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Downstream guidance performance of a bubble curtain and a net barrier for the European eel, *Anguilla anguilla*, in an experimental flume

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ABSTRACT

Populations of the European eel (*Anguilla anguilla)*, a critically endangered species, have been severely impacted by migration barriers, as losses due to turbine-induced mortality can be substantial. To prevent eels from entering turbines, effective guidance systems are needed to redirect downstream-migrating eels towards safer alternative passage routes. Although physical guidance screens may have very high guidance efficiencies, these generally come with high construction and maintenance costs and are difficult to scale up to large rivers. Behavioural guidance systems are typically less costly, but have often been ineffective. Hence, more work is needed to identify more effective behavioural solutions or physical barriers that are less costly to upscale. In this study, we assessed the performance of a physical net barrier (23 mm mesh size) and a behavioural bubble curtain guidance solution, for downstream-migrating eels and compared these with a guidance-free control at four different water velocities (0.1, 0.4, 0.7 and 1 m/s) in a large experimental flume using PIT-telemetry and video. The overall passage rate with the net barrier was 68 % higher than during the control treatment, whereas there was no significant difference between the bubble curtain and the control. We also found an effect of eel body size, where larger eels were less likely to enter the bypass than smaller eels. Velocity did not influence passage rate. Video data, in addition, revealed that b guidance along the barrier was greater, and passes through the barrier fewer, for the net barrier than for the bubble curtain and the control. The results suggest that net guidance solution for downstream guidance of eels should be explored further, whereas the bubble curtain does not appear appropriate for eel guidance.

1. Introduction

Diadromous fish have life cycles that involve migrating between freshwater and saltwater environments. These migratory journeys play a vital role in the reproduction, growth, and survival of the fish (Lucas and Baras, 2001). The obstruction of rivers by hydropower plants and their associated infrastructure disrupts natural migration routes, impeding the ability of migratory fish species (Wright et al., 2022) to reach their spawning grounds or access crucial feeding and nursery habitats (Jonsson et al., 1999; Lenders et al., 2016). As a consequence of the widespread lack of free-flowing rivers (Grill et al., 2019), diadromous fish populations have experienced sharp declines worldwide (Deinet et al., 2020) and with the changing climate these effects of river fragmentation will likely be heightened (Franklin et al., 2024). Various studies have documented severe declines in diadromous fish populations following dam construction (Chen et al., 2023; Duarte et al., 2021). These declines highlight the urgent need for conservation efforts and the implementation of effective strategies to mitigate the negative impacts of dams on diadromous fish species.

Among the most impacted species is the critically endangered catadromous European eel (*Anguilla anguilla*), which has experienced a $>$ 90 % decline in recruitment over the last 45 years (ICES, 2015).The

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European eel undertakes a long migration to the Sargasso Sea to spawn (Wright et al., 2022) and before undertaking their migration silvering of the body takes place, which represents a physiological adaptation to life at sea (Durif et al., 2005). Silver eels face many difficulties when passing downstream through hydroelectric facilities, as the risk of turbine-induced injuries and mortality is high for these long-bodied fish (Algera et al., 2020). In fact, turbine-induced mortality of adult eels may be 4–5 times higher than that of salmonid smolts (Larinier and Travade, 2002). The need for restoring longitudinal river connectivity and ensuring safe passage for eels is, therefore, pressing.

For fish in general, various solutions have been developed to restore river connectivity both in the upstream and downstream direction (Katopodis and Williams, 2011). For downstream passage, the main problem is that fish follow bulk flow (Coutant and Whitney, 2000), so they often need to be guided away from turbine intakes and towards bypasses (Calles et al., 2013b). Existing guidance devices can be grouped into three categories: physical, behavioural, and hybrid. Physical barriers do not allow fish to pass through, whereas behavioural devices rely on stimuli (sound, light, hydrodynamic, etc.) to guide the fish. Hybrid barriers combine more than one method, such as physical barriers with behavioural components (e.g., Louver screens) or barriers that combine various stimuli, such as the bioacoustics fish fence guidance system, referred to as BAFF, which combines sound with a curtain of air bubbles (Schwevers and Adam, 2020). Some hybrid guidance barriers have shown potential for successful downstream guidance of eels. For instance an electrified bar rack (e-HBR) with 51 mm bar spacing showed a fish protection efficiency of 86 % for European eel (Meister et al., 2021; Moldenhauer-Roth et al., 2022). Curved bar racks (CBR) with a bar spacing of 50 mm, on the other hand, have also been tested but have shown a low guidance effect on eels (Beck et al., 2020, 2022).

Conventional physical screens, angled sharply against the flow, have been successfully used to prevent migrating fish from entering water intakes (DWA, 2006). Conventional screens, however, are often not good solutions for eels, as eels easily get impinged on screens, resulting in injury or death (Calles et al., 2010). For the design of fish guidance screens, another important caveat is that eels are particularly good at pressing through narrow openings, aided by their mucous secretions (Knights, 1982), and therefore bar spacing may need to be smaller than typically recommended (e.g. 15–18 mm for screens in Sweden (Calles et al., 2013a) and up to 20 mm in most German federal states (Wagner, 2021)). Calles et al. (2013b) reported reduced eel mortality and increased guidance towards a collection facility on the Ätran River after reducing rack gap size, lowering the inclination angle of the rack, and adding bypasses. The practice of combining angled (angle to the vertical) or inclined (inclination to the horizontal) bar racks (10–20 mm bar spacing), oriented at 26°–45° angle with bypasses, has been reported to be effective for the downstream passage of eel (Calles et al., 2021; Kjærås et al., 2022; Økland et al., 2019; Tomanova et al., 2023). Upscaling existing guidance solutions to larger facilities, however, remains a challenge, due to high construction and maintenance costs, in addition to functional uncertainties (Emanuelsson et al., 2017). There is therefore a need for a different type of physical guidance system, one that can be easily upscaled.

Besides screens, the net barrier is another type of physical barrier that has guidance potential. Nets are used to prevent fish from entering water intakes and to guide them downstream (Guilfoos et al., 1995). Their efficiency depends on site-specific hydraulic conditions and the relationship between the size of the fish and net's mesh size (Fish Passage Technologies: Protection at Hydropower Facilities, 1995). A net made of Kevlar fibres (synthetic fibre of high tensile strength) with a mesh size 1 cm has been previously used in flumes as a guidance screen for experiments with smolts and roach, without the nets being the topic of the study (Bowes et al., 2021; Näslund et al., 2022). Furthermore Harbicht et al. (2022) reported that the guidance efficiency of 75 % for a net barrier with a mesh size 25.4 mm tested with salmonid smolts, but net screens have not been previously tested for eel guidance.

The functionality of fish passage guidance solutions usually depends on approach velocities. Behavioural guidance barriers are particularly limited by the approach velocity, which usually needs to be under 0.5 m/s for the fish to be able to respond to behavioural cues (DWA, 2006; Schwevers and Adam, 2020). Thus the use of behavioural barriers may not always be practical (Katopodis and Williams, 2011). Other stimuli that have been shown to affect the swimming behaviour of eels include acoustic (Pratt et al., 2021; Sand et al., 2000), light (Vowles and Kemp, 2021) and electric stimuli (Miller et al., 2021). One behavioural approach, which combines acoustic and visual stimuli, is the bubble curtain. It is produced by running compressed air through benthic pipes or hoses with multiple outlets, thereby creating a “curtain” of bubbles moving from the bottom to the surface (Noatch and Suski, 2012). Although hydropower companies have not yet applied stand-alone bubble curtains successfully (Schwevers and Adam, 2020; Taft, 2000), studies by Leander (Leander et al., 2021; Leander et al., 2024) found promising results for Atlantic salmon smolts in both laboratory settings and in river experiments. Meanwhile, information on the effect of bubble curtains on eel behaviour is limited, with only a couple of studies carried out (Adam, 1999; DWA, 2006).

In this study, we tested the guidance potential of a bubble curtain and a physical net barrier under four different velocity conditions using silver eels in a large indoor flume. We hypothesized that (1) at low velocities (0.1 m/s and 0.4 m/s), the guidance performance of the angled net barrier and bubble curtain would be similar for eels, but (2) at higher velocities (0.7 m/s and 1 m/s) the net barrier would have better guidance performance than the bubble curtain.

2. Materials and methods

2.1. Experimental fish

Adult silver European eel *Anguilla anguilla* (n = 180) were captured with fyke nets by a local fisherman in the south-eastern part of Lake Vänern, Sweden. Fish were caught on the 5th and 19th of October 2020 and immediately transported to the Vattenfall Research and Development Centre in Älvkarleby, Sweden. Only individuals showing morphological signs of ventral body silvering were used for the experiment, i.e., not individuals classified as “yellow eels”. This initial method of visual inspection has proven to be sufficient for identifying migratory individuals in previous eel passage studies (Calles et al., 2013b). Upon arrival, fish were placed in one of three stainless-steel circular tanks (3.5 m^3 each), where they remained until the experiments were initiated. Each tank was equipped with a bead filter (Nilefisk ATTIX 961–01), a UV filter (Aquaflex 1 AF4), a chiller (Charles Austen pump Limited HC-22000BH), an opaque plastic container to be used as a shelter for the fish, and aeration using three large air stones. The tanks were filled with filtered water from the Dalälven River (pH = 6.4, KH < 3, NO_2 = 0, NO_3 = 0), and the mean water temperature was 13.5 ± 4.9 °C. The water quality was checked daily with aquarium strips and with a water probe (ProDSS Multiinstrument, ProDSS- Conductivity and Temperature Sensor, ProDSS- Optical DO-Sensor). Partial water changes were regularly carried out to maintain water quality. The fish were not fed as they normally do not feed during the migration period (Aarestrup et al., 2009; Bruijs and Durif, 2009). One day after their transportation the fish were sedated with benzocaine (0.017 g · L^{-1}, 0.28 M), measured and weighed. Pectoral fin length (L_{PF}) was recorded (mean L_{PF} = 40.5 mm ± 4 SD), which was then used together with the total length of the fish to calculate the fin index (I_F) (mean I_F = 4.7 ± 0.4 SD), with the formula: $I_F = 100\, L_{PF}\, L_T^{\,-1}$, which was used to further confirm the “silvering” of the eels (Durif et al., 2005). The eels were tagged with 32 mm passive integrated transporter (PIT) tags (Oregon RFID, Portland, USA). A scalpel incision was made on the ventral surface about 1 cm to the left of the fish's mid-line and 2–3 cm anterior of the anal opening. The tags were then inserted through the small incision into the body cavity and no suturing was needed. All eels survived the surgery and had a minimum of one week of recovery before being used in the experiment.

2.2. Experimental facility and design

The experiment was conducted at the Vattenfall Research and Development Centre in Älvkarleby, Sweden in an oval-shaped, re-circulating flume ("Laxelerator", Fig. 1). The flume consists of two 24 m long, 4 m wide, and 2 m deep test sections, which were used as test arenas for three different guidance barrier treatments: (1) a net, (2) a bubble curtain, or (3) no guidance barrier at all (control). The guidance barriers (net/bubble) were placed at an angle of 30° from the wall of the experiment arena, dividing the arena into an upstream and a downstream part (Fig. 1). The barrier extended from the flume wall to a ramp (referred to as the bypass), terminating at a 0.6 m wide and 0.5 m high escape opening (corresponding to the bypass opening of a real fish passage solution), which emptied into a collection box. The bypass was designed as an upward-sloping ramp to mimic dewatering of the bypass flow similar to what is done in a normal hydropower plant. The net barrier was made of Kevlar netting (Ø = 2 mm; stretched-mesh size = 23 mm, Dyneema™, Pacific Netting Company, USA), attached to a removable 6.8 m long and 2 m high steel frame. The air bubble curtain barrier was produced by pumping air from a compressor into a steel pipe (with a square-shaped profile) placed on the bottom of the flume. The pipe was 6.8 m long and had 0.5 mm openings (diameter) placed every 10 cm. Fish were introduced into the flume via a start box. To detect when fish left the start box and successfully passed the bypass we placed one PIT-tag reader (Oregon RFID, USA) at the opening of the start box and one at the end of the bypass (Fig. 1).

To verify the PIT-tag readings and to analyse fish behaviour we placed eight network cameras (Hikvision, models: ds-2cd4b26fwd-izs, ds-2cd2t47g1-l, and ds-2cd5546g0-izhs) and one underwater camera (Hikvision, model ds-2xc6224g0-l) in each experimental arena. The cameras were placed outside the flume, except for the underwater one, which was situated downstream, of the guidance barrier. All cameras were set to night mode and had their IR light turned off. The cameras filmed (1) the Start Box from above (SB angle); (2) the end of the bypass ramp, where a PIT-tag reader was placed before the Bypass Exit/collection box entrance (BE angle); (3) Downstream along the Ramp in the direction of the bypass exit (DR angle); (4) Upstream view along the Barrier (UB angle); (5) the Top part of the barrier and ramp Intersect (TI angle); (6) the Bottom part of the barrier and ramp Intersect (BI angle); (7) MiDdle side of the flume looking along the Barrier on the upstream side (MDB angle); (8) Under Water camera on the downstream side of the barrier, facing Upstream (UWU); (9) the downstream part of the barrier, at the middle of flume, facing upstream (MU angle) (Fig. 1).

2.3. Experimental procedures

Downstream migration was tested using groups of 5 fish subjected to the three different guidance treatments (net barrier, air bubble curtain, or no barrier control), and four different velocity treatments (0.1, 0.4, 0.7, or 1 m$\cdot$ s^{-1}), resulting in a 3 × 4 full factorial design. All treatments were replicated three times, resulting in a total of 36 trials. Trials were conducted every night between 21 October and 1 November 2020. A nocturnal schedule was implemented as this is when European eels migrate (Bruijs and Durif, 2009). Three trials were performed each night, between 18:00 h and 05:00 h, with a 1-h break between trials to remove the fish from the flume and prepare for the next trial. The facility was illuminated by a dim light (2–5 lx at the surface). A group of 4 or 5 fish was transferred to the start box and left to acclimatize for 10 min and thereafter the start box was opened, and the trial started. The first 5 (or on a few occasions 4) fish that were caught from one of the holding tanks were the ones used. This haphazard way of selecting individuals was done to minimise stress. Our aim was to have 5 fish per trial; however, 3 eels lost their PIT tag prior to the test, and 7 eels chose not to leave the start box (hence were excluded from the experiment) which resulted in seven of the 36 trials (19.4 %) consisting of three or four participating eels. At the start of a trial, the start box was opened and the fish left the box on their own volition. The experiments lasted three hours, after which the flow and the cameras were switched off, and the video and PIT-reader data were downloaded onto hard drives. Only eels that left the start box were considered to participate in the trial. In total, 170 eels participated in the experiment (mean weight = 1278 g ± 354 SD, mean total length (L_T) = 858 mm ± 70 SD). After the trial, fish were

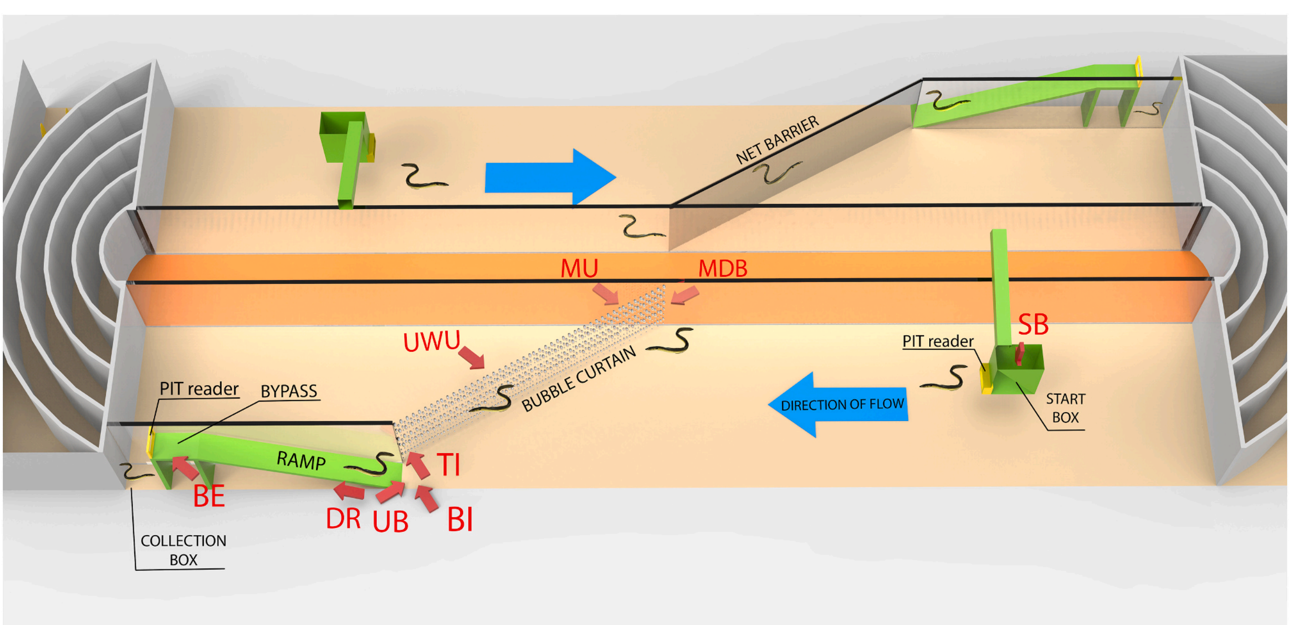

Fig. 1. Experimental setup in the flume showing a 30° angled barrier (bubble curtain or net), which was tested at velocities of 0.1, 0.4, 0.7, and 1 m/s for the downstream guidance of silver eels, *Anguilla anguilla*. A no-barrier control was also tested. The red arrows indicate the placement of the 9 camera angles. The set up was the same in both sleeves of the flume, including the camera angles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

removed from the flume and released into Dalälven River.

2.4. Data analysis and statistics

2.4.1. Guidance efficiency and passage time

We analysed guidance and passage variables as well as fish behaviour. A successful passage event was defined as detection by the PIT-antenna in the bypass. Guidance efficiency was determined by the number of eels that passed through the bypass, divided by the number of eels that left the start box and therefore participated in the trial. Although the control treatment had no guidance screen present and therefore the fish could not be guided to the bypass (they found it by chance) we still use the term guidance efficiency for comparison between treatments.

$$\%\text{Guidance efficiency} = 100\ (\text{N eels collection box}/\text{N eels in trial})$$

Passage time was calculated as the time difference from when an eel left the start box until it was detected by the collection box PIT tag reader. Because passing through the guidance screen did not prevent eels from later entering the bypass ramp in our experiment, we assumed that all eels could eventually enter a bypass given enough time. Eels that did not pass i.e., did not enter the collection box, after having left the start box, were given the maximum time: that was 180 min.

$$\text{Passage time} = \text{Time initial detection at collection box} - \text{Time last detection at start box.}$$

2.4.2. Passage rate

Cox regression, a type of time-to-event analysis, was used to model the effects of barrier type (bubble curtain, net, or control) and mean water velocity on the passage rate of eels. Time-to-event analysis is appropriate for fish passage data as it takes into account both the proportion of fish passing (guidance efficiency) and the time it takes for them to pass (passage time), and allows fish to be available for passage for different periods of time (Bravo-Córdoba et al., 2021; Harbicht et al., 2022; Motyka et al., 2024; Nyqvist et al., 2017a, 2017b, 2024). In the time-to-event context, passage rate refers to the probability of passage over time (Castro-Santos and Haro, 2003; Castro-Santos and Perry, 2012; Hosmer et al., 2008). We defined fish as available to pass from the point at which they left the start box. Passage time was defined by the time from leaving the start box until entering the collection box, based on PIT detections. Fish not passing were censored at the end of the experiment. We included all combinations of barrier type (control, bubbles, and net), velocity (0.1, 0.4, 0.7, and 1.0 m/s), their interaction, as well as fish length, among the candidate models. All models were clustered on trial, to account for the non-independence of observations from the same trial. To select the best model among candidate models, minimization of the Akaike information criterion (AIC) value was used. Models with an AIC value of 2 or less from the null model and within 2 AIC units from the best model were considered good models (Burnham and Anderson, 2004). If more than one competing model fulfilled these criteria, all were presented and used to describe the effects of covariates. For all good models, the assumption of proportionality of hazard was explicitly tested (Fox, 2002). The analysis was performed in R Statistical Software (v4.4.2; R Core Team, 2024), with packages survival (Therneau and Lumley, 2017) and mass (Ripley et al., 2013), and plotted with ggplot (Wickham, 2016) and survminer (Kassambara et al., 2017).

2.4.3. Behavioural data

Fish behaviour in relation to the barriers was obtained from the video material. We analysed three different behaviours related to guidance: (1) swimming along the barrier towards the bypass, (2) fish U-turn/ repellence by the barrier, (3) downstream passes through the barrier. These behaviours were obtained from five of the cameras MDB, UWU, DR, and TI + BI (analysed as one frame) (Fig. 1). We analysed the videos using VLC Media Player (VideoLan, 2020), with the playback speed increased 3–8 times. As individual eels could not be identified in the videos, each observation of an eel in a frame was treated as a unique record. As soon as an eel was seen in a frame, the video was paused, the action was played at normal speed (x1) and the time code was logged together with observed behaviours. The analyses of the videos resulted in count data, and the behavioural count data were statistically analysed in SPSS (IBM SPSS Statistics 27). Two-way ANOVA (barrier type and water velocity) in the General Linear Model (GLM) package was used to analyse the mean number of behavioural observations, which was the total number divided by the number of eels participating in the trial, to account for trials that had a different number of participating eels.

3. Results

3.1. Guidance efficiency and passage time

The mean guidance efficiency for the bubble curtain ranged from 20 % (at 0.4 m/s) to 47 % (at 0.1 m/s), for the control it ranged from 33 % (at 0.4 and 1 m/s) to 47 % (at 0.7 m/s) and for the net barrier- from 31 % to 73 % (at 0.7 m/s) (Table 1).

Passage time was also calculated and varied in trials from 2 min (net barrier, velocity 0.1 m/s) to 178 min (bubble curtain, velocity 1.0 m/s). Mean passage time over all velocities did not vary as much. It was 118 to 153 min, 137 to 151 min, and 109 to 147 min for the bubble curtain, barrier-free control, and net barrier respectively (Table 1).

3.2. Passage rate

The net barrier guided fish to the bypass at a 68 % higher rate than the control, while there was no difference in passage rate between the control and bubble treatments (Fig. 2). In addition, longer fish passed through the bypass at a lower rate than shorter fish (Table 2). No effect of velocity on the passage rate was found.

3.3. Behavioural data

Analyses of video data revealed significant effects of barrier, velocity and their interaction on the behaviour ‘swimming along the barrier’ (Two-way ANOVA, GLM Univariate, Table 3). The significant interaction was due to that bubble curtain and especially the net barrier showed a lower guidance behaviour at higher velocities, whereas the control did not (Fig. 3, a). Regardless of velocity, guidance towards the bypass was much higher for the net barrier than for the other two treatments (Fig. 3, a).

For the number of downstream passes, there were significant effects of barrier and the interaction (Table 3). The interaction was due to differences between the bubble curtain and the control. For the bubble curtain, more eels passed through the bubble curtain at the lowest velocity of 0.1 m/s and then decreased with the number of downstream passes being more or less constant for the other three velocities. In contrast, the number of downstream passes increased from 0.1 to 0.4 m/s to then decrease at the higher velocities for the control (Two-way ANOVA, GLM Univariate, Table 3). Regardless of velocity, the number of downstream passes was much lower for the net barrier than for the other two treatments (Fig. 3, b). Eels were repelled by the net barrier and did a U-turn significantly more often with the net in place compared to the no barrier control, while there was no significant difference between the bubble curtain and control (Fig. 3, c). This behaviour was not significantly influenced by velocity, nor was there a significant barrier x velocity interaction (Two-way ANOVA, GLM Univariate, Table 3).

For the number of U-turns at the barrier, there was a significant effect of barrier (Table 3). Eels were repelled by the net barrier and made significantly more U-turns with the net in place compared to the no barrier control, while there was no significant difference between the bubble curtain and control (Fig. 3, c). This behaviour was not significantly influenced by velocity, nor was there a significant barrier x

Table 1
Mean (±SE) guidance efficiency (expressed as a percentage) and mean passage time (in minutes) of the bubble curtain, net barrier and no barrier control at water velocities of 0.1 m/s, 0.4 m/s, 0.7 m/s, 1 m/s for downstream migrating silver eels, *Anguilla anguilla*. All treatments were replicated three times.

Velocity (m/s)	Bubble curtain		Control		Net barrier	
	Guidance % mean ± SE	Passage time (min) mean ± SE	Guidance % mean ± SE	Passage time (min) mean ± SE	Guidance % mean ± SE	Passage time (min) mean ± SE
0.1	47 ± 7	118 ± 18	35 ± 13	151 ± 20	47 ± 18	109 ± 24
0.4	20 ± 20	153 ± 27	33 ± 7	149 ± 6	53 ± 13	131 ± 8
0.7	27 ± 27	151 ± 29	47 ± 4	151 ± 9	73 ± 13	113 ± 22
1	38 ± 2	139 ± 13	33 ± 18	137 ± 26	31 ± 17	147 ± 18

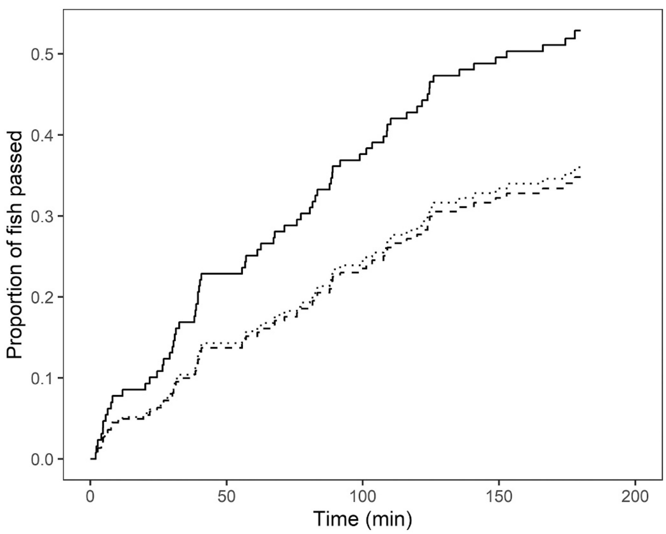

Fig. 2. Cumulative events plot showing passage rates as the estimated proportion of silver eels that found the bypass and entered the collection box for the net barrier (solid line), bubble curtain (dashed line) and control (dotted line) treatments over time (represented in minutes).

velocity interaction (Two-way ANOVA, GLM Univariate, Table 3). The number of eel observations recorded by the underwater camera on the downstream side of the arena (behind the guidance barrier) was almost 67 % higher with the bubble curtain ($n = 232$ observations) compared to the no barrier control ($n = 139$ observations) and over 8 times higher than the number of observations for the net barrier ($n = 28$ observations).

Table 2
a) Subset of Cox-regression models within 2 ΔAIC of the best model, and in excess of 2ΔAIC from the null model (good models) along with the covariate effects (hazard ratios) for the best model; b) Barrier-type (control, bubbles and net), velocity, their interaction, and fish length were included among the candidate models. For the barriers, the control constitutes the baseline covariate.

a)

AIC-table	AIC Covariates	AIC with Covariates	ΔAIC (null)	ΔAIC (min)
Barrier + Fish Length	683.89	678.62	−5.27	0
Fish Length	683.89	679.39	−4.50	*0.77*

b)

Best model Variable	HR	95 % CI	*p*-value
Barrier - Bubbles	0.96	0.50–1.85	0.90
Barrier - Net	1.68	1.03–2.76	**0.04**
Fish Length	0.96	0.93–1	**0.03**

4. Discussion

The guidance performances of the physical net barrier (mesh size 23 mm) and behavioural bubble curtain were assessed by quantifying passage rate, fish guidance efficiency, passage times and behaviour in a large flume for downstream migrating adult silver eels. We hypothesized that the guidance performance would be similar between the behavioural bubble curtain and the physical net barrier at velocities under 0.5 m/s, but at higher velocities the net barrier would function better. Our results for guidance performance did not support our hypothesis, although the fish guidance efficiency was the same at the lowest velocity of 0.1 m/s (consistent with reports of exploratory behaviour at low velocity gradients (Piper et al., 2015)) than the one for the net barrier. Nevertheless, at the next velocity 0.4 m/s, the mean fish guidance efficiency for bubble curtain was already lower (as expected with behavioural barriers at velocities over 0.3 m/s (DWA, 2006)). Overall, the net barrier performed the best and its function did not depend on velocity. The function of the bubble barrier was not better than the barrier-free control.

Passage rate is a useful way to assess fish passage solutions as it includes both time and guidance efficiency (Castro-Santos and Haro, 2003; Harbicht et al., 2022). We found that physical net barrier had a significantly higher passage rate than the behavioural bubble curtain and the control, with the latter two not differing from each other. The significant effect of barrier type on passage rate is further supported by two of the observed behaviours: guidance along the barrier towards the bypass and downstream barrier passes. These behaviours showed that the net barrier guided the eels well, with very few downstream passes through the barrier. Our video data also showed that the bubble curtain did not perform well, as there was no significant difference in guidance rate and eel behaviour when comparing the bubble barrier and the control. There were, nevertheless, some discrepancies between the video and telemetry data. For example, the guidance efficiency of the net

Table 3
Summary of two-way ANOVA, GLM Univariate, of the behavioural data for silver eels in relation to barrier type, velocity, and barrier x velocity.

Observed behaviour	Barrier type	Velocity	Barrier x Velocity	General pattern
Swimming along barrier to bypass	$p < 0.001$	$p = 0.003$	$p = 0.010$	Net > Bubble = Control
	$F_{2,24} = 72.68$	$F_{3,24} = 6.00$	$F_{6,24} = 3.70$	
Downstream passes	$P < 0.001$	$p = 0.38$	$p = 0.048$	Net > Bubble > Control
	$F_{2,24} = 41.79$	$F_{3,24} = 1.08$	$F_{6,24} = 2.54$	
U-turn/Repelled by barrier	$p = 0.005$	$p = 0.89$	$p = 0.10$	Net > Bubble = Control
	$F_{2,24} = 6.75$	$F_{3,24} = 0.21$	$F_{6,24} = 2.54$	

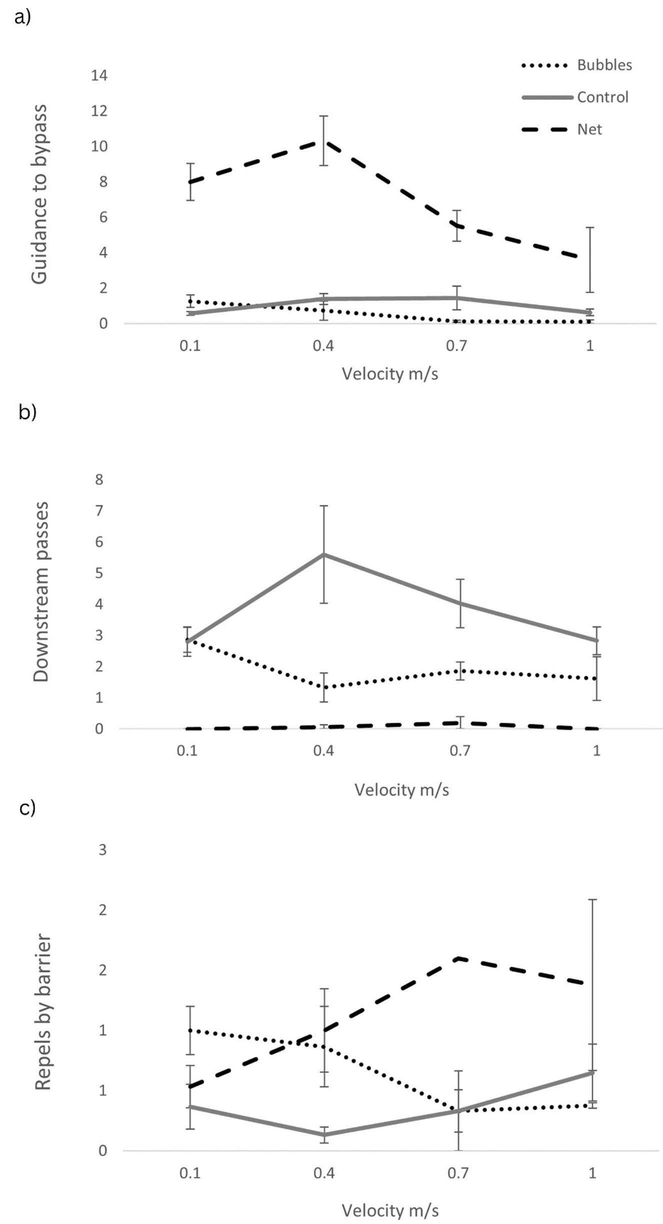

Fig. 3. Eel behaviour in relation to barrier type (bubble curtain, no barrier control and net barrier) and velocity (0.1, 0.4, 0.7 and 1.0 m/s): a) Mean number of swimming behaviours along barrier in direction towards bypass (termed as 'Guidance to bypass'on y axis); b) Mean number of observed downstream passes through the barrier.; c) Mean number of observed U-turns at barrier.

barrier was highest at 0.7 m/s, whereas the number of observed guidance behaviours along the barrier was higher at lower velocities. It is important to bear in mind that guidance efficiency simply measures how many fish made it to the bypass. It does not describe how the eels did this, nor their behaviour at different velocities. Moreover, for the behavioural data we could not follow individual fish, so some of the observations have likely been done on the same individuals on multiple occasions, which may bias our estimates of the different behaviours.

The passage rate for the physical net barrier was higher than for the behavioural bubble barrier. This likely reflects the physical properties of the net, including the net's mesh size, which hindered eels from passing through. Despite the net performing significantly better than the bubble curtain and the control, the overall guidance efficiency of 51 % was much lower than the 75 % guidance efficiency observed by Harbicht et al. (2022). This is likely due to the different species that were studied (salmonids vs eels) and their reaction to both the net and the experimental set up. The bypass ramp was the same in both these studies, made of metal and reflecting light from the ceiling, however, the salmon smolts and eel respond very differently to light, i.e., smolts are attracted to light while eels avoid it (Noatch and Suski, 2012; Stoilova, 2024). In addition, it is possible that the eels avoided the bypass ramp more than the smolts, but since we could not distinguish between guidance barrier efficiency and bypass efficiency (due to the location of the PIT tag reader), we can only speculate about this.

Furthermore Harbicht et al. (2022) found that the net barrier performed poorer than fish protection metal screens and theorised that this is due to the lower hydrodynamic disturbance caused by the net. The net is thinner than the screens, causing a lower sweeping velocity vector (current that runs along the screen and contributes to guidance (Albayrak et al., 2020)) compared to conventional screens. On the other hand, since eels often do not respond to an obstacle until they collide with it (Russon et al., 2010; Schwevers and Adam, 2020), a net guidance may be a better alternative to hard barriers for eels, if combined with some sort of jet along the net barrier. In addition, a physical structure such as a net, which is made of soft but durable material, should, in theory, cause fewer injuries upon impact. We did not observe impingement of the eels at water velocities up to 1 m/s when analysing videos for barrier-related behaviours, but further testing is needed at higher velocities to evaluate the risk for injury and impingement. Nevertheless, the risk of damage to the net from large debris is expected to be high, and, therefore placement of a standard trash rack upstream of the net may be a viable way of reducing this risk.

Interest in behavioural barriers has been high as the costs for building and maintaining these is typically lower than for physical barriers. Many behavioural barriers have, however, functioned poorly in guiding fish when put into practice (Schwevers and Adam, 2020). The low guidance efficiency of the bubble barrier reported here is consistent with the outcomes of the few existing studies on bubble curtain efficiency for the guidance of eels (Adam, 1999; Bakker and Gerritsen, 1992; Sonny and Beguin, 2020). Further indication that the bubble curtain did not deter and guide the fish towards the bypass, but maybe even attracted them to cross through it is seen in the higher number of eel sightings downstream of the bubble curtain compared to the same area in the barrier-free control. This result is also consistent with a field study conducted in the Vechte River (Netherlands), where 9 % more eels were found in the area behind the bubble curtain when it was on versus when it was switched off (Bakker and Gerritsen, 1992, cited by DWA, 2006).

Theoretically, a bubble curtain should guide the fish using visual in addition to acoustic and tactical cues. As mentioned above,- light is known to be a strong deterrent for eels (Hadderingh et al., 1992; Hadderingh et al., 1999; Velde, 1999). One possible explanation for the poor performance of our bubble curtain may have been the lack of illumination of the bubbles to allow the fish to detect them from a distance. We ran our trials at low light levels to mimic night conditions during downstream migration. Also, we used river water in the flume, which was dark in coloration due to humic substances, and thus may have also affected the eels' ability to discern the bubbles. It has been noted previously that bubble curtains can be difficult to detect by fish at night and in turbid waters (McIninch and Hocutt, 1987; Noatch and Suski, 2012). Another challenge with bubble barriers is that at high flows, the integrity of the curtain may be reduced, resulting in gaps forming in the curtain (Noatch and Suski, 2012), which is something that also occurred in our study at the highest velocity. Potentially, the bubble curtain may serve as a useful hybrid barrier component if combined with light and sound, which have individually shown some good results for the deterrence of eels: e.g., 65 % deflection rate with light reported by Hadderingh et al. (1999) and an increase of 144 % (compared to the control) with sound in a field study by Sand et al. (2000). The Bio Acoustic Fish Fence (BAFF), which combines a bubble curtain with sound and light cues, has also shown to be effective for repelling and guiding out-migrating juvenile salmonids and for limiting the dispersal of invasive carp species (Cupp et al., 2021; Perry et al., 2014; Welton et al., 2002), but to our knowledge it has not been tested with eels and the achieved results are not directly comparable for other fish species.

Velocity did not influence the passage rate in our study. We did see the same guidance efficiency between the bubble curtain and net at the lowest velocity of 0.1 m/s, (although again low: 47 % for both), which might indicate that when eels have a low approach velocity, they notice the bubble curtain in front of them and end up swimming into the bypass just as often as with the physical net barrier. The overall mean guidance efficiency did not, however, differ between velocities, nor did the mean passage time in our telemetry results. On the other hand, we did see an effect of the interaction of barrier type and velocity for two of our behavioural observations: guidance along barrier towards the bypass and passes through the barrier. Hence, guidance barriers should not be tested without the consideration of their performance under different velocities.

We found that eel body length affected the likelihood that an eel would enter the bypass, with smaller eels being more likely to enter than larger ones. Since large eels have a greater swimming ability than small eels (Clevestam et al., 2011), large eels should have a greater capacity to alter their movement in response to different flow conditions, and perhaps this has affected the size-dependent difference we observed. Nevertheless, our results differ from previous size-dependent differences in behaviour observed at fish passage facilities (Travade et al., 2010). For example, Motyka et al. (2024) found that large eels were more likely to find a bypass than small eels when guided by an angled rack. Similarly, Jens (1987) showed that large eels used a bypass more than small ones, possibly because smaller individuals (45–50 cm) were able to pass through the racks (DWA, 2006). These effects of size on passage probability may thus be context-specific and require further study.

Lastly, some important caveats regarding the study. Even if the number of tested eels was relatively high, the overall sample size per treatment was fairly low and each treatment was only replicated in 3 trials. In particular, guidance efficiency measurements, based on trial means, risk being sensitive to low sample size. The passage rate analysis, in contrast, uses the individual fish as a replicate while controlling for group effects, and hence increases the effective sample size (Nyqvist et al., 2024). All in all, even if higher sample sizes would increase the precision of the result, the overall result is likely to stand. In addition, even if experimental behavioural studies are of high value when testing fish passage theory, it is also important to remember that behaviour in forced swimming experiments does not automatically translates to field conditions. In relation to fish swimming performance estimates, for example, fish actively choosing to swim often outperform fish forced to swim (Castro-Santos et al., 2013; Peake, 2008).

5. Conclusion

Currently, eels are among the species of fish most impacted by hydropower (Ben Ammar et al., 2021), and successful alternatives to physical fish guidance screens, are not currently available. As physical guidance screens are difficult to upscale, there is a need for alternatives such as behavioural guidance. Based on our study, however, we can conclude that the behavioural bubble curtain was ineffective for the guidance of downstream migrating eels. Although the physical net barrier had a better guidance performance for eels when compared to the bubble curtain, it was still not good enough to motivate in situ tests in rivers at this point in time, especially when considering potential problems with cleaning them as well. Ultimately, the success of any guidance barrier depends not only on passage success, but also on maintenance costs and limitations.

Ethical note

The study was carried out under ethical permit license 001671, dnr 5.8.18–03390/2019 issued by the Ethical Committee for Animal Research in Gothenburg. The eels were part of a trap and transport program, and we obtained a permit to use the animals for behavioural studies (permit dnr 2649–20, issued by the Swedish Agency for Marine and Water Management), before releasing them in the River Dalälven (permit dnr 6917–2020, issued by the county council Gävleborg).

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CRediT authorship contribution statement

Velizara Stoilova: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eva Bergman:** Writing – review & editing, Validation, Project administration, Methodology, Funding acquisition, Conceptualization. **David Aldvén:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Rachel E. Bowes:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Olle Calles:** Writing – review & editing, Methodology, Conceptualization. **Nils Nyquist:** Writing – review & editing, Investigation. **Daniel Nyqvist:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Piotr Rowinski:** Writing – review & editing, Investigation, Data curation. **Larry Greenberg:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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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Data availability

Data will be made available on request.

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