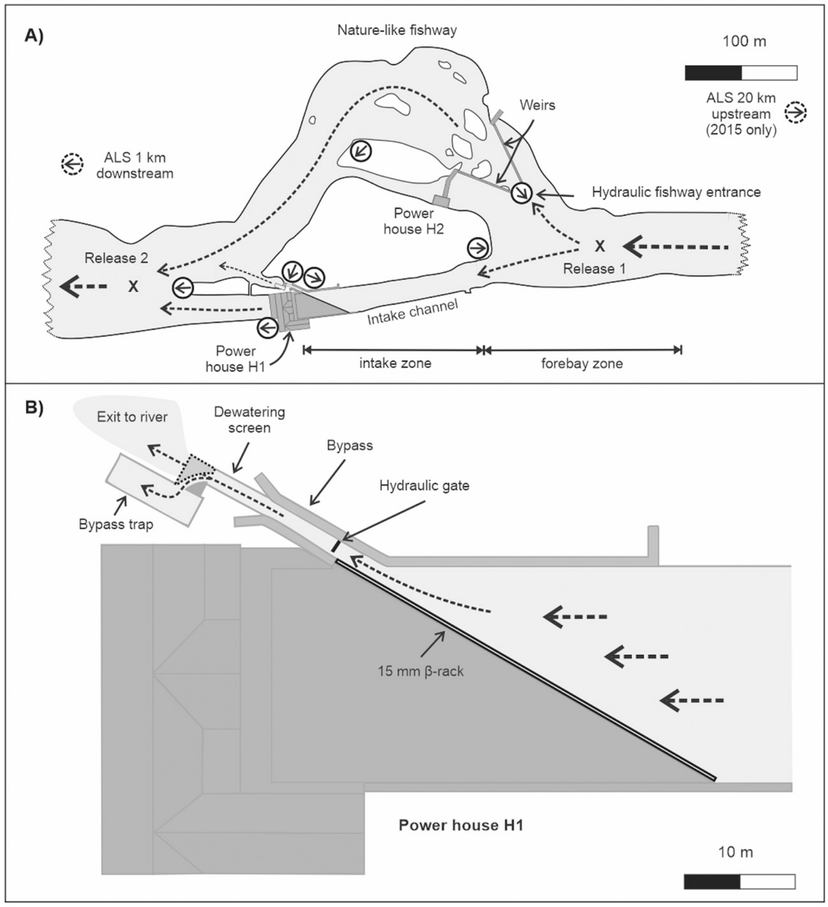

Fig. 2. The Herting hydroelectric plant after the implementation of new fish passage facilities. A) Overview of the area, fish passage facilities and powerhouses H1 and H2 with the position and direction of automatic listening stations (ALSs), and B) a detailed sketch of the angled rack and bypass at powerhouse H1. Figures modified from (Nyqvist et al., 2018).

x H) and a bottom slot (200 × 200 mm), are open, allowing water to flow through the bypass at a rate of 0.6 $m^3 s^{-1}$. When the pressure gradient across the rack exceeds a pre-specified level, the gate opens fully, permitting a rack cleaner to push accumulated debris from the rack through the bypass. During this process, the discharge through the bypass temporarily increases to a maximum of 3.0 $m^3 s^{-1}$. The bypass channel is also equipped with a dewatering feature which can be used to divert fish into a holding facility for counting or tagging (described further in Nyqvist et al., 2017b). No modifications to the turbine intake were made at the H2 powerhouse during the facility upgrades. Instead, to protect downstream migrating fish, the turbine at H2 is not in operation during fish migration seasons and only generates electricity between December and February. At the H2 powerhouse, downstream migrating fish can pass via a nature-like fishway (i.e., the modified original main stem of the river) which discharges a minimum of 11 $m^3 s^{-1}$, both through the hydraulic fishway entrance and over the two adjacent weirs (Fig. 2A).

2.2. Tagging and release

Downstream migrating silver eels were caught in four eel traps located 13–70 river km upstream from the Herting HEP, radio tagged, and transported downstream for release (for more information about the traps, see Calles et al., 2010). Evaluation of the Herting HEP passage solutions followed the same procedure as in Calles et al. (2010, 2012a, 2013), while the tagging and handling procedures followed those of Jepsen et al. (2002). Briefly, captured eels were anaesthetized using benzocaine (0.2 g/L) before a radio tag (F1540, Advanced Telemetry Systems, Isanti, MN, U.S.A.) weighing 2.0 g was surgically implanted into the peritoneal cavity via an incision (4–5 mm) on their ventral surface. The following morphological parameters were recorded during tagging: total length (mm), weight (±10 g), degree of silvering (0–3), left pectoral fin length (±0.1 mm), and eye diameter (both vertical and horizontal, ±0.1 mm). The sexual maturation of each individual was estimated from the degree of silvering and by calculating the Eye Index (left eye) according to Pankhurst (1982), and the Fin Index (left pectoral fin) according to Durif et al. (2009). Median time to full anesthesia was 6.1 min, while median total handling time was 4.0 min (range: 2.6–8.3 min). Eel recovery was monitored for 1–5 h prior to release and no mortality or signs of injury resulting from the tagging procedure were observed during the study. Tagged eels were released after dusk on the same day they were tagged (17:00–20:00).

Table 1
Silver eel radio telemetry tagging schedule at the Herting hydropower facility.

Tagging date	Tagged eels	Release location	
		Upstream[a]	Downstream
Sep 2, 2014	9	7	2
Sep 11, 2014	11	8	3
Sep 18, 2014	10	8	2
Sep 26, 2014	10	7	3
Sep 18, 2015	13	10	3
Sep 23, 2015	13	10	3
Oct 15, 2015	14	10	4
Total	80	60	20

[a] Release site differed between years as specified in the main text.

Eighty tagged individuals were released on four separate occasions in 2014, and three separate occasions in 2015 (Table 1). To differentiate between handling effects and dam passage effects, tagged eels were assigned to either a passage group ($n = 60$; released upstream from the Herting HEP) or a control group ($n = 20$; released downstream from the Herting HEP). Eels from the control group were released at the confluence of the H1 and H2 outlets (Release site 2, Fig. 2A) while eels from the passage group were released either immediately upstream of the Herting HEP in 2014 (Release site 1, Fig. 2A) or in the tailrace of the Ätrafors HEP, 24 km upstream of Herting HEP in 2015 (Fig. 1).

2.3. Telemetric tracking

An array of automatic listening stations (ALSs, $N = 15$), each consisting of a 4–6 element Yagi-style antenna and a receiver (model R4500; ATS), were positioned at eight sites around the Herting HEP and up to 1 km downriver from the H1 powerhouse (Fig. 2A). An additional ninth ALS was positioned at the release site below the Ätrafors HEP in 2015. Each ALS listened for transmissions from activated tags in their vicinity and stored the tag's unique code along with a timestamp and a reading of the signal strength. The array operated continuously throughout the study period and recorded activated tags until a tag was detected below the HEP, leaving the system, or until the end of each study period (December 23 in 2014 and November 27 in 2015). Median time between detections on a single ALS was 1 min (IQR = 1–2 min). Radio tagged eels were also manually tracked on a weekly basis during the study period in the vicinity of the Herting HEP and downstream as far as the river mouth, as well as upstream as far as Ätrafors HEP in 2015, using a 3 element Yagi-style antenna and a handheld receiver (model R2100; ATS, Isanti, MN, U.S.A.).

2.4. Passage efficiency analysis

To assess the efficiency of the new fish passage solutions implemented at the Herting HEP for safe downstream passage for European eel, we quantified efficiency of the two FPSs using methods outlined by the European standard "Water quality — Guidance for assessing the efficiency and related metrics of fish passage solutions using telemetry" (CEN, 2021). The passage efficiency was evaluated in two ways, with the overall impediment passage efficiency (η_{ip}) which includes both passage solutions to assess total passage survival, and with FPS-specific efficiencies (η_{fps}) for the two passage solutions separately to allow for transferable comparison between systems. The overall impediment passage efficiency for the Herting HEP, regardless of the specific route chosen for passage, was calculated as.

$$\eta_{ip} = f_g / f_a \times 100 \quad (1)$$

in which f_g is the number of eels leaving the area of influence of the impediment after downstream passage, and f_a is the number of eels approaching the impediment (i.e. detected by the forebay ALS). The FPS-specific efficiencies for the nature-like fishway at the H2 powerhouse as well as the combined angled rack and bypass at the H1 powerhouse were calculated as.

$$\eta_{fps} = f_{ex} / f_e \times 100 \quad (2)$$

where f_{ex} is the number of eels exiting each FPS AND leaving the area of influence of the impediment after passage (i.e. moving downstream below the dam). When calculating η_{fps} for each of the two fish passage solutions, f_e was calculated as the number of fish that entered the area immediately upstream of the relevant fish passage solution. For the H2 powerhouse's fishway this meant eels detected within the HEP forebay, while for the H1 powerhouse's angled rack and bypass, this meant only those eels detected within the intake channel. In addition to these two metrics, we also assessed passage time as a measure of migrational delay caused by the HEP, defined here as the duration of time between the first detection of a tag at the HEP forebay to the time of passage. Finally, the effect of the dams on travel times was assessed by comparing time from release to arrival at the downstream ALS between the control groups (both 2014 and 2015) and the passage groups (2014 only – released just upstream the dam), as these times all included post-release recuperation and any effect of the dam.

2.5. Time-to-event analysis

To model the effects of discharge variables and time-of-day (day/night) – and potential behavioral effects of water temperature and moon phase (Tesch, 2003) - on passage, approach, and rejection rates, a Cox proportional hazards regression (Castro-Santos and Haro, 2003; Castro-Santos and Perry, 2012; Hosmer et al., 2008), a type of time-to-event analysis, was used. Detections by ALSs situated at the Herting HEP were first used to define presence in the two passage zones of interest: the HEP forebay and the H1 powerhouse intake channel (Figs. 2A and 3). Once inside a passage zone, eel movement was classified into one of several mutually exclusive options (Fig. 3). From within the HEP forebay, eels could *i)* bypass the HEP and continue downstream via the nature-like fishway, *ii)* progress from the forebay into the H1 powerhouse intake channel, or *iii)* reject the forebay by retreating upstream. Eels that progressed into the intake channel, could *iv)* bypass the H1 powerhouse and continue downstream via the angled rack and bypass or *v)* reject the intake channel and retreat into the forebay. Eels were classified as rejecting the forebay following a period of >2 h outside the forebay, and the intake channel after a period of >30 min outside the intake channel. All tagged eels present within one of the two passage areas (forebay or intake channel) were considered capable of passage and comprised the risk set in time-to-event parlance. Since individual eels could exit and reenter a passage area multiple times, creating correlated event histories, a marginal model was used and data were clustered on a fishID variable. Robust variance values were therefore used to assess the significance of coefficient estimates (Therneau and Grambsch, 2000). Similarly, analyses were stratified based on year to account for unmeasured differences between the two study replicates (Hosmer et al., 2008; Allison, 2010; Kleinbaum and Klein, 2012).

A separate analysis was conducted for each of the five movement categories described above using a set of different discharge variables. For modelling the rejection rates from the forebay (*i*), we used total river discharge (Fig. 4). To model progression through the HEP forebay (i.e., intake approach (*ii*) or fishway passage (*iii*)), total river discharge was replaced by relative discharge (fishway discharge/total river discharge; Fig. 4) as this was thought to be more relevant for these models. Similarly, the movement of eels within the H1 powerhouse intake channel (i.e., intake rejection (*iv*) and bypass passage (*v*)), was modelled as a function of discharge rates through the turbines rather than total or relative discharge. To trace diel behavioral changes often reported for migrating eels, diel period (day/night) were included in all analyses.

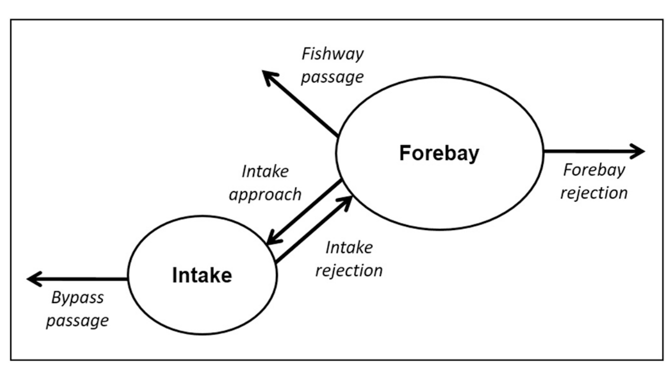

Fig. 3. A schematic diagram showing modelled eel movement options (arrows) and risk groups (ellipses) for fish present in the forebay and the intake channel.

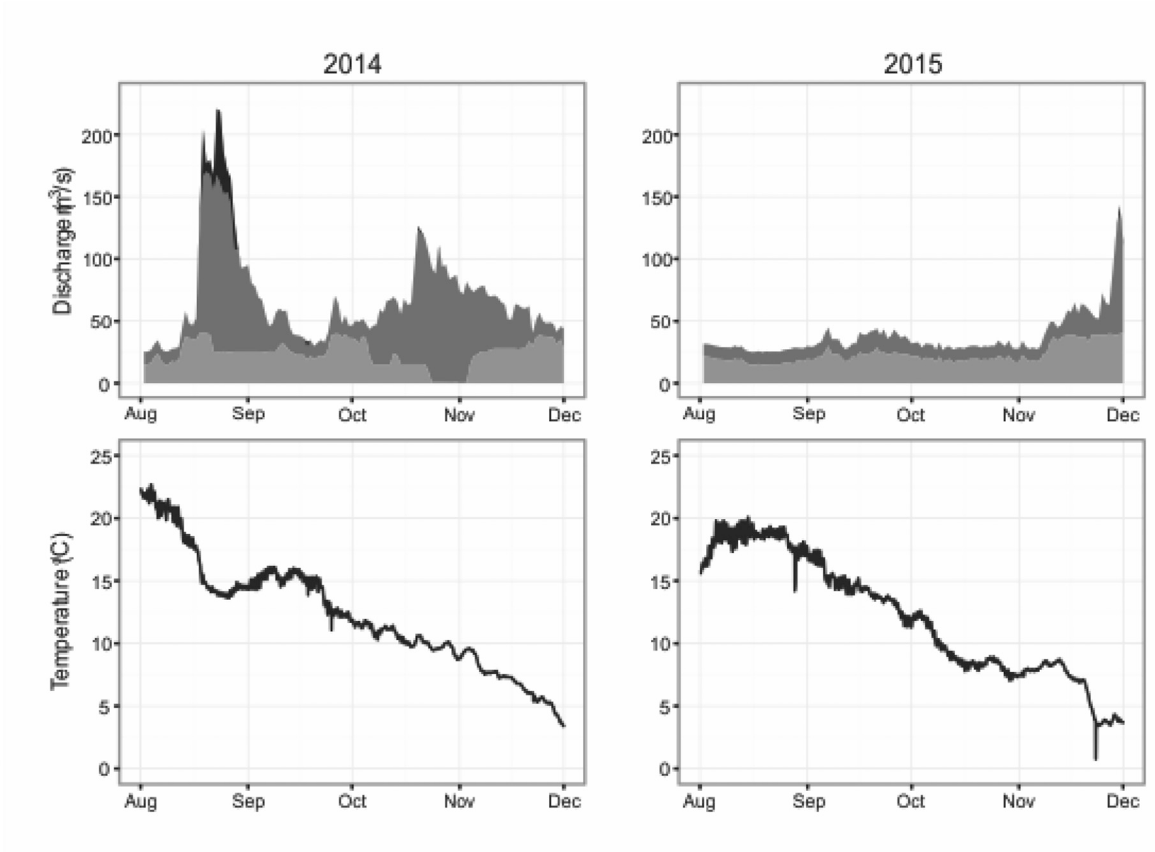

Fig. 4. Discharge through turbines at the Herting H1 powerhouse (light grey), fishway (dark grey) and spill gates (black) and water temperature during the eel migration period (August–November) for 2014 and 2015. Data from Falkenberg Energi AB.

Temperature and lunar phase (illumination fraction; Kelley et al., 2018), were also included among the candidate models for all five movement categories. The resulting set of 15 candidate models were then ranked according to their Akaike information criterion (AIC) value. A subset of good models with ΔAIC values within 2 units of the best fitting model (lowest AIC value) and at least 2 units above the null model was then selected from among the candidate models for each analysis. The most parsimonious model, the simplest model with the fewest parameters, from among the subset of good models for each analysis was considered the best model (Burnham and Anderson, 2003; Richards, 2008). The proportionality of hazards assumption was tested for all good models using the cox.zph() function from the survival package in R (Therneau and Lumley, 2015).

Differences between groups of fish or times were tested using Mann-Whitney *U* tests (continuous data) or Fisher's Exact tests (count data). All statistical analyses were performed using base R (R Core Team, Austria) or the Survival v3.2-7 package (Therneau and Lumley, 2021).

3. Results

Over 2 years, eighty European eels were radio tagged and released upstream ($n = 60$) or downstream ($n = 20$) of Herting HEP. Based on their individual size and the marked sexual dimorphism in European eels (Tesch, 2003), all individuals were identified as females. Generally, eels included in this study tended to be larger in 2014 than in 2015. Eels in 2014 were, on average, 9% longer (Mann-Whitney U test, $p < 0.01$; Table 2) and 32% heavier (Mann-Whitney U test, $p < 0.01$; Table 2) than eels in 2015. Similarly, study eels tended to show more signs of sexual maturity in 2014, in terms of their eye index (Mann-Whitney U test, $p < 0.006$) and silvering (Fisher's exact test, $p < 0.01$, Table 2). No significant difference was present among the study years in terms of their fin index (Table 2).

Table 2
Biometric summaries (range) for eels in a dam passage study conducted on the river Ätran in southern Sweden during the fall migration period in 2014 and 2015.

	2014	2015
Length (mm)	787.95 ± 100.43 (586–955)	715 ± 84.28 (610–1040)
Weight (g)	1000.04 ± 329.94, (450–1800)	679 ± 270.5 (420–1890)
Eye index	8.96 ± 1.36, (5.76–11.94)	8.14 ± 1.31 (5.58–10.85)
Fin index	5.12 ± 0.39 (4.32–5.9)	5.11 ± 0.34 (4.44–5.97)
Silvering index (1/2/3)	0/38/2	10/27/3

3.1. Migration characteristics and passage efficiency

Upon release, tagged eels generally remained at their release site for some time before recommencing their downstream migration. In 2014, as the passage group were released directly into the HEP's forebay (Fig. 2A), these eels ($n = 30$) were considered to have entered the forebay passage zone upon release, barring one exception that was never detected due to tag failure. In contrast, the 2015 passage group ($n = 30$) were released an additional 20 km upriver and were observed to remain at their release site for a median of 163 min (range: 3 min to 12 days) before recommencing their downstream migration. Among the 2015 passage group, all eels reached the Herting HEP during the study period, though travel times between the Ätrafors and Herting HEPs ranged from

7 h to 36 days (median = 7 days). This corresponds to a median travel speed of 3.14 km/day (range = 0.6–71.7 km/day). All arrival times at the Herting HEP occurred at night.

Of the 59 eels that were detected to enter the HEP forebay over both study years, 56 were observed passing the HEP via one of the two FPSs to continue their downward migration as indicated by detections at the lowermost ALS or the combination of diminishing downstream detection strengths in combination with an absence of detections during manual tracking sessions below the HEP. Only three eels (5%) failed to pass the HEP and were still present (and moving) within the reservoir at the end of the study periods. This result represents an impediment passage efficiency (η_{ip}) for the Herting HEP of 95% (56 of 59 eels). The overall FPS efficiency (η_{fps}) for the nature-like fishway near the H2 powerhouse (i.e., the proportion of eels that entered the forebay and passed via the nature-like fishway) was 49% (29 of 59 eels). Not all eels that passed via the fishway did so directly upon entering the forebay, however. A total of 39 eels moved from the forebay into the H1 powerhouse's intake channel and among these, 12 (31%) returned to the forebay and either passed via the fishway or remained in the forebay. The remaining 27 eels in the intake channel passed via the bypass, resulting in a η_{fps} for the angled rack and bypass of 69%. Among eels that passed via the H1 powerhouse's bypass, 20 did so on their first visit to the intake channel, five required a second visit, and two eels required three or more visits.

The median passage time for eels passing the HEP, i.e., from the first detection at the forebay to passage of the HEP, was 24 h and exhibited a large degree of variation, from 5 min to 49 days. In 2014, when fish were released in the forebay, the median passage time was 79 h. In 2015, on the other hand, when fish were released 20 km upstream and reached the dam on their way downstream, the median passage time was 1 h (median). This difference was, however, not significant (Wilcoxon, p = 0.12). Some eels initially retreated upstream from the forebay, only to return to the HEP one or more times before eventually passing. The median number of retreats from the HEP forebay, among eels that eventually passed the dam (n = 56), was one, but as many as 14 retreats were detected. Eels failing to pass did so after 1–3 visits to the dam. Failed passage attempts resulting in rejection of the forebay occurred after a median of 52 h (range: 105 min to 26 days) and were significantly longer than successful passage attempts which occurred after a median of only 41 min (range: 2 min to 4 days, Wilcoxon test, p = 0.003). Within the H1 powerhouse intake channel, successful passage attempts occurred after a median of 8 min (range: 1–81 min) while failed passage attempts required significantly longer (median = 37 min, range: 2 min to 6.4 days, Wilcoxon, $p < 0.001$).

Among the control group (20 eels released immediately below the Herting HEP), all but one eel (95%) successfully moved downstream and left the river. Among these successful outmigrants, 16 were detected by the lowermost ALS but all are assumed to have reached the sea (no detections in the river). Across study years, the control group required a median of 7 days (range: 31 min to 23 days) to reach the downstream ALS. The corresponding time from release to detection at the lowermost ALS for eels released just upstream the HEP in 2014 was 23 days (range: 34 min–47 days; n = 25), which was significantly longer (Wilcoxon test, p = 0.002) than for the downstream release group. Time from passage, on the other hand, hence looking at eels that can be assumed to be actively on their way downstream, was 36 min (median; range from 10 min to 23 days; n = 51) from passage to detection at the downstream ALS (passing the ALS, time from first to last detection, took them on average 10 min; range 1 min–3 days). There were no differences in migration speed below the dam with regards to which passage option (bypass vs. fishway) used by eels (Wilcoxon test, p = 0.41).

3.2. Time-to-event analysis

For eels that entered the forebay, movement patterns were most strongly associated with variation in discharge (relative) and diel period. Eels that rejected the forebay (Table 3i), departing in an upstream direction, did so at a rate 84% higher at night relative to during the day. This effect was not significant however. Among eels that progressed through the forebay, the best models for both passage via the fishway (Table 3ii) and approaching the H1 powerhouse intake channel (Table 3iii) were significantly affected by the amount of water discharging through the fishway relative to the total river discharge. According to these models, a 1% increase above the average relative discharge resulted in a 5% increase in passage rates via the fishway and a 2% decrease in passage rates into the intake channel. Passage rates via the fishway were also significantly affected by the diurnal period, such that eels were over 7-fold more likely to pass the HEP via the fishway at the night relative to the day (Table 3ii).

For eels that entered the H1 powerhouse intake channel, we found no models that explained the passage rates better than a null model, while the rate of retreat from the intake channel into the HEP forebay were reduced by 9% with each additional 1 m^3 s^{-1} increase in turbine discharge; a significant effect.

4. Discussion

By tagging and tracking mature European eels as they migrated down the river Ätran in southern Sweden, we assessed the efficiency of two fish passage solutions recently integrated into the Herting hydroelectric plant (HEP). The combination of a new bypass, paired with an angled rack, and a large nature-like fishway provided downstream migrating silver eels with a highly effective combination of passage solutions, with high impediment passage success and relatively short passage times. Route selection was associated with variation in discharge and the success we observed of the present fish passage solutions in accommodating the passage of silver eels mirrored previous observations at this facility for downstream migrating Atlantic salmon kelts and smolts (Nyqvist et al., 2017b; Nyqvist et al., 2018). The high levels of passage success observed for both silver eels and multiple life stages of Atlantic salmon makes the Herting HEP a good example of what can be achieved, in terms of fish passage solutions, when best practice recommendations are followed.

In a previous assessment of the Herting HEP, prior to the installation of the new FPSs, all eels passed through the racks and turbines and the impediment passage efficiency (η_{ip}) for silver eels migrating downstream was estimated at only 70% (Calles et al., 2012a). The present η_{ip} of 95% for both study years, with all eels passing the HEP via the bypass or fishway, represents an improvement to the impediment passage efficiency of 36% over the former baseline of 70%. Furthermore, with the control group (released below the HEP) also demonstrating a migratory success rate of 95%, the escapement to sea was equal for eels released upstream and downstream of the Herting HEP. Increases in passage efficiency such as this are necessary, particularly in systems where multiple power plants can have a cumulative effect on the overall survival of migratory species (MacGregor et al., 2014; Nyqvist et al., 2016). As most of the river systems occupied by European eel contain multiple power plants, silver eels are regularly subjected to the cumulative effects that multiple dam passages have on their survival (Marohn et al., 2013; Trancart et al., 2020). For this reason, increasing downstream passage success and survival, such as that observed at the Herting HEP, would likely have a significantly positive effect on silver eel escapement from regulated rivers. In the river Ätran's catchment, for example, eels are required to pass seven HEPs when migrating between their primary rearing areas and the sea. Consequently, cumulative survival would potentially increase from ~8% to 70% if all HEPs in this catchment were equipped with downstream passage solutions as efficient as evaluated here. Moreover, rivers with low eel abundance mainly produce large and highly fecund females, as is the case for the river Ätran (Calles et al., 2010) and most catchments in northern Europe, and increasing the escapement for such stocks should be of a particularly high conservational value for a critically endangered species like the European eel.

Table 3
Subset of models within 2 ΔAIC of the best fitting model and in excess of 2ΔAIC from the null model (good models) along with the covariate effects for the best (most parsimonious, in bold) model based on marginal Cox-proportional hazard models for event rates (passage, approach, rejection) for eels within zones upstream (forebay, intake channel) of the Herting hydropower facility.

Event	Good models				Best model			
	Mode parameters	AIC	$\Delta AIC_{null\ model}$	ΔAIC	Variable	HR	95% CI	*p*-value
(i) Forebay rejection	**night**	**687.5**	**−3.1**	**0**	Night	1.84	0.98–3.45	0.058
	night + temp	688.5	−2.2	0.9				
(ii) Fishway passage	**relative + night**	**178.5**	**−33.6**	**0**	Relative	1.05	1.03–1.07	<0.001
	relative + night + moon	179.1	−33.1	0.6	Night	7.36	1.89–28.7	0.004
	relative + night + temp	180.5	−31.7	2				
(iii) Intake approach	relative + night	487.7	−2.3	0	Relative	0.97	0.95–0.99	0.009
	relative	**487.9**	**−2.1**	**0.2**				
(iv) Bypass passage	No good model							
(v) Intake rejection	**H1**	**156.2**	**−7.8**	**0**	H1	0.91	0.88–0.95	<0.001
	H1 + temp	157.7	−6.3	1.5				
	H1 + moon	158.1	−5.9	1.9				
	H1 + night	158.1	−5.8	1.9				

Note: HR represents the hazard ratio or hazard function for the discrete or continuous variables respectively. A HR of 1 represents no effect on the baseline probability of an eel experiencing the event of interest. 95% confidence intervals were calculated using the robust variance estimates.

There are few published studies on the passage performance of downstream passage solutions for fish in general and silver eels in particular. Among the studies currently published, the 95% η_{ip} recorded in this study represents a uniquely high passage efficiency for eels and lends strong support for the use of angled racks with a marginal bypass. Alternatively, inclined racks with lateral bypasses can be employed, as those produced a similarly high η_{ip} of 90% at the Ätrafors HEP, some 20 km upstream of the Herting HEP (Calles et al., 2013). In fact, the inclined racks at the Ätrafors HEP actually exhibited a higher overall FPS efficiency (η_{fps} = 82%) than at Herting HEP's angled rack and bypass (η_{fps} = 69.2%), though this may be due to differences in the available alternative passage routes. At the Herting HEP, eels that rejected the bypass could still select the nature-like fishway, while at the Ätrafors HEP, the only available alternative was for eels to pass via a bottom fed spill gate. A more common level of impediment passage efficiency for a HEP employing an inclined rack and bypass system (η_{ip} = 63–87%) was recorded by Okland et al. (2019) at the Unkelmühle power station (intake capacity 27 m^3s^{-1}) on the River Sieg. As with the Herting and Ätrafors HEPs, several downstream passage routes were available at the Unkelmühle HEP, though the authors did not report the η_{fps} for the three inclined racks at the turbine intake, instead stating that it was in the range of 30%. In another study, Travade et al. (2010) reported a low η_{ip} of 59% for the Baigts HEP (intake capacity 102 m^3s^{-1}), where an angled rack and bypass system demonstrated an η_{fps} of only 17.4% for eels. In this case, eels were observed to preferentially pass the HEP via spill gates (n = 48) instead of the available bypasses (n = 17). On the Connecticut River, Brown et al. (2009) found that most silver eels passed the large-scale Cabot station (intake capacity 300 m^3s^{-1}) by passing through the racks and turbines, resulting in a low η_{fps} of only 9% for the bypass and an unknown, but likely low, η_{ip} because of the relatively high head of the Cabot HEP and the presence of Francis runners. The precise mechanisms behind the relative efficiencies between solutions may be of possibly system-specific biological and behavioral origin, which deserves attention in future work.

One of the few published evaluations of a downstream fish passage solution comparable in rack design to the Herting facility comes from a small hydroelectric plant (intake capacity 10 m^3s^{-1}) on the Franconian Saale River in Germany (Egg et al., 2017). In that study, downstream migrating eels encountered an angled rack with horizontal bars that guided eels towards a sluice gate. Along the base of this rack was a zig-zag bypass pipe which eels could enter via holes in the pipe, allowing them to travel directly to the HEP's tailwater. The authors reported that none of the silver eels they tracked entered the zig-zag bypass. Instead, eels passed via the upward opening sluice gate located 6 m downstream the end of the rack. Unfortunately, this evaluation was performed using a sonar so the individual eels could not be tracked and, hence, the η_{ip} could not be determined. Other evaluations of angled racks suffer from similar limitations, i.e. silver eels are observed being deflected by the rack and caught in the bypass, but at unknown efficiencies (Verreault and Therrien, 2005; Anonymous, 2010; Ebel, 2013). Still other studies evaluating silver eel downstream passage using conventional (steep) racks do not incorporate route selection and, hence, do not provide route-specific passage efficiency. η_{ip} reported in studies of steep racks with bypasses, however, tend to be considerably lower than those reported for inclined and angled racks with bypasses, e.g. 23% at the Tange HEP (intake capacity 36 m^3s^{-1}) on the River Gudenaa (Pedersen et al., 2011) and 56–64% at the Halsou HEP (intake capacity 30 m^3s^{-1}) on the River Nive (Gosset et al., 2005).

For fish passage solutions to perform well they must offer both efficient and timely passage for migrating fish. Though there was substantial variation among individuals, the median passage time for silver eels at the Herting HEP (from the first arrival in the forebay to passage) was only 1 h for eels encountering the dam after having recommenced their downstream migration (but 79 h for eels released in the proximity of the forebay). Similarly, successful passage attempts occurred after eels spent <1 h in the forebay (fishway passage) or the intake channel (bypass). This passage time is similar to the median passage time of 0.29 (2014) and 1.3 h (2015) recorded for eels passing the aforementioned Unkelmühle HEP on the River Sieg (Okland et al., 2019), but considerably lower than the 2.9 days median passage time recorded for eels encountering the inclined racks at the Ätrafors HEP (Calles et al., 2013). It is worth noting that the release sites both for the Ätrafors study and the current study (forebay released eels in 2014), were situated relatively close to the evaluated FPS and it was therefore uncertain if the observed passage times were a measure of delay, or an artifact of tagged eels not yet having recommenced their downstream migration. Nevertheless, there are few comparable evaluations of inclined and angled racks that report passage times for silver eels, so it is unclear how these observations fit the bigger picture. The observed passage time, for eels that had recommenced their downstream migration, was however very limited and so any long-term impact on the migration success of eels passing the Herting HEP seems unlikely.

The quantitative performance of passage facilities is typically described as total survival (here termed impediment passage efficiency, η_{ip}), fish guidance efficiency (overall FPS efficiency, η_{fps}) and passage time. The η_{ip} for the evaluated facility in this study was very high, 95% as all eels that successfully passed the dam also continued downstream, whereas the η_{fps} were comparably low for the nature-like fishway (η_{fps} = 46%) and moderate for the angled rack and bypass (η_{fps} = 69%). From a conservation point of view, however, the η_{fps} values for our two fish passage solutions are not directly relevant, as the two passage routes complement each other and most eels passed the HEP successfully. Even though the overall passage survival (i.e. η_{ip}) is the most important measure from a conservation and management point of view, η_{fps} of particular fish passage solutions is important for making comparisons across sites (i.e. transferability). Furthermore, η_{ip} can be the outcome of a combination of various η_{fps} for available passage routes, and includes the number and quality of available alternatives at a site. For instance, we would expect the η_{fps} for the angled rack and bypass at the Herting HEP to have been higher if the alternative route had been less attractive. Similarly, what η_{fps} should we expect if an angled rack and bypass were implemented at a site where no alternative passage routes were available? Nevertheless, we argue that the combined effects of the downstream fish passage solutions evaluated at the Herting HEP show great promise for providing safe and efficient passage for multiple species and life stages at any hydroelectric plant of similar size and with a defined intake channel. To date, full-depth mechanical screening solutions with bypasses have been successfully implemented at hydroelectric facilities with an intake capacity of less than 170 m^3 s^{-1}, and it is currently not known to what extent the technique can be upscaled to larger systems with more flow.

Water flow upstream of hydropower dams and the type of fish passage solution employed are considered the most important factors influencing fish behavior and passage performance (Silva et al., 2020). Although eels are often considered to move in relation to structures, they are also guided by the hydrodynamic environment (Piper et al., 2015). In our study, although we were not able to track the eels at high spatial resolution, nor map the flow fields upstream of the dam, we did observe a substantial influence of water flow on the fish behavior. Eels passed the HEP via the nature-like fishway at substantially higher rates when a greater proportion of the total discharge was released through this route, and, correspondingly, approached the turbine intake channel at a higher rate when a higher proportion of water was allocated to this route. This corroborates the common assumption that downstream migrants to a high extent follow the bulk flow of water (Coutant and Whitney, 2000), and is consistent with similar findings for European eel in other locations (Jansen et al., 2007; Travade et al., 2010). In addition, eels were less likely to retreat upstream from the intake channel, but not from the forebay, under higher discharges. Identifying the exact nature of the relationship between relative discharge and passage behavior is difficult, however, as collected data are from naturally varying circumstances. Future studies would therefore greatly benefit from experimental manipulation of the proportion of discharge passing through different potential swim routes (beneficial or detrimental for passage) to identify under what situations eels decide to commit to a passage option.

Promisingly, no eels were found impinged on the intake rack, and turbine discharge did not seem to influence bypass passage for fish present in the intake channel, indicating that the angled rack guided eels to the bypass at similar rates independent of discharge variations during the study period. Similar results were found for Atlantic salmon (smolts and kelts) at the same site (Nyqvist et al., 2017b, 2018). These results agree with the theory that sweeping flow velocity effectively guides even weak swimmers towards the bypass (Larinier and Travade, 2002). To fully understand the behavioral choices of eels and to improve our understanding of the effectiveness of downstream fish passage solutions like angled and inclined racks, we require detailed information on small-scale movements of eel, along with the hydrodynamic environment they inhabit. Future studies can address this knowledge gap using 3D-acoustic telemetry and state-of-the-art habitat mapping tools (Piper et al., 2015; Silva et al., 2020).

The evaluations performed at the Herting HEP have shown that the angled rack with a bypass in combination with a large nature-like fishway offered efficient and timely downstream passage for salmon smolt (Nyqvist et al., 2018), kelt (Nyqvist et al., 2017b) and silver eels (current study). There are very few examples of evaluations of downstream passage facilities for both salmonids and eels, in spite of the fact that the two species are highly prioritized for conservation in many countries.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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