

# Bubble barriers to guide downstream migrating Atlantic salmon (*Salmo salar*): An evaluation using acoustic telemetry

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## ABSTRACT

Structures for guiding fish around migration barriers are frequently used for maintaining connectivity in regulated riverine systems. However, for non-physical barriers, experimental studies providing direct and detailed observations of fish–barrier interactions in rivers are largely lacking. In this study, we quantify the efficiency of bubble barriers (alone or in combination with light stimuli, and in both daylight and darkness) for diverting downstream migrating Atlantic salmon (*Salmo salar*). Both a laboratory-based migration experiment and a large-scale field experiment in a regulated river were used to evaluate efficiency of bubble barriers. In the latter, we used acoustic telemetry to provide in situ measurements of how downstream migrating Atlantic salmon smolts interact with bubble barriers. We show that bubbles divert smolts with high efficiency in both a laboratory flume (95%) and in natural settings (90%). This latter efficiency is higher compared to an already present physical barrier (46%) covering the upper two meters of the water column in the large river. The bubble barrier did not affect flume migration in darkness, suggesting that visual cues are crucial for the observed repelling effect of bubbles. We conclude that bubble barriers can be effective, largely maintenance free and low-cost alternatives to physical structures currently used to divert salmon away from high-mortality passages.

## 1. Introduction

Over half of the world's large river systems are regulated by dams (Nilsson et al., 2005). One often crucial measure to maintain connectivity in these regulated rivers is to divert migrating fish away from passages associated with high mortality (e.g. hydropower turbines). These preferred migratory pathways are generally referred to as fishways and are designed in a multitude of ways; from semi-natural creeks functioning as both migration routes and habitats for rheophilic fish species (Gustafsson et al., 2013; Pander et al., 2013), to technical fishways focusing solely on allowing strong migrants to pass an obstacle (Williams et al., 2012).

The Atlantic salmon (*Salmo salar*)—a species with iconic status and high socioeconomic value—can migrate to spawn several times during its lifetime, and thus relies strongly on high riverine connectivity both at juvenile (smolt) and adult life stages. Atlantic salmon is a common target species when designing fishways (Clay, 1995). Despite this, present fishways seldom meet intended objectives to provide satisfactory connectivity even for such a species (Brown et al., 2013). Here, a key challenge is to guide salmon away from the main current, that the

salmon typically follows, and towards often small fishways with much weaker currents (Northcote, 1998). A common method to guide salmon towards fishways during downstream migration is by using physical structures, e.g. racks or guide walls. The initial installation costs for these structures are high and they will, aside from guiding salmon, also accumulate debris brought by currents, which leads to a high maintenance demand for keeping physical guiding structures functional (Clay, 1995; Noatch and Suski, 2012). In addition, it is challenging to cover the full water column depth with physical guiding structures in larger rivers, due to high hydraulic pressure. Therefore, guiding structures are often constrained to shallower river stretches or placed in specific parts of the river known to be used by the focal species. For example, Atlantic salmon smolts are known to primarily use the surface layers during downstream migration (Thorstad et al., 2012) and physical barriers covering only the upper meters of the water column are often used to overcome the hydraulic forces encountered in rivers (Calles et al., 2013; Scruton et al., 2003). The drawback of this approach, besides the large work effort needed to remove accumulated debris, is the inability of this structure to steer deeper migrants, which also a migration mode that Atlantic salmon smolts can adopt (Davidsen et al., 2005; Hvidsten and

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Johnsen, 1997; Svendsen et al., 2007).

Earlier studies have highlighted that bubble barriers may be used to prevent fish from entering undesired areas (Flammang et al., 2014; Welton et al., 2002; Zielinski and Sorensen, 2016). However, the underlying mechanism for the diverting role of bubbles is uncertain (Solomon, 1992), and both visual (Welton et al., 2002) and auditory (Popper and Carlson, 1998; Zielinski et al., 2014) cues have been put forward as the cause of the response. If functional, artificial bubble structures are highly attractive as they avoid the issue with floating debris and, thus, generate low maintenance costs. Despite this, the efficiency of bubble barriers has mostly been quantified in laboratory settings, not in large-scale natural systems, where their function is most relevant (Dawson et al., 2006; Miehl et al., 2017; Patrick et al., 1985; Zielinski et al., 2014). Studies that have been conducted in full scale have used indirect approaches based on downstream fish detections (Welton et al., 2002; Zielinski and Sorensen, 2015) and catches further up- or downstream from the barrier (Ruebush, 2011), but see Perry et al. (2014) for studies on Chinook salmon (*Oncorhynchus tshawytscha*).

The endpoint of fish guiding structures is to keep fish away from areas associated with high mortality risk, and any means to increase risk aversion will de facto have positive effects on population numbers. For an anadromous species that rely on sea-to-river connectivity to complete their life cycle, Atlantic salmon has since the development of hydropower suffered a global decrease in population numbers (Limburg and Waldman, 2009; Parrish et al., 1998). Due to the socioeconomic status of salmon there are high potential gains associated with higher population numbers, both recreational (Arlinghaus and Cooke, 2009; Ignatius and Haapasaaari, 2018) and economic values (Kulmala et al., 2008) have been quantified in studies showing the benefits of Atlantic salmon to the society.

Our aim with this study was to quantify the ability of bubble barriers to guide downstream migrating Atlantic salmon smolts over large distances in rivers. We hypothesized that bubble barriers alone, or in combination with light stimuli, diverts downstream migrating Atlantic salmon smolt.

## 2. Material and methods

The study was conducted in two parts; first in a laboratory setting and later in a large river where migrating Atlantic salmon needs guidance away from potentially lethal passages through the turbines of a hydropower plant. In both parts, the fish were released upstream of a

barrier and were then faced with a binomial option; 1) to pass through the barrier or 2) to avoid it (i.e. being guided by it) and thus steer to the bubble-free side. Underwater footages from flume and river experiments are shown in Fig. 1.

### 2.1. Flume experiment

To test our hypotheses, we conducted a laboratory study from the 19th of April to the 28th of April in 2017. This period was selected to overlap with the salmon smolt stage and thus, being most appropriate for migration studies. We tested the guiding effect of barriers with different combinations of bubbles and stroboscopic light in a flume specifically designed to study fish behavior (Fig. 2). The oval flume measured 11 m long, each raceway 1.4 m wide, and was filled with water (65 cm deep) that circulated at  $0.31 \pm 0.06 \text{ m s}^{-1}$  (mean  $\pm 1$  S.D.). A flow through of groundwater was used to keep temperature ( $8^\circ\text{C}$ ) and other abiotic factors constant over time. We used hatchery-reared Atlantic salmon smolts bred from the River Dalälven broodstock to quantify the guiding effect. To capture the migrating behavior, we selected two-year-old smolts, which during this time of the year smoltifies and actively swims downstream. The fish were surgically tagged with passive integrated transponders (PIT; for details, see below). To quantify migratory decisions in the smolts, a barrier that covered half the width of the raceway was positioned in a  $45^\circ$  angle with the current. Two  $60 \times 60$  cm antennas, connected to a reader (Oregon RFID, Multi-Antenna HDX Reader), were used to collect data on fish movements (i.e. when and where a PIT tag was detected). With one antenna positioned downstream of the open half and the other downstream of the barrier (Fig. 2), the detections revealed if the salmon passed through the barrier or through the open space next to it.

The bubbles were generated by an air compressor (Dewalt DPC16PS, operating at a pressure of 5 bar) connected to a plastic hose (inner diameter = 8 mm) perforated with a 1-mm diameter needle creating small holes every 1 cm. The hose was weighed down and double folded creating a two-layer bubble barrier with an effective length of 150 cm. Four stroboscopic LED-lights (iGuzzini, E-101 5w, flashing simultaneously at 480 bpm) was installed between the perforated hoses to generate the stroboscopic light treatment. Sound treatment was produced by a spherical transducer, 17.5 m in diameter (Model ITC-1007), transmitting sound chirps between 53 and 350 Hz was originally part of the study. However, due to high levels of background noise, we were not able to detect these sound signals, hence, this treatment was excluded



### Treatments

Guidance efficiency =  $f(\textit{Bubbles}, \textit{Stroboscopic light}, \textit{Bubbles} + \textit{Stroboscopic light}, \textit{Bubbles} + \textit{Darkness}, \textit{Bottom structure}, \textit{Bottom structure} + \textit{Darkness})$

Rationale: 1) Determine most effective treatment  
2) Quantify importance of visual cues

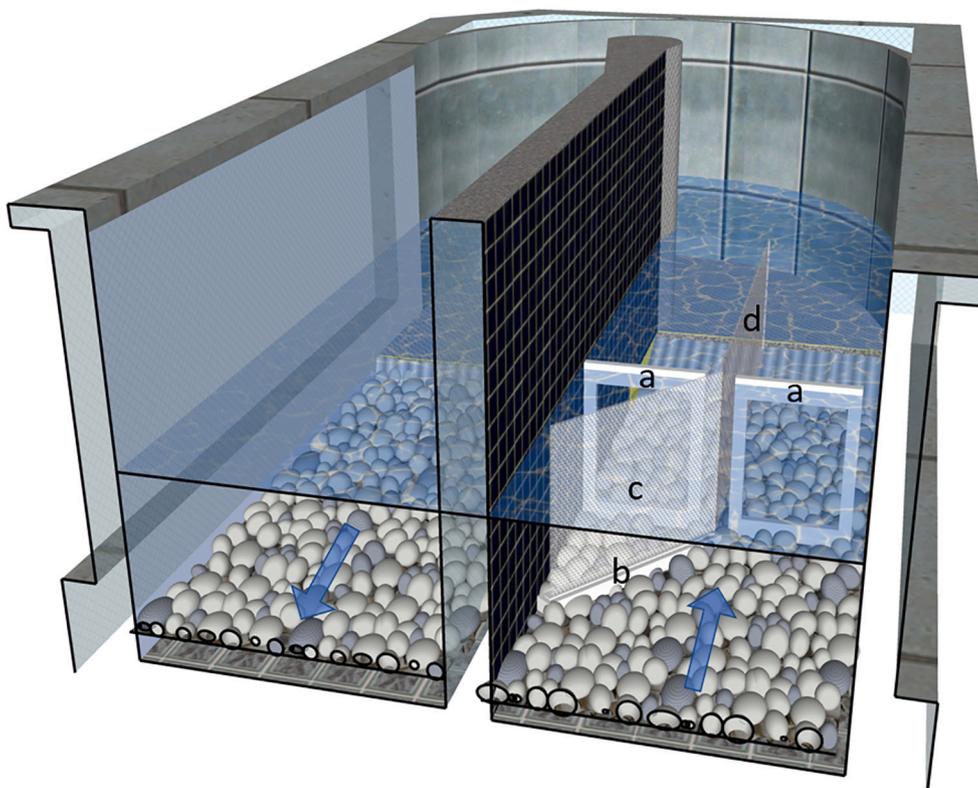


### Treatments

Guidance efficiency =  $f(\textit{Bubbles})$

Rationale: Validate laboratory predictions on a large scale

Fig. 1. Underwater footages of the flume (a) and river (b) experiments and their corresponding treatments (in *italic*). Note that fish in both experiments are presented with the same two options, either go through the barrier or steer to the side to avoid passage. Also shown are the rationale for the individual experiments.



**Fig. 2.** Schematic cross section of the flume used to study the effect of bubble barrier on migrating Atlantic salmon smolt. Blue arrows show the counter clockwise water current in the flume. Two PIT-antennas (a) detected if tagged smolt passed on either the left or right side of the raceway. The barrier consisted of a ramp (b) with a perforated hose and four stroboscopic lights, positioned in a 45° angle to the current. When the compressor was turned on it generated a bubble curtain (c), which was altered between a right and left position between replicates. The gap between the end of the barrier and the antennas was screened off with a plastic net (d) to prevent false positives by fish moving from one side to the other downstream of the barrier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from the study.

We tested guidance effects of bubbles and stroboscopic light, both separate and in combination, by comparing fish migration in these treatments with no treatment (i.e. control). Furthermore, to distinguish visual cues from other sensory systems, the effects of both the control and bubble treatment were tested in daylight and in complete darkness. Each treatment consisted of five replicates, except for daylight control (six replicates) and bubbles in complete darkness (three replicates). To account for potential differences in current velocity between the inner and outer part of the flume, the position of the bubble barrier was moved between replicates of each treatment.

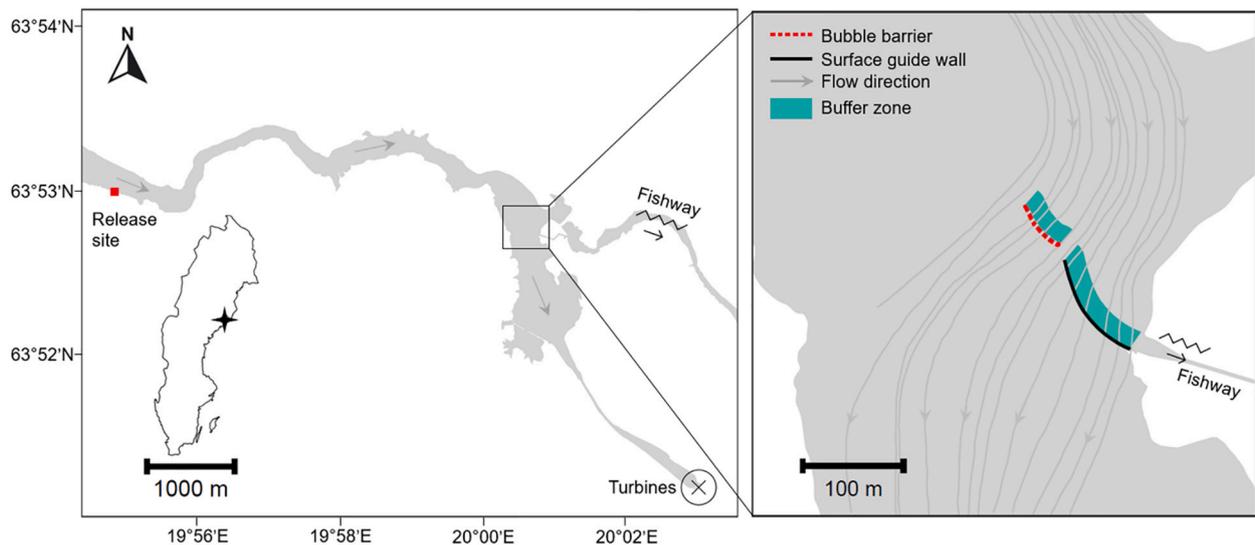
Each replicate run consisted of 10 novel individuals adding up to a total number of 290 individuals (body length =  $203.6 \pm 13.6$  mm, mean  $\pm 1$  S.D.). The smolts were anaesthetized with tricaine mesylate (MS-222) and measured for length, after which a 23 mm PIT tag (Oregon RFID, HDX+ PIT Tag) was surgically inserted into the abdominal cavity of each individual. Fish were kept overnight in a holding tank ( $100 \times 100 \times 40$  cm) with flow-through water (between 5 and 7 °C) from the adjacent river Dalälven. Each trial started the following day after tagging with 10 smolts being haphazardly netted from the holding tank, moved to the flume, and then left undisturbed for 30 min for habituation. At this point, we estimated that >95% of the smolts had initiated active downstream movement. After the habituation, we initiated the experiment with one of the six treatments, and all antenna detections during one hour were used in subsequent statistical analyses. The experiment was run over ten consecutive days, and treatments were randomly assigned to different days to avoid confounding effects of time. At termination of the experiment, all hatchery-reared smolts were euthanized, as described in the ethical permit (Dnr C 169/14) issued by the animal ethics board in Sweden.

## 2.2. River experiment

To test our hypothesis at longer distances, we used a bubble barrier (without light stimuli) in Ume River, which is a large regulated river in

northern Sweden with an average discharge over one thousand times higher than the flume ( $400 \text{ m}^3 \text{ s}^{-1}$  vs.  $0.3 \text{ m}^3 \text{ s}^{-1}$ ). Here, a bubble barrier was installed adjacent to a hydropower station with an available fishway. A surface guide wall designed to divert downstream migrating salmon towards the fishway was already in place, but only covered a quarter of the total river width. We used this setting, with the surface guide wall only, as a control for two years, followed by a third year with the addition of a 50-m long bubble barrier, installed as an extension of the guide wall, as the experimental treatment (Fig. 3).

To track the downstream movement of smolts in their natural setting, we used acoustic telemetry. Over the three years, 89 wild smolts native to the river was caught in a smolt trap, adjacent to the fishway. When caught in the trap, the smolts were kept in tanks ( $100 \times 100 \times 60$  cm, with flow-through water from the Ume River) until tagging, which happened within 6 h. In 2016 and 2017, a total of 49 smolts were surgically tagged with Vemco V5-2x transmitter (weight: 0.77 g, length: 12.7 mm, signal delay:  $0.7 \pm 0.1$  s) between the 30th of May and 17th of June 2016 (24 individuals) and between the 8th of June and 14th of June 2017 (25 individuals). These individuals only encountered the surface guide wall and not the bubble barrier and were used as control. In 2018, 40 smolts were surgically tagged between the 13th of June and 21st of June, half of them with Vemco V5-2x transmitter and half of them with Vemco V7P-4x (weight: 1.5 g, length: 22 mm, signal delay:  $20 \pm 5$  s). The latter is equipped with a pressure sensor, which aside from generating XY-positions also provides depth measurements for every transmission. Before tagging, the smolts were anaesthetized with tricaine mesylate (MS-222) and measured for weight and length. Transmitters were placed in the body cavity through a 15 mm long scalpel incision on the ventral side between the pectoral and pelvic fins. Tag burden in weight was on average  $3.59\% \pm 0.15\%$  (mean  $\pm 1$  S.E.). This weight is well below tag burdens of 7–8% reported to have no effect on swimming performance, and likelihood of survival in the wild for salmonids (Chittenden et al., 2009; Smircich and Kelly, 2014). The incision was closed using sutures and two surgeon's knots after which the fish were returned to the flow-through tank and allowed to recover for a



**Fig. 3.** Map of Ume River (light grey) around Stornorrforss hydropower plant. Left panel shows the geographical position (black star) of the study site at perspective of Sweden (lower left corner) and the release site (red square) 6 km upstream of the dam. Here, the river divides into two branches where the southern leads to the turbines (black cross in a circle) and the northern leads to a fishway (black zigzag) around the turbines. Right panel shows a detailed map of the area around the surface guide wall (black line, leading to the fishway entrance), bubble barrier (dashed red line), and 20-m buffer zones upstream of the two barriers (turquoise polygons) used to define fish encounters with the guiding structures. Dark grey arrows represent the main flow direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

minimum of six hours. After visual inspection of activity and flight behavior, to ensure that the fish were in good conditions, they were moved to an oxygenated 1.5 m<sup>3</sup> transport tank, trucked 6 km upstream of the barrier, and released back into the river (Fig. 3). All handling and tagging of wild-caught fish were approved by the animal ethics board in Sweden (Dnr 5.2.18–3060/17).

Each year we deployed 15 receivers (Vemco HR2) in a 16-ha grid (average receiver spacing: 54 m) around the barriers, to detect signals from tagged fish. Fish positions were derived via hyperbolic positioning using Vemco positioning system (VPS) as described by Smith (2013) and erroneous positions were filtered out using swimming speeds and turning angles as described by Leander et al. (2020). After filtering, the median offset from a towed reference tag to a high precision GPS track (i.e. accuracy) was  $1.27 \pm 0.11$  m (median  $\pm$  1 S.E.) and the average number of positions generated by each tag transmission was  $0.36 \pm 0.023$  and  $0.44 \pm 0.033$  (mean  $\pm$  1 S.E.) depending on signal type, pulse position modulation and binary phase shift keying, respectively. For further details on telemetry performance see Leander et al. (2020).

### 2.3. Statistical analyses

To examine the barriers ability to guide smolt in the flume, a generalized linear mixed effect model for binomial data was used, where number of passages fishway/barrier per replicate was treated as a response variable, and treatment as a six-level fixed effect. The factor barrier position, used to account for possible differences between outer and inner curve of the flume, and replicate, to account for the 10 individuals used in each run, were both treated as random effects. Differences between treatments were tested using Tukey's all-pair comparisons.

The effect of the bubble barrier in the river was tested by using the ratio of smolts encountering the barrier and smolts that passed through the barrier. Encounters were defined as smolts with more than two detections within a polygon covering the area from the barrier and 20 m upstream (Fig. 3). To examine differences in ratios for control vs. bubbles, as well as bubbles vs. guide wall, we used Fisher's exact test on contingency tables arranged with number of smolts passing the barrier and number of smolts not passing the barrier as columns and treatment (control/bubbles) or structure (bubbles/guide wall) as rows. To counter

possible confounding effects of the fixed barrier positions (i.e. the guide wall was always situation inside of the bubble barrier), we also performed a general linear model (binomial, of logistic type) where passages (yes/no) were treated as a response variable explained by the fixed effects 'barrier structure' (bubbles/guide wall) and 'distance from fishway entrance' (m), and their interaction term. Efficient guiding by the physical or non-physical structure was defined as a fish encountering the structure but not passing to downstream areas. All analyses were performed using R (version 3.6.0).

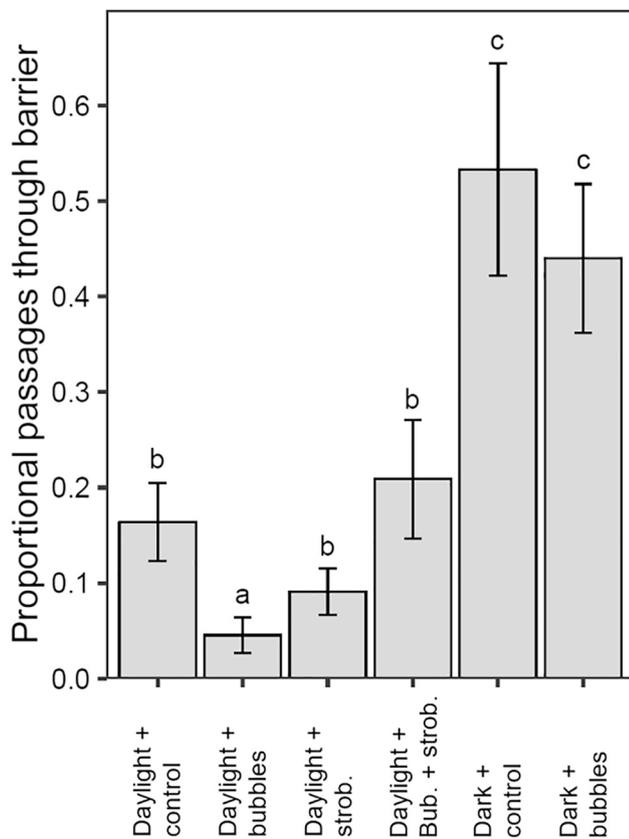
## 3. Results

### 3.1. Flume experiment

The bubble treatment alone was most efficient in guiding salmon and lowered the passages through the barrier to  $4.6 \pm 1.9\%$  (mean  $\pm$  1 S.E.). This was a 70% reduction of passages compared to the daylight control ( $Z = 3.28, p = 0.001$ ). In the daylight control treatment (barrier present but both bubbles and stroboscopic light turned off),  $16.4 \pm 4.1\%$  of the smolts passed the barrier, indicating that the supporting bottom structure in itself affected (repelled) smolt. Stroboscopic light alone had a nearly significant, negative effect on barrier passages, but when combined with bubbles this trend was instead positive, neither of those treatments differed significantly from the daylight control. Importantly, bubbles repelled fish in daylight but not in darkness (Fig. 4).

### 3.2. River experiment

The total number of 89 tagged and released salmon smolt generated 56 encounters with the guidance structures or control area. Remaining individuals never reached the study site at all (most likely due to predation) or approached the study site in a western trajectory and consequently missed the guiding structures/control area located on the eastern river shore. Ninety percent of the individuals encountering the bubble barrier did not pass through it (Table 1), which was significantly higher than the control (28%,  $p = 0.004$ , Fisher's exact test) and the surface guide wall (46%,  $p = 0.025$ , Fisher's exact test). Few smolts that encountered either one of the barriers made it through the fishway, only one out of 30 encounters for the control and four out of 17 encounters



**Fig. 4.** Bar chart showing proportional of smolt that passed through the barrier (y-axis) for the different treatments, control, bubbles and stroboscopic light in either daylight or darkness (x-axis). Error bars represent  $\pm 1$  S.E. and different lower-case letters denote significant differences ( $p < 0.05$ ) from Tukey’s all-pair comparisons.

**Table 1**  
Number of tagged smolt released, barrier encounters, and barrier passages.

Treatment	No. of released individuals	No. of barrier encounters	No. of barrier passages	Fisher’s exact test Bubbles vs. Treatment
Control	49	18	13 (72%)	$p = 0.004$
Surface guide wall	89	28	15 (54%)	$p = 0.025$
Bubble barrier	40	10	1 (10%)	$p = 1.000$

Significant differences of proportional passages (Fisher’s exact test) was tested for the bubble barrier versus the control and surface guide wall separately and presented in the right most column. Note that the guide wall was present on all releases, hence the higher number of encounters.

with the bubble barrier present. Due to a low sample size, this difference was marginally significant ( $p = 0.051$ , Fisher’s exact test).

The logistic regression supported that the different probabilities to pass the bubble barrier and the surface guide wall were dependent on the different barrier structures ( $p < 0.001$ ) and not on their positions ( $p = 0.701$ ), although distance to fishway entrance in itself had a negative effect on fish guidance efficiency ( $p = 0.024$ ). Examples of fish trajectories are shown in Fig. 5.

**4. Discussion**

Clearly, both our laboratory study as well as our field experiment validated our main hypothesis: bubble barriers effectively divert

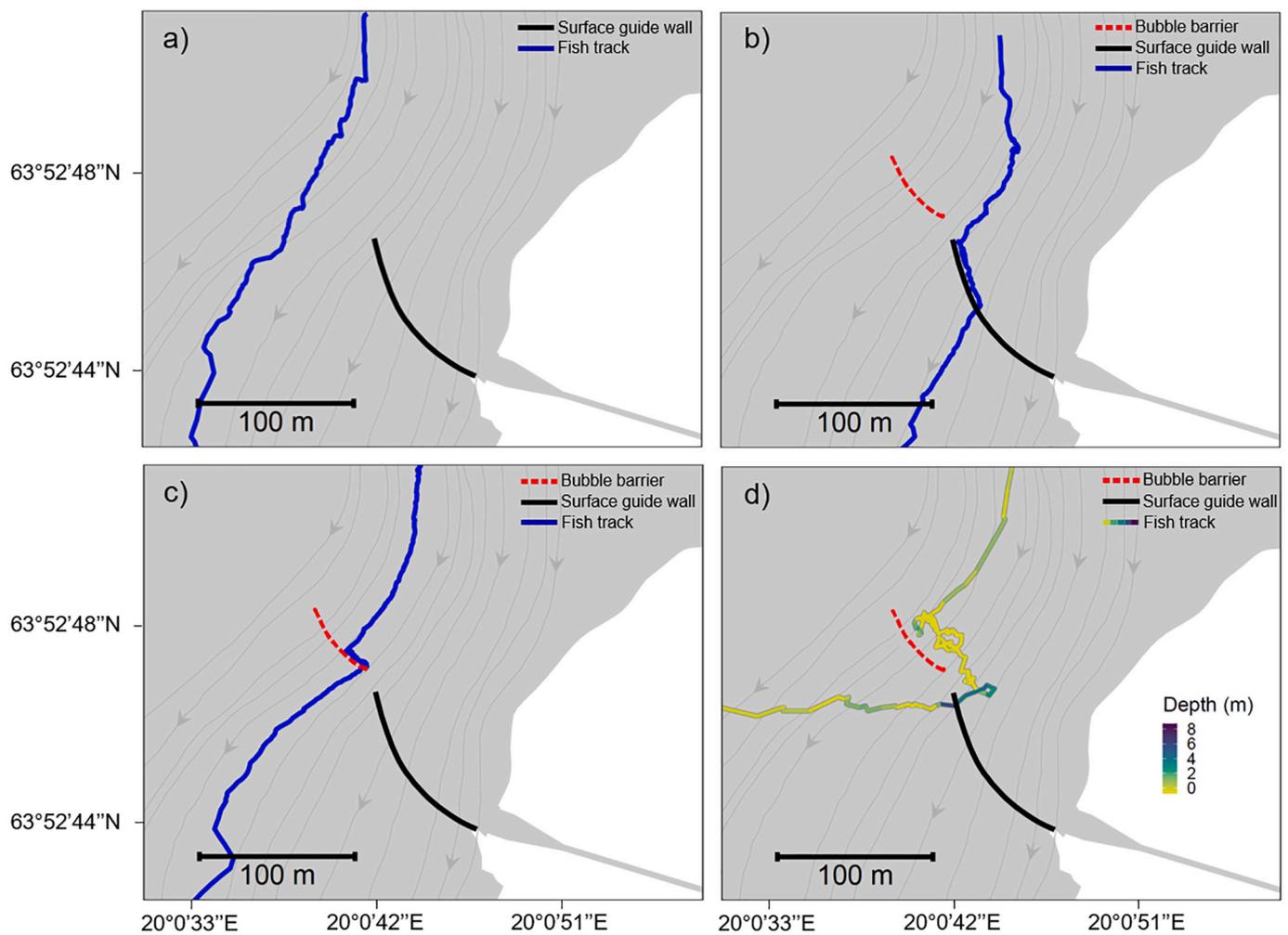
migrating Atlantic salmon. Indeed, this agreement between laboratory predictions and field behavior support recent works suggesting that fish performance in behavior trials can be used to predict fish behavior in more complex ecosystems (Fahlman et al., 2020). Moreover, our study shows that the efficiency of the bubble barrier (and bottom structures) for guiding fish is not effective during dark conditions, indicating that they respond to the visual cues when diverting from bubbles. However, the efficiency of the bubble barrier was also reduced with distance from the fishway entrance, suggesting that environmental conditions that change gradually away from the shore, such as increasing flow velocity and depth, may also reduce the efficiency in which of bubble barriers divert salmon smolt.

Earlier studies investigating have speculated that fish (e.g. walleye and common carp) uses both visual and auditory cues to navigate in relation to the bubble barriers (Flammang et al., 2014; Zielinski et al., 2014). However, our results seem to partly contrast this and those of Welton et al. (2002) who showed that a barrier using both bubbles and sound was more effective in guiding Atlantic salmon smolt during night compared to daytime. Their interpretation was that during daylight the smolt could locate gaps in the barrier using visual cues, but this possibility was limited during night when they instead, as suggested by the authors, relied on auditory cues in their movement. Yet, with our results in mind—demonstrating that bubbles alone divert salmon only when fish can visually see them—the finding by Welton et al. (2002) seems more likely to be an artefact of the sound treatment being more effective during dark conditions. Nevertheless, we cannot exclude that fish in the study by Welton et al. (2002) still had some visual cues from moonlight in their night time experiments—conditions that contrast with our dark treatment where visual cues were completely removed.

Although the river-scale barrier intercepted few individual trajectories ( $N = 10$ ), only one of them passed the 50 m long barrier. This single individual did, however, clearly avoid the barrier at first with a 90° turn (Fig. 5c) but passed in the very end of the barrier. Since the barrier did not cover the full water column in each end (i.e. bubble hose was slightly U shaped), this passage could potentially be a dive under the barrier, but we lack depth data on this individual to confirm this interpretation. Indeed, our limited depth data show that smolts are able to dive under the two-meter deep surface guide wall (Fig. 5d). The early view of smolt as ‘passive migrants’ only following the current (Thorpe et al., 1981; Tytler et al., 1978) has been revised in studies that have shown migration velocities faster than the water current (Davidsen et al., 2005; Svendsen et al., 2007). Here, our results validate an active migration mode also for the vertical axis, with individuals diving to avoid large structures covering the upper two meters of the water column.

**4.1. Application of bubble barriers in rivers**

A manager of fishways is challenged by high construction and maintenance cost for physical barriers, a challenge that has warranted the development of non-physical barriers (Noatch and Suski, 2012). Interestingly, the calculated guidance efficiency of the surface guide wall is lower than for the bubble barrier; hence, a higher proportion of individual smolt passed the former. Further, since the physical barrier had a more strategic position for guiding fish following the near-shore currents in comparison to the bubble barrier, it seems rationale that the latter guidance structure could have guided an even higher number of individuals if placed closer to the fishway entrance. In other words, our findings suggest that a low-cost bubble barrier extending from the bottom to the surface seems more efficient in diverting salmon than a physical barrier that only covers the upper two meters of the water column. Furthermore, the average water velocity at our laboratory experiment ( $0.31 \text{ ms}^{-1}$ ) and field site ( $0.27 \text{ ms}^{-1}$ ) is of the same magnitude as typical for rivers worldwide (Schulze et al., 2005; Verzano et al., 2012), creating a large application potential for the use of bubble barriers.



**Fig. 5.** Example of individual smolt movements around the two guiding structures; surface guide wall (solid black line) and bubble barrier (dashed red line). Blue and colored lines represent trajectories from tagged smolts where a) is an individual passing with no bubble barrier present and remaining panels shows different examples of smolt behavior with both surface guide wall and bubble barrier present. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Our near-continuous measurements of fish behavior around the bubble barrier enabled us to both quantify the efficiency at which bubble barriers are able to divert downstream-migrating salmon, but also in detail study how migrating smolt interact during downstream migration with bubbles. Results from previous studies, based solely on downstream catches or other indirect measures of fish guidance efficiency (Welton et al., 2002; Zielinski and Sorensen, 2015), have been unable to show that migrating fish is strongly repelled by the bubbles per se, which is evident from our findings. However, what is also apparent from our results are that guiding the fish towards the fishway is not enough for a successful passage through the fishway. In our case, most fish were successfully guided to the inlet of the fishway but did not in the end enter the fishway. Instead these fish spent time near the inlet, turned around or swam under the guide wall and towards the turbines. Here, our findings of diverting effects on migrating fish from simple structures, such as the turned off barrier in our laboratory experiment, highlight that small visual stimuli can have an important negative impact on the attractiveness of a fishway. This stresses that accurate quantification of fish guidance structures needs to involve adequate tools to reveal the full picture of the barrier effectiveness. Clearly, previous findings of poor fish guidance efficiency of bubble barriers (Flammang et al., 2014; Welton et al., 2002), may be an artefact of the non-appealing or non-existing alternative next to the barrier rather than the guidance function of the bubble barrier itself.

#### 4.2. Conclusions and recommendations

Our results show that a bubble barrier can repel migrating Atlantic salmon and function as a guiding method to lead them into a preferred direction and that bubbles alone, with no stroboscopic light, proved to be most efficient in doing so. Interestingly, without any visual cues for the salmon, the guiding function of the bubble barrier ceased to exist. Nevertheless, the limited visibility in a natural colored boreal river still proved to be sufficient to generate enough visual cues of the bubble barrier to effectively affect and divert Atlantic salmon. The significant repelling effect observed in two very different settings, i.e. on hatchery reared salmon in a flume and on wild salmon in a large river, indicate a high potential for guiding juvenile salmonids in water velocities around  $0.3 \text{ m s}^{-1}$ . However, for this method to be implemented as a holistic solution, future studies should evaluate the effects of bubble barriers on other and life stages, other migratory species, as well as a range of water velocities.

#### Authors' contributions

Conceptualization, J.L., G.H. and M.J.; Data curation, J.L.; Formal analysis, J.L., J.K. and M.J.; Funding acquisition, G.H. and J.K.; Investigation, J.L.; Methodology, J.L., G.H. and M.J.; Project administration, J.L., G.H. and M.J.; Resources, G.H. and J.K.; Software, J.L.; Supervision,

J.K. and M.J.; Validation, J.K. and M.J.; Visualization, J.L.; Writing - original draft, J.L.; Writing - review & editing, J.L., J.K., G.H. and M.J. All authors have read and agreed to the published version of the manuscript.

#### Data availability statement

All data used in this manuscript are available through the Figshare database: <https://doi.org/10.6084/m9.figshare.13536758.v1> and <https://doi.org/10.6084/m9.figshare.13536740.v1>

#### 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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