# Survival and movement behaviour of Atlantic salmon smolts (*Salmo salar* L.) migrating through impounded lakes and natural standing waters

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Contents

*Abstract*

Juvenile Atlantic salmon *(Salmo salar L.)* smolts were tracked through two lakes impounded by large hydropower dams (> 10 m) in head height), and one natural standing water located in the River Conon system, Northern Scotland using telemetry. Eighty smolts were tagged with acoustic transmitters and were tracked for an eight-week period from May to June 2017 using Acoustic Monitoring Receivers deployed across the three lakes (Loch Garve, $N$ = 10; Loch Meig, $N$ = 8; Loch Achonachie, $N$ = 10), and a single receiver positioned in the Cromarty Firth estuary. High mortality rates were found between the river release location and the three lakes; Loch Garve (25% $km^{-1}$), Loch Meig (28% $km^{-1}$) and Loch Achonachie (10% $km^{-1}$) which was likely the result of predation. In addition, mortality rates in lakes was generally high, with an average mortality rate of 16% $km^{-1}$ in natural standing waters and 32% $km^{-1}$ in impounded waters. Modelling showed that successful lake migration was lower if the lake was impounded, and if individuals were migrating earlier in the study period. Survival rate of tagged fish from the three upstream river release sites to the estuary ranged from 0 to 20%. Modelling found that successful migration (river release to estuary) was lower if the lake was impounded, and if fish were travelling in smaller release groups. The mean time taken for a fish to exit a natural standing water ($N = 15$) was 8 ± 14 days, and to exit an impounded lake ($N$ = 16) was 9 ± 7 days (mean ± SD). The absolute minimum lake transit speed ranged between 0.0008 and 0.0433 m/s.  Smolts that successfully exited the natural standing water travelled the shortest total distance during the study period (35 ± 3 km per fish), with impounded smolts travelling on average 103 km further (138 ± 114 km per fish) before exiting their respective lakes. There was no significant difference in fish swim speeds between natural standing waters and impounded lakes. Tagged smolts that exited a natural standing water carried out on average 12% more downstream directional movement than upstream, in contrast tagged smolts that exited an impounded water carried out on average 2.7 % to 54.9% more upstream (outflow to inflow) directional movement than downstream. These findings highlight differences in fish behaviour and movement between natural standing waters and those impounded by large (<10 m head height) hydropower dams.

## 1. Introduction

Migration is a common resource exploitation strategy whereby individuals move from one area to another in search of food, shelter or breeding sites (Aidley 1981). This movement is often seasonal and timed to match key life stages, for example birds migrating between breeding sites with low predation levels to feeding areas with greater food resources (Newton 2010). Migration may also occur in species that undergo several ontogenetic stages with different ecological constraints and physical needs. For example, juveniles developing into adults with high energetic demands which requires a certain type of feeding grounds, as seen in the mosquitofish (*Gambusia affinis)* which exhibits an ontogenetic shift from caladocerans (branchiopod crustaceans) to larger prey as it matures (Garcia-Berthou 1999; Milner-Gulland et al. 2011). According to evolutionary ecology theory, the benefits of migration must outweigh the cost of the movement itself for the mechanism to persist (Gross 1987). With the potential costs of migration including, but not limited to: energy expenditure, mortality (increased risk of infection and predation), and behavioural and morphological body adaptation (McCormick et al. 1998; Alerstam et al. 2003).

Advances in the field of animal tracking and telemetry has facilitated the tracking of migratory species across terrestrial, aerial and aquatic biomes. Biotelemetry describes the use of technology to remotely track individuals, and includes the use of; radio and acoustic transmitters, archival tags (also known as data storage tags), satellite tags and passive integrated transporter tags (PIT-tag). Typically this technology involves the attaching of a tag to an individual which records information on their movement, and other environmental and physiological parameters which is then (wirelessly) transmitted to a stationary logger or mobile receiver in range (Thorstad et al. 2013). Each tag type has a different functionality which can be matched to a study design and environment.

The use of archival tags (or DST tags) has been used to unravel the mystery of some of the largest migrations in the world, including that of the sooty shearwater (*Puffinus* griseus) which undertakes an annual trans-equatorial flight pattern covering around *ca*. 75, 000 km (Shaffer et al. 2006). A limitation of archival tags is that sensor information is recorded and stored inside the tag, therefore an individual must be recaptured to retrieve the stored data, which is difficult for individuals which do not show strong site fidelity or inhabit the open ocean. Radio tags offer an affordable alternative to tracking species over large distances. Radio tracking has been used mainly to study terrestrial species, and aquatic individuals inhabiting streams, rivers and shallow lakes (Lucas & Baras 2000). Radio tags also offer the option of 'active tracking' using a hand-held antenna to position tagged individuals in real time. However, radio tags are limited in aquatic environments as radio waves attenuate rapidly in the dissolved salts abundant in saline or brackish environments, making it only usable to study individuals in shallow freshwater habitats (Kuechle & Kuechle 2012). The advancement of acoustic telemetry has facilitated the tracking of individuals through saline and deep-water habitats using coded sound signals. The ability for sound to travel five times faster in water than air (Forrest 1994) allows acoustic tracking to monitor the movements of individuals to almost real-time accuracy over long distances, such systems are also capable of recording temperature, heart rate, depth and acceleration data (Thorstad et al. 2013). Acoustic telemetry has provided the technology to investigate the dispersal and movement ecology of aquatic species of high conservation and economic value, including sharks and cetaceans (Carey et al. 1981; Holland et al. 1992; Gasper et al. 2008).

Biotelemetry has also been pivotal in understanding the effect of anthropogenic induced stressors in aquatic systems. The development of coastal and riverine infrastructure has created obstacles that can alter the ability and efficiency of an individual navigating its environment (Marschall et al. 2011). Accurate navigation is essential to achieve successful migration, and to minimise energy expenditure (Wiltschko & Wiltschko 1987). Modification of the river corridor through hydropower development poses in a physical barrier, and has been found to cause delays in migrating freshwater species (Welch, Rechisky, Melnychuk, Porter, Ward, et al. 2008; Caudill et al. 2007; McCormick et al. 1998; Cushman 1985). For species which show seasonal migration with a narrow migratory window, for example mature adult sockeye salmon (*Oncorhynchus nerka*) travelling to spawning sites (Lee et al. 2003), delayed migration may lead to increased energy expenditure as they attempt to overcome or navigate past obstacles, which will reduce energy available for reproduction (Chanseau and Larinier, 1999; Naughton *et al.*, 2005; Kinnison *et al.*, 2016). Recent studies have also found a negative cumulative effect of barriers, with a 6-7% reduction of survival in the estuary with each dam passed (Baisez et al. 2011; Stich et al. 2015).

Atlantic salmon (*Salmo salar*) migration is well documented, with migration forming an important part of a generally diadromous life history (Gross 1987). Adult Atlantic salmon spawn in freshwater in autumn and winter, preferring well oxygenated gravel to lay eggs. In March to April eggs hatch into alevins and emerge from the gravel as feeding fry. After a year in freshwater, fry are described as parr (Pyefinch & Mills 1963; McLennan 2016). Juvenile salmon typically spend 2-3 years in rivers in the UK (Miller et al. 2012), in northern Europe 1-8 years has been recorded (Thorstad, Whoriskey, et al. 2012), before undergoing the process of 'smolting'. They become silver in colouration with specialised chloride cells developing in the gills which allows them to adapt to salt water (McCormick et al. 1998). In addition to morphological and physiological changes, behavioural changes have also been observed including a shift from previously aggressive and territorial parr to shoaling individuals (Damsgard & Arnesen 1998). Migration from freshwater to salt-water enables increased energy intake due to increased food availability, which leads to increased growth, and results in improved individual fitness (Gross et al. 1988). In females, increased maternal body size has been linked to a greater number and size of eggs (Thorpe et al. 1984; Jonsson et al. 2016). As a result, larger eggs leads to larger fry which have a competitive advantage due to their size, resulting in a higher initial survival rate as they are able to exploit and control high-quality feeding territories (Einum et al. 2002; Moffet et al. 2006).

In general, smolt migration lasts three to seven weeks from April to July, with populations in lower latitudes showing the earliest timings of migration (Verspoor et al. 2005; Stewart et al. 2006). Timing of migration has been significantly associated with migration success and survival (McCormick et al. 1998). The effect of migration delays at river barriers has been found to not only result in a mismatch in time of migration and optimal conditions (feeding opportunities and reduced thermal stress) which facilitate success, but can also increase the exposure of smolts to predators thus leading to heightened mortality (Jonsson and Ruud-Hansen, 1985; Friendland, 1998; Jepsen *et al.*, 1998).

Existing research suggests that juvenile fish migrating downstream through rivers utilise the water's flow, with the fastest ground speeds seen during times of high flow (Youngson et al. 1989). While movement of fish through riverine and estuarine environments is currently well documented (Stich et al. 2015b; Welch, Rechisky, Melnychuk, Porter, Walters, et al. 2008; Welch, Rechisky, Melnychuk, Porter, Ward, et al. 2008; Aarestrup et al. 2002; Gowans et al. 2003; Thorpe et al. 1981; Gauld et al. 2016; Baisez et al. 2011), knowledge of the movement of fish within lakes remains limited. The broad aim of this study was to improve the understanding of how Atlantic salmon juveniles (smolts) migrate downstream through three lakes, two impounded by large (> 10 m head height) hydropower dams (Loch Meig and Loch Achonachie) and one natural standing water (Loch Garve).

I hypothesised that the presence of large hydropower dams would negatively affect the survival of smolts migrating downstream due to migratory delays, which in turn would lead to increased predation rates. With fewer smolts successfully exiting, the number of successful migrants from the river release site to the estuary would be lower in lakes impounded by large (> 10 m head height) hydropower dams. In addition, I hypothesised that fish that had prior experience of successfully navigating past hydropower dams would be more successful traversing dam another than those with no prior experience.  To test this general hypothesis I addressed a series of very specific questions related to survivorship of tagged *S. salar* smolts:

1.1 How can we define survival from telemetry observations?

1.2 Does lake migration success differ between lakes?

1.3 Is lake migration survivorship affected by lake impoundment?

1.4 Does the successful migration of smolts to the estuary differ between lochs?

1.5 Is estuary migration survivorship affected by lake impoundment?

1.6 What factors might be driving survivorship of S. salar smolts?

1.7 Does the role of experience (whether a fish had exited a hydropower dam before) affect lake migration success?

I also hypothesised that the presence of large hydropower dams would pose a physical barrier which would hinder navigation downstream, leading to a reduction in swim speed and more variable movement patterns. To test this general hypothesis I addressed a series of very specific questions related to movement behaviour of tagged *S. salar* smolts:

2.1 How long did it take for successful smolts to exit their respective lakes?

2.2 Is the time taken for a smolt to exit a lake significantly different between lakes, and between impounded and not impounded lakes?

2.3 What was the minimum transit speed of fish that successfully exited a lake?

2.4 Is the minimum transit speed of fish that exited a lake significantly different between lakes, and between impounded and not impounded lakes?

2.5 What was the mean total distance travelled by successful and unsuccessful fish in three lakes?

2.6 Is the total distance that smolts travel in a lake significantly different between lakes and between impounded and not impounded lakes?

2.7 What was the average speed of successful and unsuccessful fish in the three lakes?

2.8 Was there a difference in the proportion of downstream to upstream movements between successful and unsuccessful fish within, and between lakes? Did this differ significantly between natural standing waters and those impounded by large hydropower dams?

# 2. Materials and methods

## 2.1 Study site

The study was conducted over five months from March to July 2017 in the River Conon catchment located in Northern Scotland (57° 60N, 4°63'W; Fig. 1). Hydroelectric power was developed in the Conon system between 1941 and 1961 (Payne 1988), and includes more than 32 km of tunnels, 24 km of aqueducts, and seven main dams and power stations (Gowans et al. 2003).

Loch Garve is a standing water body, 1.83 $km^2$ in surface area (2 km long, 0.79 km wide) in the middle reaches of the River Blackwater (57.5991°N, 4.6636° W; Fig. 2). The outflow from Loch Garve flows east into Loch na Croic, joining the main stem of the River Conon 10.5km downstream. This confluence is 9.4km from the head of tide of the Cromarty Firth.

Loch Meig is a water body 0.45 $km^2$ in surface area (2.54 km long and 0.12 - 0.3 km wide) impounded for hydropower on the River Meig (Fig. 3). The Meig Dam was constructed to collect water from the River Meig for transfer to Loch Luichart via a 2.5 km long, 3 km diameter tunnel (Payne 1988). Fish migrating downstream exit Loch Meig via a Borland fish pass with an inbuilt counter where the number of individuals passing downstream is automatically recorded (Stephens, pers comm., 3 July 2017). The River Meig then continues east, and is met by the confluence of the River Bran 2.4 km downstream.

The confluence of the River Meig and River Bran flow a further 3.8 km east into Loch Achonachie. Loch Achonachie is a small 0.69 $km^2$ loch (1.92 km long and 0.39 km wide) which was formed by the construction of the Torr Achilty dam and power station (57.5563°N, -4.6114°W; Fig. 4). The level of this loch fluctuates due to irregularities in discharge from upstream power stations and heavy run off, combined with varying rates of hydro-electric generation (SSE 2017). Water is on a controlled release, with water fed into the 15 MW power station built into Torr Achilty dam as required. Water from Torr Achilty continues east for 2.53 km before meeting water from the River Blackwater.

## 2.2 Acoustic monitoring receivers

In total, 31 Acoustic Monitoring Receivers (AMRs) were deployed for a period of eight weeks in early-April (prior to smolt capture) and were retrieved in early June 2017 (Fig 1). Acoustic Monitoring Receivers (AMRs) included 12 Vemco VR2W and 9 Vemco VR2Tx receivers (Vemco, Bedford, Nova Scotia, Canada), and 10 Biotel TBR-700 receivers (Thelmabiotel, Trondheim, Norway) all operating at 69 kHz. AMRs were positioned across the lakes in lines to form 'gates' of receivers so that all passing fish would be detected and recorded as they moved within their respective lochs. Biotel TBR-700 AMRs were positioned at the loch outflows in 'clusters' so that the option of 3D mapping of fish exiting the lakes might be possible. This cluster formation was not necessary in Loch Garve as the lake outflow was > 300m in width.

In total 10 AMRs were positioned in Loch Garve, forming 5 detection gates of receivers (Fig 2). A further 8 AMRs were positioned in Loch Meig forming 6 detection gates, with a pair of receivers at the lake's outflow. A single receiver was deployed 200 m upstream of the first loch receiver in Loch Meig so to detect fish entering the loch (Fig 3). In total 10 AMRs were deployed in Loch Achonachie forming 4 detection gates (7 AMRs) with a further 3 AMRs positioned at the loch's outflow (Fig 4). A single AMR was also placed in the Cromarty Firth estuary to identify successful fish that had made it to tidal waters (Fig 1).

Range tests were undertaken prior to AMR installation to ensure site coverage, and to reduce the incidence of acoustic breaches by tagged individuals. Tests were carried at Loch Meig from 2 May to 15 May 2017. Six Vemco VR2Tx receivers (Vemco, Bedford, Nova Scotia, Canada) were placed at fixed distances from a sentinel acoustic tag (Model LP-7.3, 139dB re 1 μPa power, Thelma Biotel AS, Trondheim, Norway 2013), following the procedure outlined by Hornbeck, 2009 and Topping and Szedlmayer, 2011. Four of the receivers had an integrated sync tag which was used to transmit signals to the surrounding receivers, transmitting receivers were also able to receive and store detections. This data was analysed using the *fossil* package (Vavrek 2011) in *R* (R Core Team 2015). AMR array design was adjusted so to ensure an overlap in detection range at each deployment site.

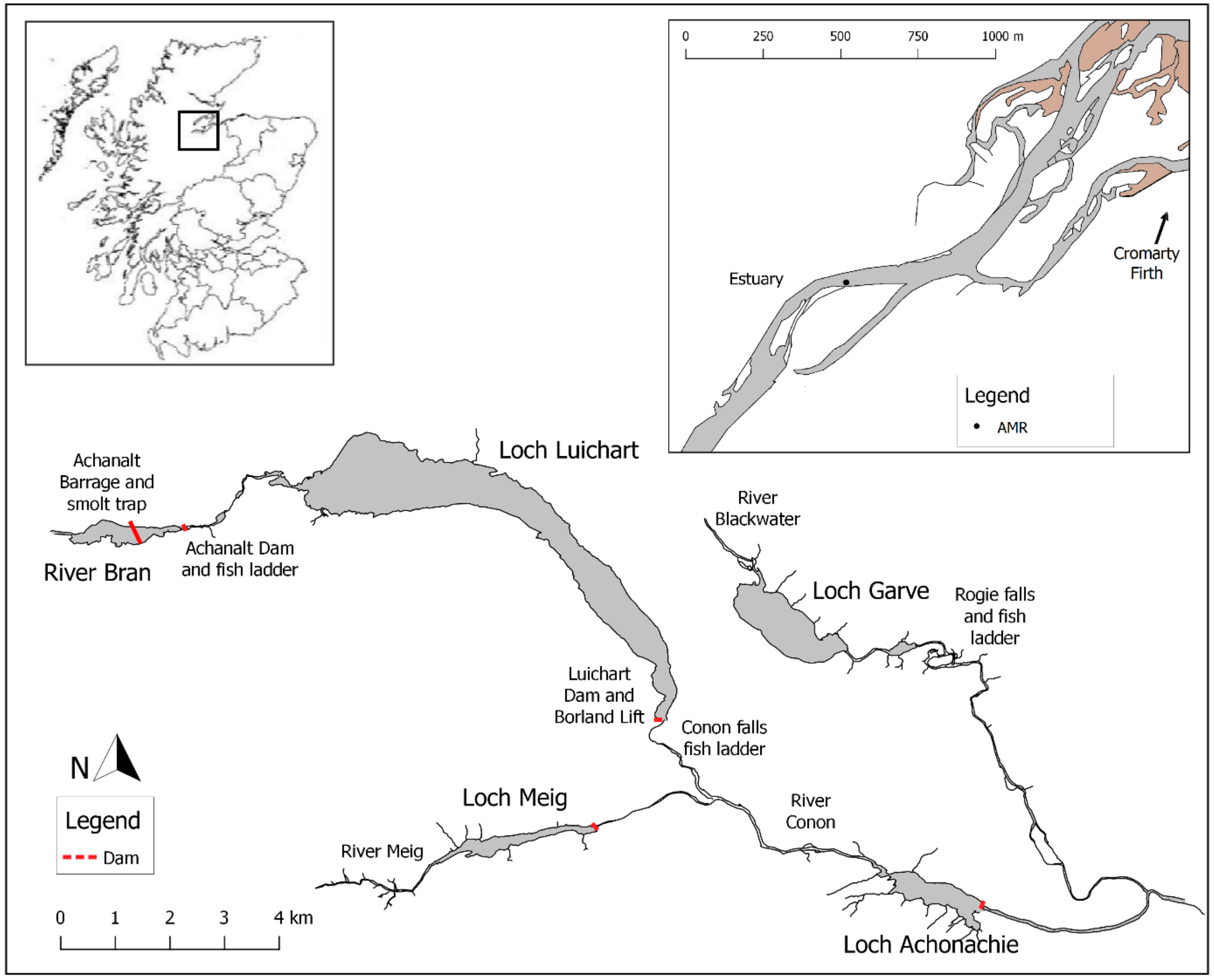


Fig. 1. Map of the main study area on the River Conon, Northern Scotland (top-left inset). Includes the three study sites (two impounded; Loch Meig, Loch Achonachie and the natural standing water, Loch Garve), and the site of fish trapping for acoustic tagging (Achanalt Barrage on the River Bran). A single Acoustic Monitoring Receiver (AMR) was also deployed in the Cromarty Firth estuary (top right) 8.76 km downstream from the confluence of the River Blackwater and River Meig shown on the map (bottom right).

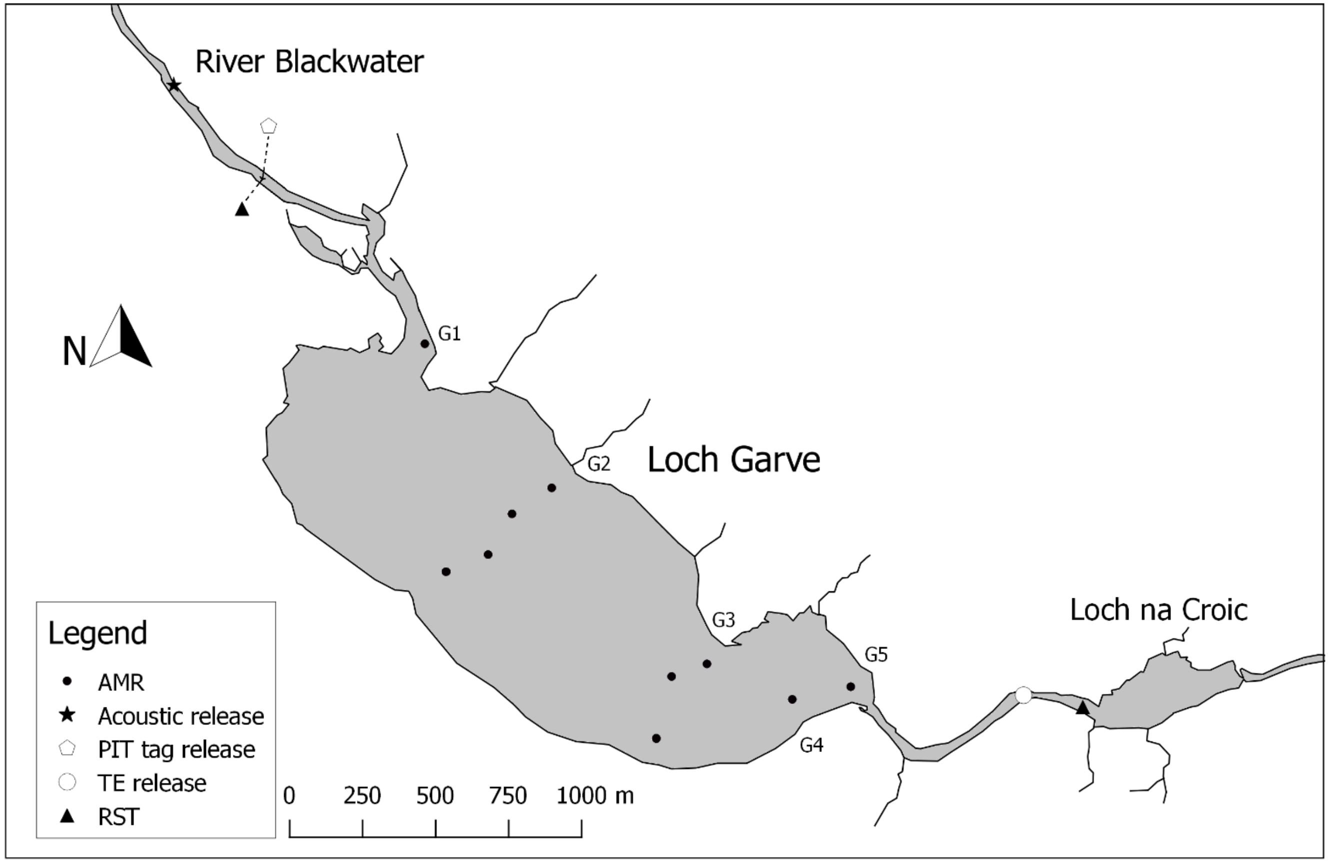


Fig. 2. Map of Loch Garve, showing the position of the Acoustic Monitoring Receivers (AMRs) along the loch (solid points), the name of the AMR gates are given next to the AMR gate positions. G2 includes 4 AMRs, G3 includes 3 AMRs, and G1, G4 and G5 include a single AMR. *S. salar* with acoustic tags were released at the site indicated by the star. PIT tagged fish were caught and released 0.82 km upstream of Loch Garve (hollow pentagon and solid triangle) at the same location, therefore where the two dashed lines meet is their relative position. The rotary screw trap (RST) closest to Loch na Croic (solid triangle) was used for trap efficiency (TE) experiments, and the corresponding TE fish release site was 0.2 km upstream (indicated by the hollow circle).

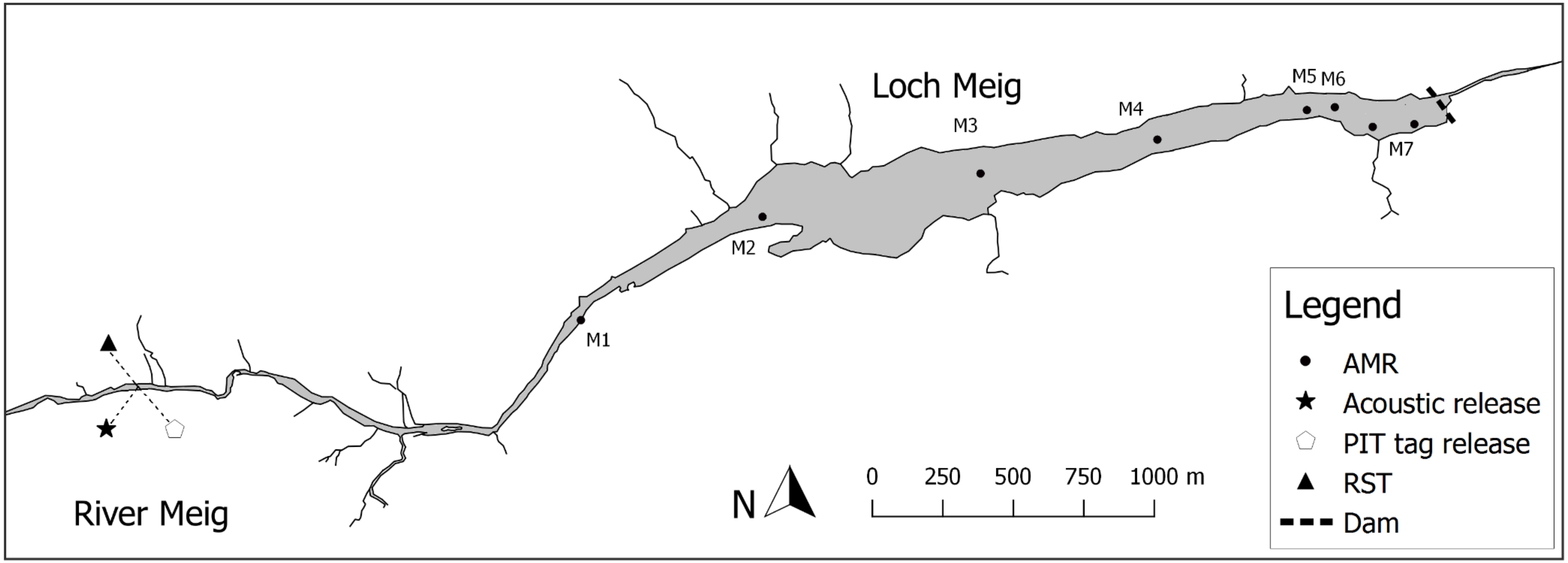


Fig. 3. Map of Loch Meig, showing the position of the Acoustic Monitoring Receivers (AMRs) along the loch (solid points), single AMRs were positioned throughout the lake (M1-M6), with a cluster of 2 AMRs forming gate M7 at the lake's outflow. PIT tagged *S. salar* smolts were caught and released (hollow triangle) at a rotary screw trap (RST; solid triangle) 1.6 km upstream of Loch Meig. Acoustic tagged smolts were also released at this coordinate (solid star). Where the three dashed lines intersect is the relative position of PIT and acoustic tagged *S. salar* release and the Meig RST. The location of the Meig dam wall is indicated by the thick dashed line. Names of AMR gates are given next to the AMR gate positions. The River Meig continues east and flows into Loch Achonachie 6km downstream.

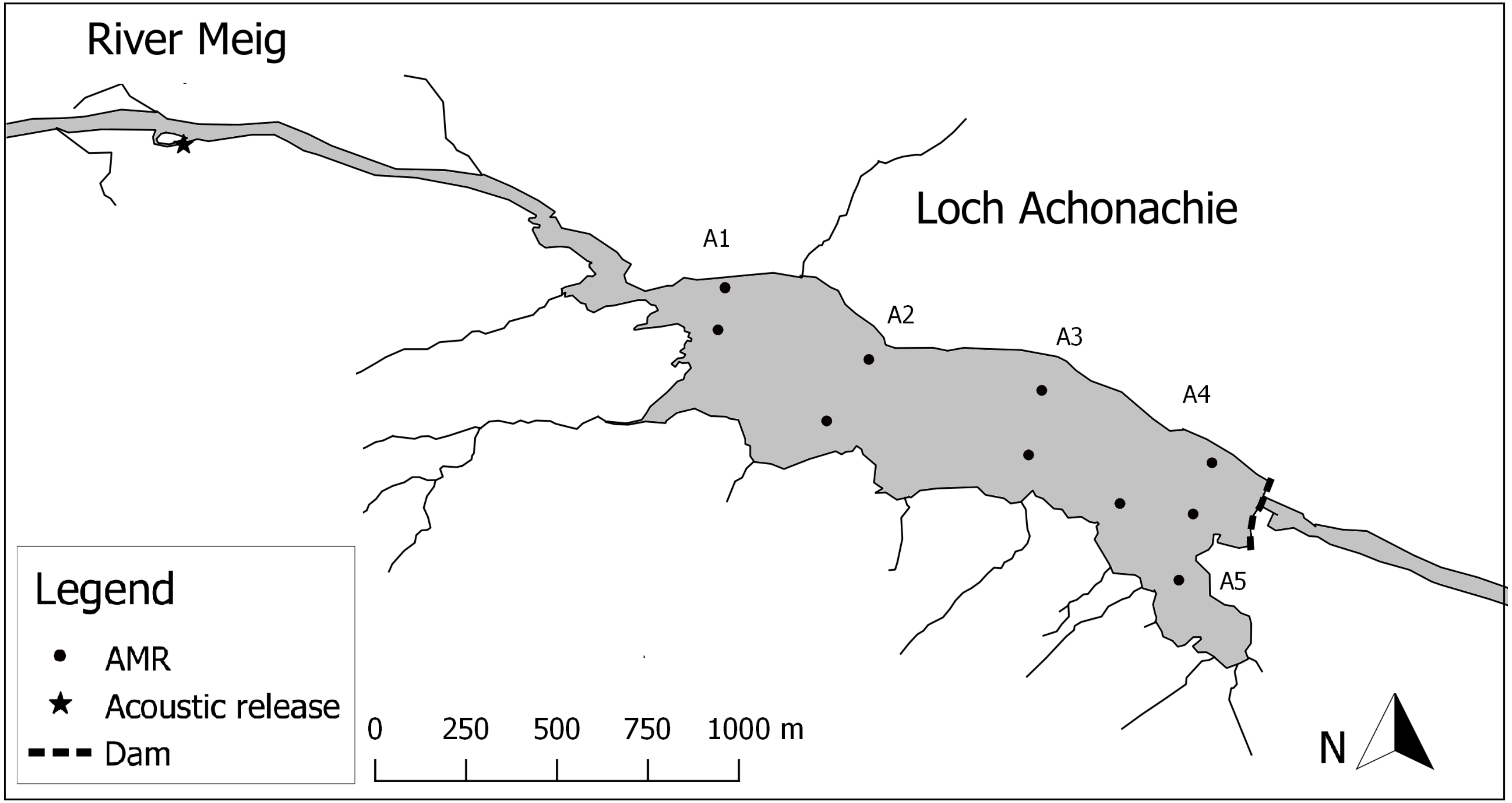


Fig. 4. Map of Loch Achonachie, showing the position of the Acoustic Monitoring Receivers (AMRs) along the lake (solid points) and the release site of acoustic tagged *S. salar* smolts (solid triangle). Gates include: A1 (2 AMRs), A2 (2 AMRs), A3 (2 AMRs), A5 (1 AMR), and gate A4 comprising of a cluster of 3 AMRs at the lake's outflow. Names of individual AMR gates are given next to the AMR gate positions. Also included is the position of the Torr Achily dam wall (dashed line).

## 2.3 Smolt capture and tagging

### 2.3.1 Acoustic tagging

*S. salar* smolts were captured by a 20 m wide wolf trap built into the Achnault barrage. The Achanault barrage is fed by the River Bran and flows into the River Conon 23 km downstream (Fig. 1). It is located 0.8 km upstream of Achanault Dam and is used to store water for Achanault Power Station for short periods (Pyefinch & Mills 1963). Prior to hydroelectric installations an impassable waterfall at Conon Falls meant that the River Bran was inaccessible to Atlantic salmon (Menzies 1928; Mills 1964). To compensate for loss of habitat in the Conon watershed, it was agreed that the North of Scotland Hydroelectric Board would provide a means of fish passage at these falls. Stocking operations began on the River Bran in 1953 with smolts transported from the Conon hatchery (Mills 1964), and in recent years has been reduced, with smolts now resulting from wild spawning (McKelvey, pers. comm., 1 August 2017). Trapping on the Bran was abandoned in the late 1960s, and restarted in 1994, with 4 000 to 12 000 (7 000 on average) *S. salar* smolts migrating downstream annually since 1994 (McKelvey, pers. comm., 1 August 2017).

Atlantic salmon smolts were captured, tagged and transported over the course of five days in 2017 on the; 20 April, 27 April, 28 April, 1 May and 2 May. In total 80 fish over 130 mm in length were chosen for surgical implantation with a 69 kHz coded acoustic transmitter (Vemco V7, 7 mm diameter, 18 mm length, 1.4 g mass in air, dB re 1 µPa power output at 1m, Vemco Ltd, Nova Scotia, Canada). Tags were programmed to have an acoustic transmission repeat cycle of 25 s ± 50%, and had an approximate tag life span of 100 days.

Prior to surgery, all surgical equipment and transmitters for insertion were sterilised with 90% ethanol and then rinsed with distilled water. Selected smolts were then anaesthetised with clove oil (0.5 mg $L^{-1}$) and metrics including mass (g) and fork length (mm) were recorded. Once under anaesthesia, the smolt was placed on a V-shaped surgery table and a small incision (11-14 mm) was made along the ventral surface of the smolt anterior to the pelvic girdle and a tag was subsequently inserted into the peritoneal cavity. The incision was closed with two independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK). Smolts were aspirated with a combination of clove oil (0.5 mg $L^{-1}$) and 100% river water throughout the procedure.

After tagging, smolts were placed into a recovery bucket with an aerator and 100% river water and allowed to recover prior to transport (< 30 minute trip duration). Smolts were visually assessed to ensure they were healthy before release within their respected tagging groups (Table 1). Fish were released: 1.2 km upstream of Loch Garve (57.61376°N, -4.68407°W; Fig 2), 1.55 km upstream in the river above Loch Meig (57.56222°N, -4.64858°W; Fig 3), and 1.5 km above Loch Achonachie (57.55683°N, -4.7678°W; Fig 4).

Table 1. Fish release location and number of individuals in the release group (group size). In total 80 fish were released at the three locations. *These fish were caught and released at Loch Meig.

| Date released | Release location | | |
|---|---|---|---|
| | Loch Meig | Loch Achonachie | Loch Garve |
| 20 April 2017 | 3* | | |
| 27 April 2017 | 10 | 10 | 10 |
| 28 April 2017 | 7 | | 7 |
| 1 May 2017 | 5 | 5 | 7 |
| 2 May 2017 | 5 | 5 | 6 |
| Total no. tagged | 30 | 20 | 30 |

### 2.3.2 PIT tagging

In addition to acoustic tagging, 463 and 127 smolts were tagged with passive integrated transponder (PIT) tags (2 x 12 mm, 0.1 g mass in air, UKID, Lancashire, United Kingdom) at Loch Garve and Loch Meig respectively to assess mortality through these two lakes.

To catch smolts at Loch Garve; a 0.91 m diameter temporary rotary screw trap (RST) was placed in the Upper Garve river 0.82 km above the upstream entrance to Loch Garve (location of RST indicated by the triangle symbol in Fig. 2). The trap was checked daily from 21 April to 17 May and smolts deemed large enough for tagging (at least 90 mm in length), and without signs of significant damage, were removed on the day of capture and anaesthetised with clove oil (0.5 mg $L^{-1}$) and metrics including mass (g), fork length (mm), and presence of minor damage (e.g. scale loss) were recorded. Once anesthetised a small incision (4-6 mm) was made along the ventral surface of the smolt anterior to the pelvic girdle, and a PIT tag was subsequently inserted into the peritoneal cavity. Tagged fish were allowed to recover in a bucket of 100% river water before release as close as possible to the location from which they had been collected. Each PIT tag had a unique code which allowed for subsequent identification, should the same smolt be re-captured. A second RST (1.22 m diameter) was placed 0.2km downstream at the upstream entrance of Loch na Croic (location of RST designated by the triangle symbol in Fig. 2). The trap was checked daily from 21 April to 24 May for PIT tagged smolts using a handheld PIT tag decoder. Smolts were categorised as 'survived' if they had been recaptured at the Loch na Croic fish trap.

To catch smolts at Loch Meig; a temporary RST (1.22 m diameter) was placed in the Upper reaches of the River Meig; 1.6 km from the entrance into Loch Meig (location of RST designated by the triangle symbol in Fig. 3). The trap was checked daily from 18 April to 14 May 2017 and smolts of adequate size (at least 90 mm in length) and without significant damage were removed on the day of capture for tagging. The same tagging procedure as described above was carried out. PIT tagged fish would be subsequently re-detected if they made it successfully 4.26 km downstream through the Meig dam (Fig. 3) which contains an inbuilt PIT tag decoder in the dam's Borland fish lift. This inbuilt decoder recorded the unique code of each passing fish as it exited the river. There are no other possible passage routes from which smolts can exit Loch Meig, therefore survival through Loch Meig was categorised by this redetection.

## 2.4 Trap efficiency

RST only capture a proportion of migratory fish. To estimate the percentage of PIT tagged fish not re-captured in the Loch na Croic RST due to inefficiency, two trap efficiency (TE) studies were carried out on; 11 to 21 April (TE1) and 15 to 24 May (TE2) 2017. RST efficiency was calculated using a 1.22 m diameter temporary RST installed at Loch na Croic (solid triangle symbol in Fig 2). In the trap efficiency studies 220 (TE1) and 203 (TE2) smolts were fin clipped to enable re-identification. Fin clipped smolts were placed in a bucket of 100% river water for thirty minutes to recover before transport and release two riffle-pool sequences (200 m) upstream of the capture site (location indicated the star symbol in Fig. 2). This methodology assumes there is no mortality between the release and recapture site.

Trap efficiency differed between the two assessment exercises. To account the large variation in trap efficiency between the two assessment periods the difference between the trap efficiency studies (TE1, 20.45%; TE2, 39.41% = 18.95%) was divided by the time interval between the first day of TE1 and the last day of TE2 (43 days). From this an incremental increase (0.44%) was applied to the previous day’s trap efficiency value to generate a cumulative value.

Using this result the number of PIT tagged recaptured fish caught on a given day were inflated by the sum of 1 plus the cumulative value of trap efficiency calculated for that day to get a more accurate prediction on the number of smolts that exited the lake, accounting for trap inefficiency.

## 2.5 Statistical analyses

The raw dataset for the 80 tagged fish included more than 2.6 million detections. Prior to analysis each transmitter (tagged fish) was reviewed individually to assess if (and where) mortality had occurred, and remove any false detections that may have occurred due to ping echoes or tag collisions. After reviewing this data, the detection time frame was defined to remove uninformative detections e.g. when a fish died in the detection range of a receiver the inserted transmitter continued transmitting, which in some cases lead to an excess of 100 000 detections. Almost a third of the detections in the raw data set were due to false detections, likely caused by the low (25 sec ± 50%) interval between pings and the proximity to concrete dam walls, which resulted in a high number of false code detections due to sonic collisions (Binder et al. 2016). Of the 80 tagged fish, 24 fish had less than 3 detections at any logical receiver (if the first three detections were not recorded by AMR positioned in the lake directly downstream from the release site this transmitter was discarded) and were thus excluded from further analysis. After these exclusions 55 fish, with a cumulative 691 953 detections remained.

The first set of analyses was carried out to address the following questions regarding survivorship and success:

*1.1 How can we define survival from telemetry observations?*

Lake survival for PIT tagged fish was defined by whether the fish at Loch Meig were redetected at the inbuilt PIT tag decoder, or if fish PIT tagged at Loch Garve were redetected at the RST (downstream of Loch Garve) at Loch na Croic. Chi squared analysis was used to test for a difference in the frequency of PIT tagged smolts exiting Loch Garve and Loch Meig. No survival data from PIT tagged fish was available for Loch Achonachie.

Lake survival of acoustic tagged fish was determined by the meeting of one or two criteria. Firstly, exit was assumed if a tagged smolt was detected by a downstream receiver e.g. if smolts in Loch Meig were detected in Loch Achonachie, or if a smolt was detected by the estuary AMR. Secondly, if an individual was detected on the last receiver gate and subsequently no further detections were received at this gate or any preceding it, it was assumed this smolt had exited the loch.

To address each survivorship question the data was split into two different types. A dataset which included all the data regardless of whether the fish were detected at the first receiver ($N$ = 80), and a subset of this data which was refined to only include detected fish (*N* = 55) so to account for any potential effect of delayed tagging mortality.

*1.2 Does lake migration success differ between lakes?*

*1.3 Is lake migration survivorship affected by lake impoundment?*

*1.4 Does the successful migration of smolts to the estuary differ between lochs?*

*1.5 Is estuary migration survivorship affected by lake impoundment?*

Chi squared analysis was used to test for a difference in the frequency of fish successfully exiting the three studied lakes, and between lakes with and without hydropower dam impoundment. To test for differences in lake exit success in impounded and natural standing lakes, data for the two impounded sites (Achonachie and Meig) was combined. The same process was followed to assess for differences in the frequency of tagged smolts that migrated successfully to the estuary.

*1.6 What factors might be driving survivorship of S. salar smolts?*

To assess factors which may be underpinning the success of PIT tagged fish that exited Loch Garve (natural standing water) and Loch Meig (impounded lake) general linear mixed models (GLMM) were created using a binomial distribution with a logistic regression, using R v. 3.3.2 (R Core Team 2015) and the *lme4* package (Douglas et al. 2015). Explanatory variables including: fish length (96 – 156 mm), day of year (range of 106 to 137), and group size (ranged from 1 to 84). Location (Loch Garve or Loch Meig) and individual (unique tag number) were included as random effects. Descriptions of variables can be found in Table 2. Fish weight was highly correlated with fish length therefore only fish length was included in the model. Continuous variables were scaled using the *scales* base function to create z-scores (values of -2 to 2). Model selection was based on the Akaike information criterion (AIC) between nested models, with model terms tested systematically. This procedure was repeated until the model with the minimum AIC, and therefore with the most significant terms explaining survival remained.

To assess factors which may be driving the successful migrating of acoustic tagged fish in response to addressed questions (above) a number of general linear mixed models (GLMM) were created using a binomial distribution with a logistic regression, using R v. 3.3.2 (R Core Team 2015) and the *lme4* package (Douglas et al. 2015). Explanatory variables included: fish length, day of year (DOY), impoundment (Y/N), and group size (3- 10). Location (lake) and surgeon were incorporated as random effects (Table 2). Continuous variables were scaled using the *scales* base function to create z-scores. Model selection was based on the Akaike information criterion (AIC) between nested models, with model terms tested systematically. This procedure was repeated until the model with the minimum AIC, and therefore with the most significant terms explaining survival remained. To further assess the relative contribution of each variable in explaining the observed variation, the *MuMin* package (Barton 2016) was used. The relative importance of each variable is the sum of all the AIC-weights from the model which contain that variable. The sum of all AIC weights are standardised to the sum of 1 across all model sets, and the relative weight of each variable can range from 0 to 1.

### *1.7 Does the role of experience (whether a fish had exited a hydropower dam before) affect lake migration success?*

To test for the differences in the frequency of successful migrants and the role of experience (whether a fish had migrated successfully through an impounded loch before) a chi squared test was carried out using a dataset comprising of all tagged fish.

Table 2. Description of variables used in the model selection process, with random fixed effects indicated by (*).

| Variable | Description |
|---|---|
| Day of year (DOY) | The julien calendar date that the fish was released (1-365) |
| Impounded | Whether a site was impounded by a large hydropower dam (10 > m in head height) |
| Group size | The number of fish that were released at the same date and time at a given site |
| Length | Length of a fish |
| Individual* | A individual fish identified by a unique tag number |
| Surgeon* | The individual that carried out the acoustic transmitter insertion |
| Location* | The site that the fish was released |

The second set of analyses address whether differences in exit success (whether a smolt had exited a lake) were due to differences in the movement behaviour of fish. For each question the significance of differences in these metrics for tagged fish that successfully exited their respective loch, and those that did not; within lochs, between lochs, and between impounded lakes and natural standing waters was tested.

This analysis was carried out exclusively for movement within lochs, therefore data was restricted from the first detection on the first receiver gate (entrance) to the last detection on the last receiver gate (exit) within each loch. Movement analysis aimed to address several key questions including:

2.1 *How long did it take for successful smolts to exit their respective lakes?*

2.2 *Is the time taken for a smolt to exit a lake significantly different between lakes, and between impounded and not impounded lakes?*

To calculate the time taken for fish to successful exit a lake the *plyr* package (Wickham 2011) was used to first manipulate and summarise the data. The time taken was then calculated as the time difference between the first detection on the first lake AMR gate to the last detection on the last AMR gate using the *difftime* base *R* function. An analysis of variance (ANOVA) was used to test for a significant difference in the time taken for successful fish to exit their respective lakes, and between impounded lakes and natural standing waters. A post hoc Tukey test was used to test for significant pair-wise comparisons.

*2.3 What was the absolute minimum transit speed of fish that successfully exited a lake?*

To assess whether the differences seen in exit time were due to the size of the lake crossed, the absolute minimum lake transit speed of fish that had successfully exited each lake was calculated. This was calculated by dividing the total length of the lake by the time taken for each fish to exit a lake (described above). The calculated absolute minimum lake transit speed assumes a strictly positive direction of movement (from inflow to outflow).

*2.4 Is the minimum transit speed of fish that exited a lake significantly different between lakes, and between impounded and not impounded lakes?*

An ANOVA was used to test for significant differences in the absolute minimum lake transit speed between lakes. A post-hoc Tukey test was then used to assess pair-wise comparisons of absolute minimum lake transit speed between lakes.

*2.5 What was the mean total distance travelled by successful and unsuccessful fish in three lakes?*

To calculate a more realistic measure of distance that tagged fish travelled during the study period I used the *GenerateDirectDistance* and *RunResidenceExtraction* function in the *VTrack* package (Campbell et al. 2012). The distance function generated a matrix with the corresponding distance between each receiver gate (centroid) location and release site. I then used this matrix in the residence extraction function to extract all movements between AMR gates, and from this calculated the total distance as a sum of all these movements by an individual. I used the *dplyr* package (Wickham 2011) and *R* base functions to extract and summarise the data so to facilitate between lake comparisons.

*2.6 Is the total distance that smolts travel in a lake significantly different between lakes and between impounded and not impounded lakes?*

An analysis of variance (ANOVA) was used to test for a significant difference in the mean total recorded distance travelled by tagged fish that exit a lake, and those that did not during the entire study period. A post hoc Tukey test was used to test for significant pair-wise comparisons.

*2.7 What was the average speed of successful (exited a lake) and unsuccessful (did not exit a lake) fish in the three lakes?*

The average swim speed of fish that exited a lake was calculated by calculating the total detection time for each tagged individual: the difference in seconds between the first detection on the first AMR gate and last detection on the last AMR gate in each lake. For smolts that did not exit a lake, this was the difference between the first detection on the first AMR gate, and the last detection on an AMR gate. The total recorded distance travelled by each smolt (described above) was then divided by the total detection time to calculate speed in m/s.

*2.8 Was there a difference in the proportion of downstream to upstream movements between successful and unsuccessful fish within and between lakes? Did this differ significantly between natural standing waters and those impounded by large hydropower dams?*

To further understand how smolts were moving within each lake I used the list of movements carried out by each fish from *VTrack* (described in 2.3). Movements were then assigned to two categories: downstream (inflow to outflow movement e.g. from G1 to G2) and upstream, (outflow to inflow e.g. from G4 to G1) movements. It was assumed that detections on gates which were not directly adjacent to the initial detection gate was due to breaks in the gate detection wall. For the purpose of this analysis a single cluster of receivers was regarded as a receiver gate. A chi squared test was used to calculate whether there was a difference in the relative frequency of downstream and upstream movement for all fish within a given lake. AMR gate A5 (Loch Achonachie) was excluded from movement analysis as it was deemed neither a downstream or upstream directional movement.

# 3. Results

## 3.1 Range testing

Range testing found a mean detection efficiency of; 80.05 ± 14.17 % at 101 m, 77.82 ± 14.73 % at 212 m, 74.07 ± 19.34 % at 327 m and 65.48 ± 24.43 % at 400 m (Table 3). There was increased variability in detection efficiency with increasing distance from a transmitter (Fig. 5). These results were used to adjust the AMR spacing to minimise the possibility of a fish passing undetected through the lake.

Table 3. Detection efficiency (mean and standard deviation to 2 d.p.) of a receiver with increasing distance from a transmitter.

| Distance (m) | Probability of detection (%) | |
|---|---|---|
| | Mean | SD |
| 0 | 90.59 | 11.16 |
| 48 | 80.05 | 14.16 |
| 101 | 80.05 | 14.17 |
| 115 | 75.34 | 20.79 |
| 122 | 67.15 | 24.51 |
| 212 | 77.82 | 14.73 |
| 216 | 77.36 | 17.32 |
| 232 | 63.07 | 25.78 |
| 285 | 63.13 | 24.27 |
| 327 | 74.07 | 19.34 |
| 332 | 50.12 | 27.83 |
| 400 | 65.48 | 24.43 |
| 448 | 57.99 | 27.65 |

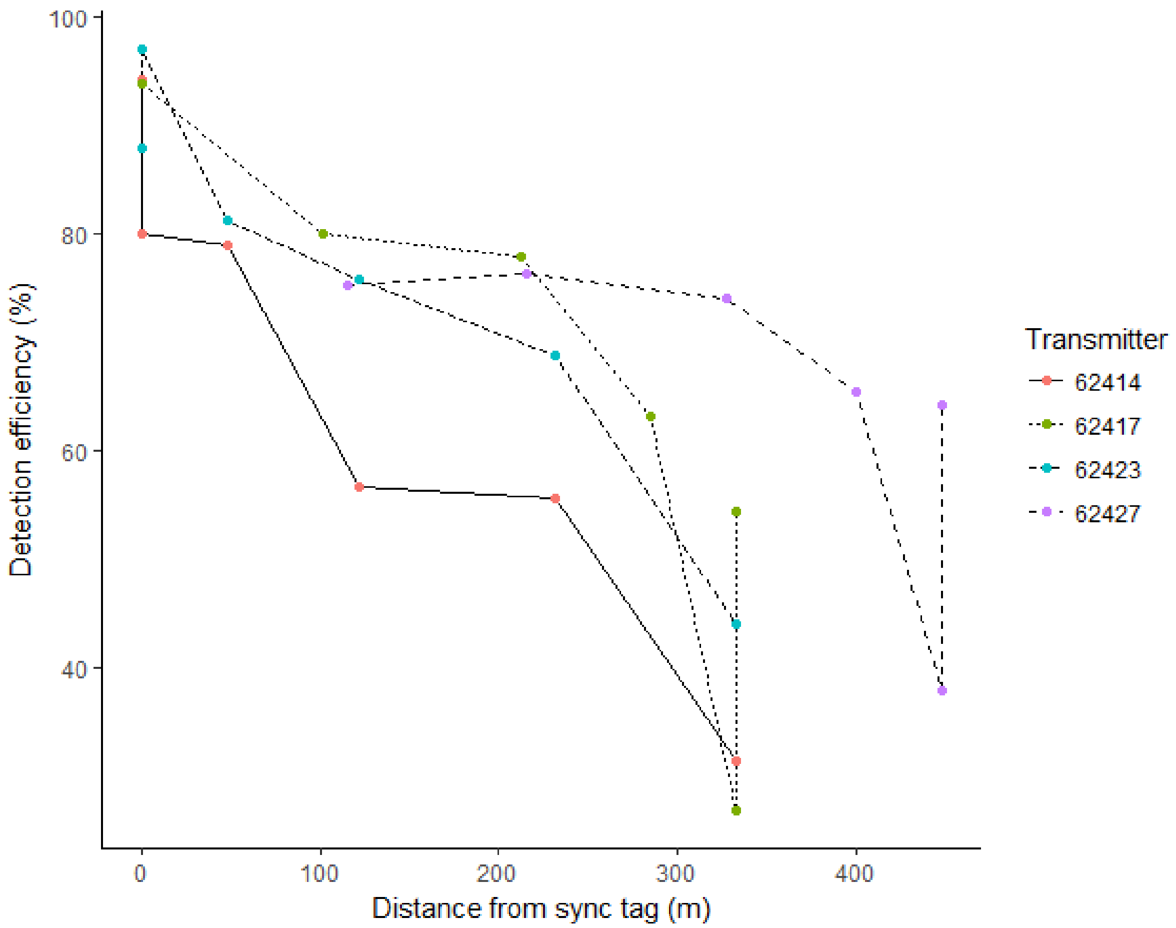


Fig. 5. Probability of signal detection emitted by four unique transmitters with increasing distance from a receiver.

## 3.2 Survivorship and migration success

### 3.2.1 PIT tag fish survivorship

Of the 453 fish PIT tagged at Loch Garve, 49 successfully migrated from the release site (hollow pentagon symbol, Fig. 2), to the Loch na Croic RST 4.16 km downstream (triangle symbol, Fig. 2). Corrected by the calculated trap efficiency increases this value to 153 smolts (33.8 % of those tagged). The mean length of PIT tagged fish at Loch Garve was 117.67 ± 10.49 mm (range = 96 – 151 mm), and the mean weight was 16.60 ± 4.65 g (range = 8.3 – 36 g).

Of the 127 fish PIT tagged and released in the river above Loch Meig (hollow pentagon symbol, Fig. 3), 42 (33.07%) were recorded passing through the inbuild PIT loop in the Meig dam 4.28 km downstream (dashed line, Fig. 3). The mean length of fish PIT tagged at Loch Meig was 122.50 ± 9.59 mm (range = 104 – 156 mm), and the mean weight was 20.20 ± 17.51 g (range = 8.3 – 40.6 g).

There was no significant difference in the frequency PIT tagged smolt survival between Loch Garve and Loch Meig, $x^2(1, N = 580) = 1.417$, $P > 0.05$. In a mixed effect model testing the effect of DOY, fish length, group size, and using location (Loch Meig/Loch Garve), and individual (tag ID) as a random effect group size was a significant predictor of success, with earlier migrants more likely to exit a lake (GLMM: -0.525 ± 0.151, Z = 3.471, P = <0.001).

### 3.2.2 Acoustic tagged fish survivorship

80 *S. salar* smolts were tagged during the study period; mean fork length = 148.4 ± SD 8.7 mm, mean mass = 32.9 ± SD 5.7 g. There was no significant difference in the length (ANOVA, $F_{2,78} = 0.162$, P = 0.851) or weight (ANOVA, $F_{2,78} = 0.068$, P = 0.934) of tagged smolts that were released at the three locations.

Of the 30 tagged smolts released at Garve, 21 (70%) were detected on the first lake AMR (G1). 50% (15) of tagged fish released in Loch Garve exited the loch successfully, with 40% (6) of those exiting the loch detected 12.4 km downstream at the estuary AMR (E1) (Fig 6a).

In Loch Meig, of the 30 tagged smolts released 17 (57%) were detected on the first lake AMR (M1). 8 (47%) fish detected successfully exited the lake, with 3 fish detected 5.7 km downstream of the last AMR gate (M7) in Loch Meig, at the first AMR in Loch Achonachie (A1) (Fig 6b).

Of these 3 fish, 2 (66%) successfully exited Achonachie, but were not redetected in the estuary (Fig. 5b). Of the 20 fish that were released at Achonachie, 85% were detected on the first lake AMR (A1), with 7 (41% of those that entered) exited the loch, and 2 (10% of those tagged) were detected 9.9 km at the estuary AMR (E1) (Fig. 6c).

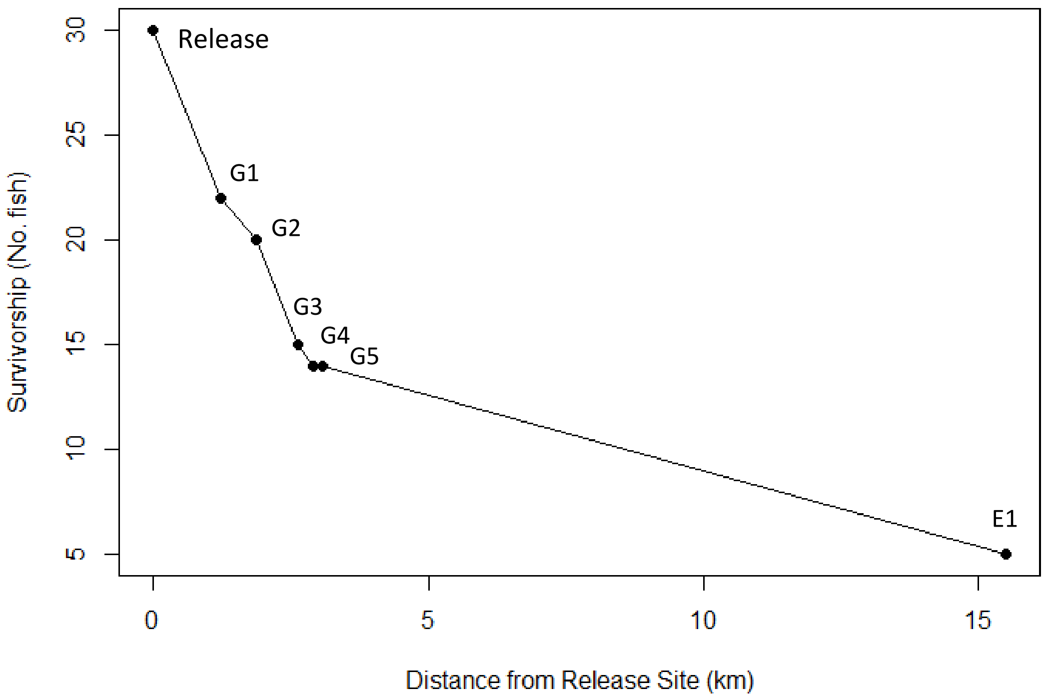


Fig. 6a. Survivorship of acoustically tagged *S. salar* smolts in Loch Garve, in terms of number of fish detected at each AMR gate in the array. Each AMR are represented by solid circles. Includes: release site, 5 AMR gates in Loch Garve (G1-G5) and the estuary AMR (E1).

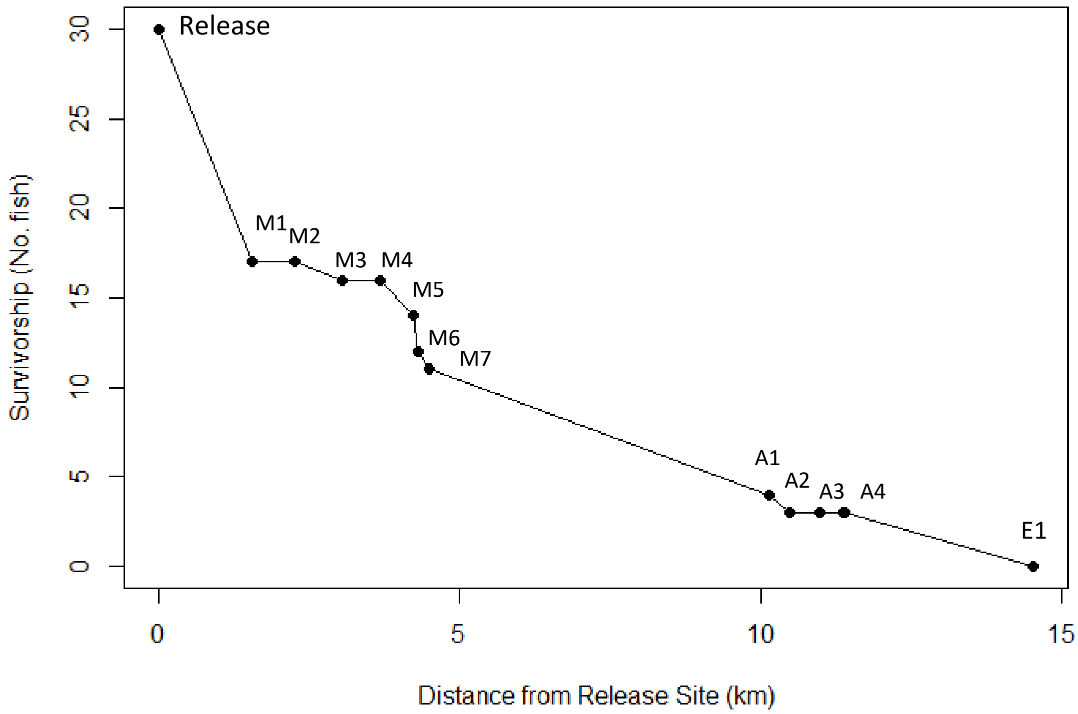


Fig 6b. Survivorship of acoustically tagged *S. salar* smolts in Loch Meig, in terms of number of fish detected at each AMR gate in the array. Each AMR gate is represented by solid circles. Includes: release site, 7 AMR gates in Loch Meig (M1-M7), 4 AMR gates in Loch Achonachie (A1-A4) and the estuary AMR (E1).

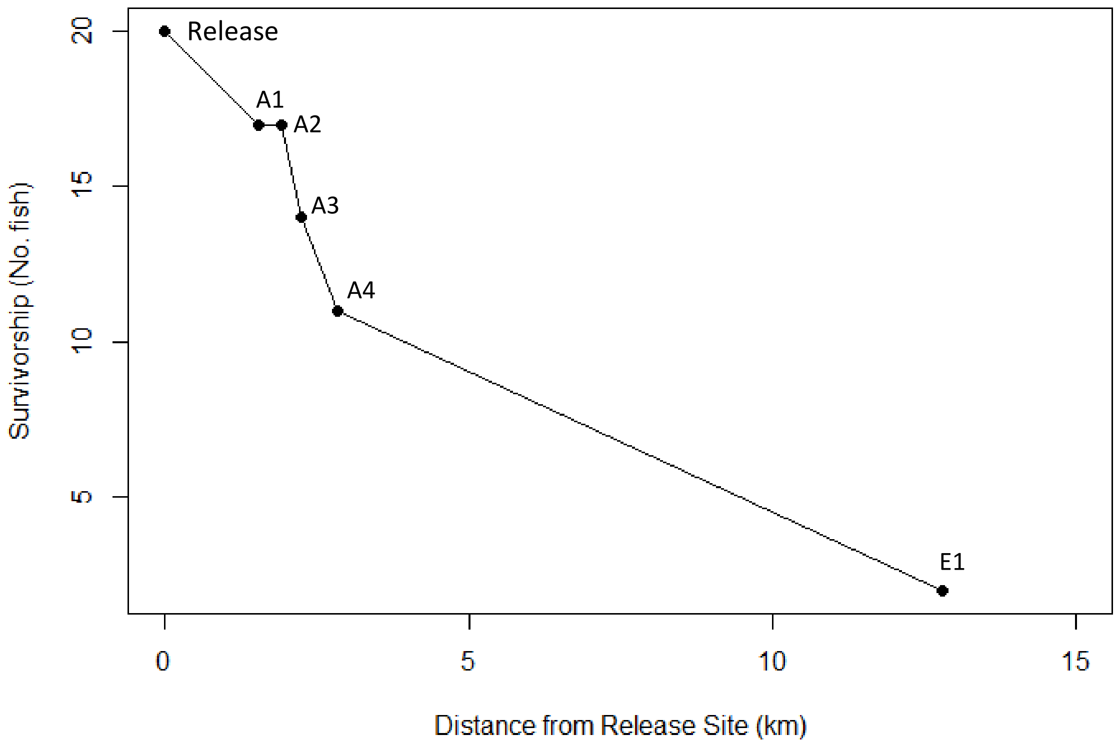


Fig. 6c. Survivorship of acoustically tagged *S. salar* smolts in Loch Achonachie, in terms of number of fish detected at each AMR gate in the array. Each AMR gate is represented by solid circles. Includes: release site, 4 AMR gates in Loch Achonachie (A1-A4) and the estuary AMR (E1).

## 3.3. Exit success

### 3.3.1 Lake exit success

All tagged fish

There was no significant difference in the relative frequency of fish that successfully exited a lake between lakes, $x^2(2, N=80) = 3.556$, $P = 0.169$. However, there was almost a significant difference in the frequency of fish that successfully exited the impounded lakes and natural standing lakes, $x^2(1, N=80) = 3.2$, $P = 0.074$. In a mixed effect model testing the effects of DOY, lake impoundment, fish length, DOY and group size, and using surgeon and lake as a random effect lake exit success was significantly predicted by; day of year (GLMM: -0.690 ± 0.274, Z = -2.517, $P = 0.018$) and impoundment (GLMM: -1.181 ± 0.520, Z = -2.274, $P = 0.048$). The calculated variable weights of DOY (0.967) and impoundment (0.808) supports these variables being a significant predictor of success (Table 4a).

Table 4a. AIC values of competing models, with subsequent single term deletions from the most complex (model 1) to least complex model (model 3).

| Model. No. | AIC | Weighting (3.d.p) | Incorporated fixed effects | | | |
|---|---|---|---|---|---|---|
| | | | Impoundment | Length | DOY | Group size |
| 1 | 107.4 | 0.084 | * | * | * | * |
| 2 | 105.5 | 0.216 | * | | * | * |
| 3 | 103.9 | 0.481 | * | | * | |
| 4 | 105.8 | 0.186 | | | * | |
| 5 | 109.3 | 0.032 | * | | | |
| Relative weighting | | | 0.813 | 0.084 | 0.968 | 0.300 |

Detected fish analysis

The proportion of total tagged and released fish that exited a lake differed between three sites (Fig. 7a). However, this difference was not significant between the three lakes, $x^2(1, N = 69) = 4.024$, $P =$

0.134. Survivorship out of impounded lakes (44% of the total released upstream) was lower, than found in non-impounded sites (50% of the total released upstream) (Fig. 7b). There was a significant difference in lake survival of individuals migrating through the natural and impounded lakes, $x^2(1, N= 55) = 3.906$, $P = 0.048$. In the mixed model with the lowest AIC (Table 4b) impoundment was the only significant predictor of lake exit success, with individuals in impounded lakes less likely to succeed (GLMM: $-1.265 \pm 0.642$, $Z = 1.972$, $P = 0.053$). The calculated variable weights of impoundment (0.998) and DOY (0.716) supports these variables being a significant predictor of success (Table 4b).

Table 4b. AIC values of competing models, with subsequent single term deletions from the most complex (model 1) to least complex model (model 3).

| Model. No. | AIC | Weighting (3.d.p) | Incorporated fixed effects | | | |
|---|---|---|---|---|---|---|
| | | | Impoundment | Length | DOY | Group size |
| 1 | 81.8 | 0.086 | * | * | * | * |
| 2 | 80.2 | 0.192 | * | | * | * |
| 3 | 78.7 | 0.496 | * | | * | |
| 4 | 89.0 | 0.192 | | | * | |
| 5 | 79.5 | 0.034 | * | | | |
| Relative weighting | | | 0.998 | 0.090 | 0.716 | 0.290 |

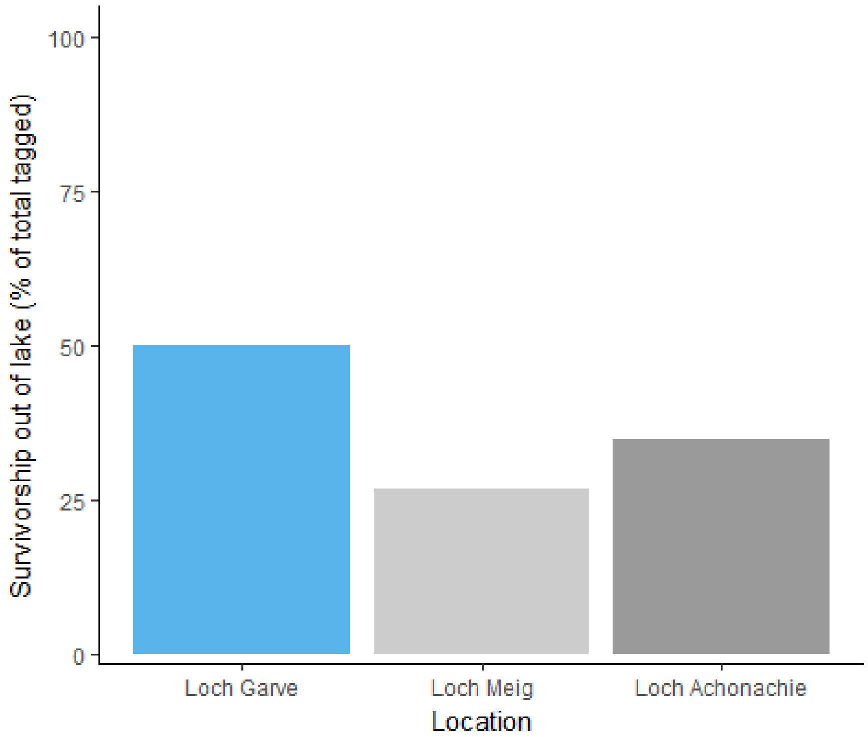


Fig. 7a. Lake survivorship of acoustic tagged *S. salar* smolts through Lake Garve (*N* tagged = 30), Loch Meig (*N* tagged = 20) and Loch Achonachie (*N* tagged = 20).

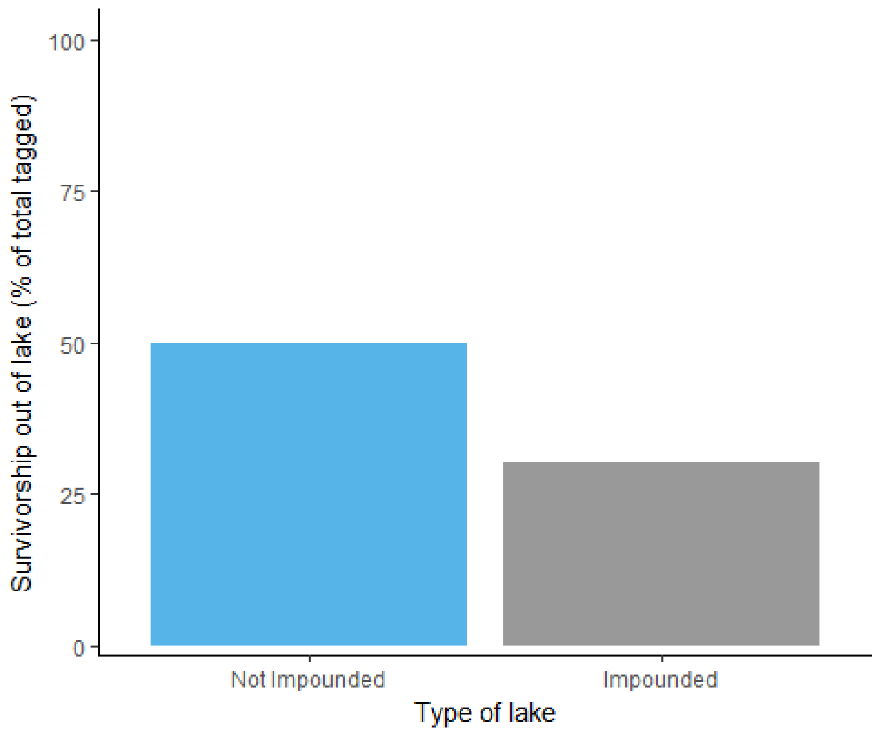


Fig. 7b. Lake survivorship through impounded (Loch Meig and Loch Achonachie; *N* tagged = 50) and not impounded sites (Loch Garve; *N* tagged = 30).

### 3.3.2 Estuary migration success

All tagged fish

The number of tagged *S. salar* smolts that migrated from the upstream release site to the estuary differed between lakes (Fig. 8a). There was a significant difference in the number of successful estuary migrants between the three lakes, $x^2(2, N = 80) = 6.667$, $P = 0.036$. There was also a significant difference in survivorship to the estuary between impounded and not-impounded lakes, $x^2(1, N = 80) = 5.333$, $P < 0.05$. In a mixed model testing the effects of DOY, lake impoundment, fish length and group size, and using surgeon and location a random effect, individuals migrating through impounded lakes were less likely to succeed than those in natural lakes (GLMM: -2.098 ± 0.991, Z = -2.303, $P = 0.033$). In addition, individuals belonging to larger groups were more likely to succeed (GLMM: 1.264 ± 0.552, Z = 2.290, $P = 0.041$). The calculated variable weights of group size (0.956) and impoundment (0.805) supports these variables being a significant predictor of success (Table 5a).

Table 5a. AIC values of competing models, with subsequent single term deletions from the most complex (model 1) to least complex model (model 3).

| Model. No. | AIC | Weighting (3.d.p) | Incorporated fixed effects | | | |
|---|---|---|---|---|---|---|
| | | | Impoundment | Length | DOY | Group size |
| 1 | 52.8 | 0.118 | * | * | * | * |
| 2 | 51.9 | 0.186 | * | | * | * |
| 3 | 50.1 | 0.457 | * | | | * |
| 4 | 54.8 | 0.044 | * | | | |
| 5 | 51.8 | 0.195 | | | | * |
| Relative weighting | | | 0.805 | 0.118 | 0.304 | 0.956 |

Detected fish analysis

Tagged fish from Loch Garve and Loch Achonachie successfully migrated from the upstream release site to the estuary, but no tagged fish released above Loch Meig were redetected in the estuary (Fig. 8a). There was a significant difference found in the number of individuals successfully migrating to the estuary between lakes, $x^2(2, N = 55) = 6.323$, $P = 0.042$. Fewer smolts migrated from the release site to the estuary in impounded lakes than not impounded lakes (Fig. 8b). There was a significant difference in survivorship to the estuary and between impounded and natural lakes, $x^2(1, N = 55) = 5.377$, $P = 0.02$. Impoundment and group size were found to be significant predictors of successful migration to the estuary. Individuals belonging to large release group sizes were more likely to succeed (GLMM: 0.994 ± 0.474, Z = 2.096, $P = 0.05$), and impoundment had a negative effect on exit success (GLMM: -1.735 ± 0.917, Z = -1.892, $P = 0.041$). The calculated variable weights of group size (0.908) and impoundment (0.815) supports these variables being a significant predictor of success (Table 5b).

Table 5b. AIC values of competing models, with subsequent single term deletions from the most complex (model 1) to least complex model (model 3).

| Model. No. | AIC | Weighting (3.d.p) | Incorporated fixed effects | | | |
|---|---|---|---|---|---|---|
| | | | Impoundment | Length | DOY | Group size |
| 1 | 48.1 | 0.101 | * | * | * | * |
| 2 | 47.1 | 0.167 | * | | * | * |
| 3 | 45.1 | 0.455 | * | | | * |
| 4 | 48.3 | 0.092 | * | | | |
| 5 | 46.9 | 0.185 | | | | * |
| Relative weighting | | | 0.815 | 0.101 | 0.269 | 0.908 |

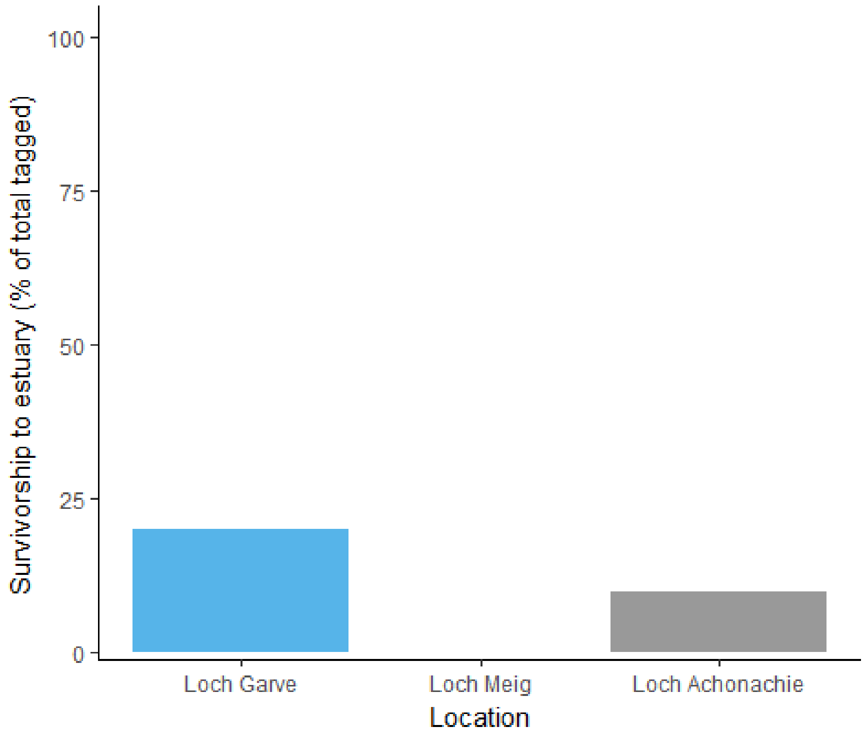


Fig. 8a. Tagged smolt survivorship from release site to the estuary AMR in Loch Garve (*N* tagged = 30), Loch Meig (*N* tagged = 30) and Loch Achonachie (*N* tagged = 20).

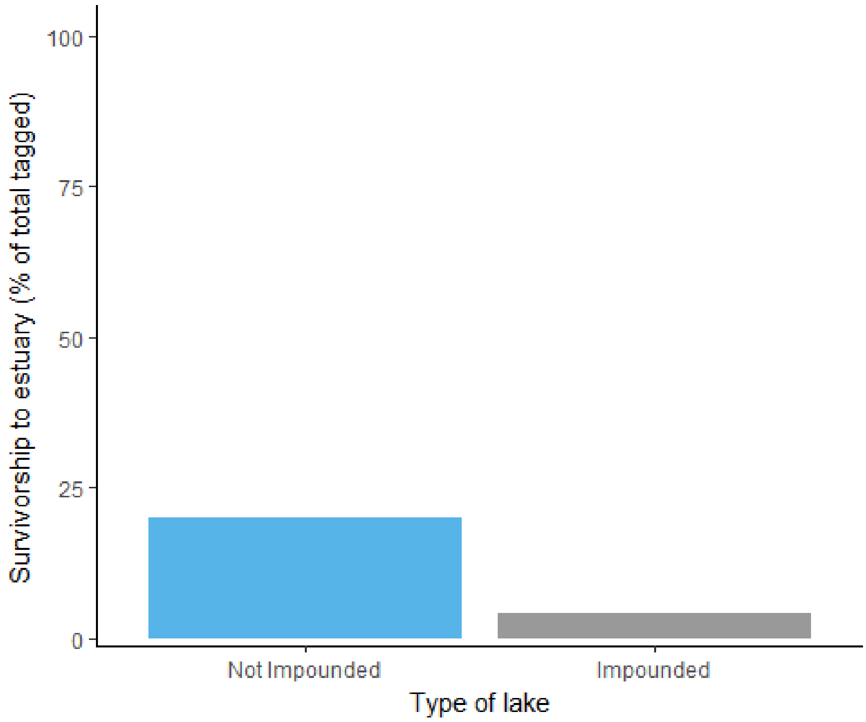


Fig. 8b. Tagged smolt survivorship from release site to the estuary AMR in impounded (Loch Meig and Loch Achonachie; *N* = 50 tagged) and not impounded sites (Loch Garve; *N* = 30 tagged).

### 3.3.3 Experience and lake exit success

There was no significant difference the frequency of successful migrants through an impounded lake as a result of experience (using all the tagged fish data), $x^2$(1, N= 23) = 1.098, *P* = 0.295. A general linear mixed model found that there were no significant predictors of success.

## 3.4 Movement analysis

### 3.4.1 Lake escape time

The time taken for fish to exit their respective lakes was highly variable (Fig. 8). *S. salar* smolts in Loch Garve took the least amount of time on average to exit the lake; range = 0.5 – 30.2 days, mean time = 7.8 ± 13.9 days, median = 2.5 days. Followed by Loch Meig; range = 0.9 – 14.6 days, mean time = 14.5 ± 14.6 days, median = 11.6 days. Smolts in Loch Achonachie took the longest amount of time on average to exit the lake; range = 7.2 – 46 days, mean time = 29.4 days, median = 29.7 days. An analysis of variance (ANOVA) of fish exit time found there was a significant difference in the exit time of fish between lakes ($F_{2,27}$ = 5.423, P = 0.011). A post hoc Tukey test found a significant pair-wise comparison of exit time between fish at Loch Garve and Loch Achonachie (P = 0.008). There was also a significant difference in the fish exit time between impounded and not impounded sites (ANOVA, $F_{1, 27}$ = 9.054, P = 0.006)

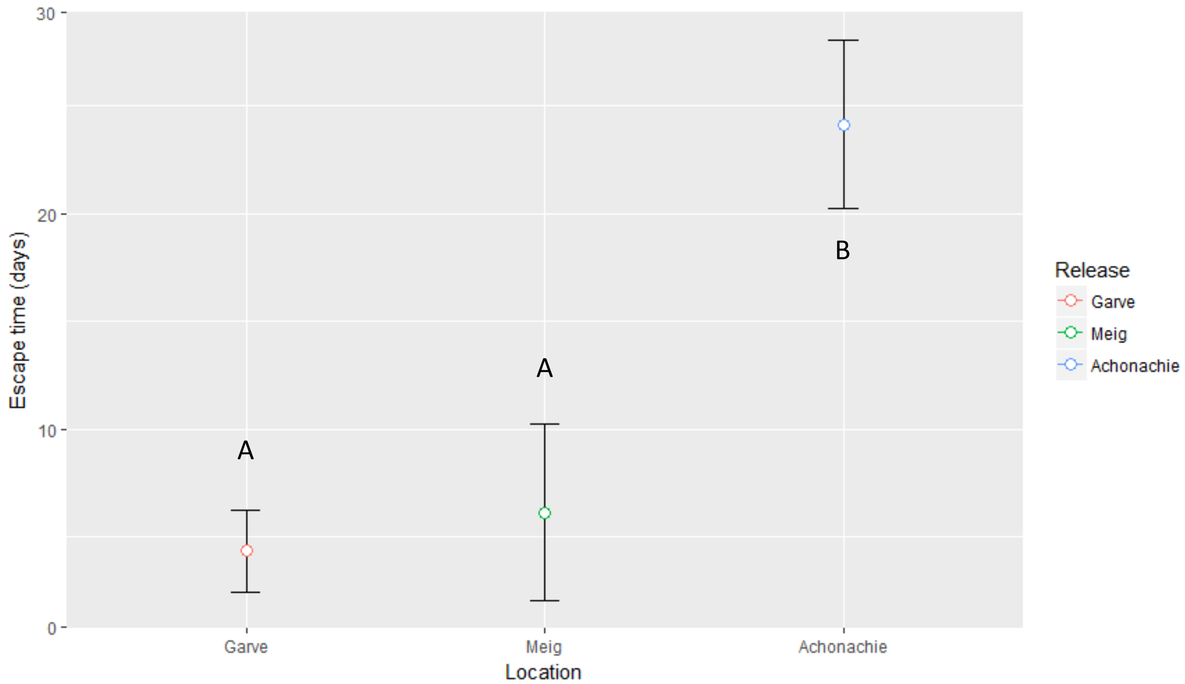


Fig. 8. Escape time of *S. salar* that exited a lake, calculated as the number of days between the first detection on the first AMR gate, to the last detection on the last AMR gate within each lake. The median time (minutes), 75% quantile (upper limit), and 25% quantile (lower limit) are indicated. Similar alpha characteristics indicate no significant differences at a P < 0.05 significance level in a pairwise post hoc Tukey test.

### 3.4.2 Absolute minimum lake transit speed

Smolts that had successfully exited Loch Garve had the highest absolute minimum lake transit speed of 0.0118 ± 0.0109 SD m/s (median = 0.0087 m/s, range = 0.0043 – 0.0433 m/s) (Fig. 9). This was followed by fish exiting Loch Meig, which travelled at a mean absolute minimum lake transit speed of 0.0008 ± 0.0007 SD (median = 0.0031 m/s, range 0.0003 – 0.0021 m/s). Fish exiting Loch Achonachie had the slowest mean absolute minimum lake transit speed of 0.0093 ± 0.0007 m/s. (median = 0.0005 m/s, range 0.0008 – 0.00021 m/s). There was an almost significant difference in the absolute minimum transit speed of fish migrating through the three lakes (ANOVA, $F_{2,27} = 2.866$, $P = 0.074$). The only near significant pair-wise comparison of absolute minimum lake transit speed was between Loch Garve and Loch Achonachie (0.061). There was no significant difference in the absolute minimum lake transit speed of fish migrating through impounded and not impounded lakes ($ANOVA, F_{2, 26} = 1.902, P = 0.17$).

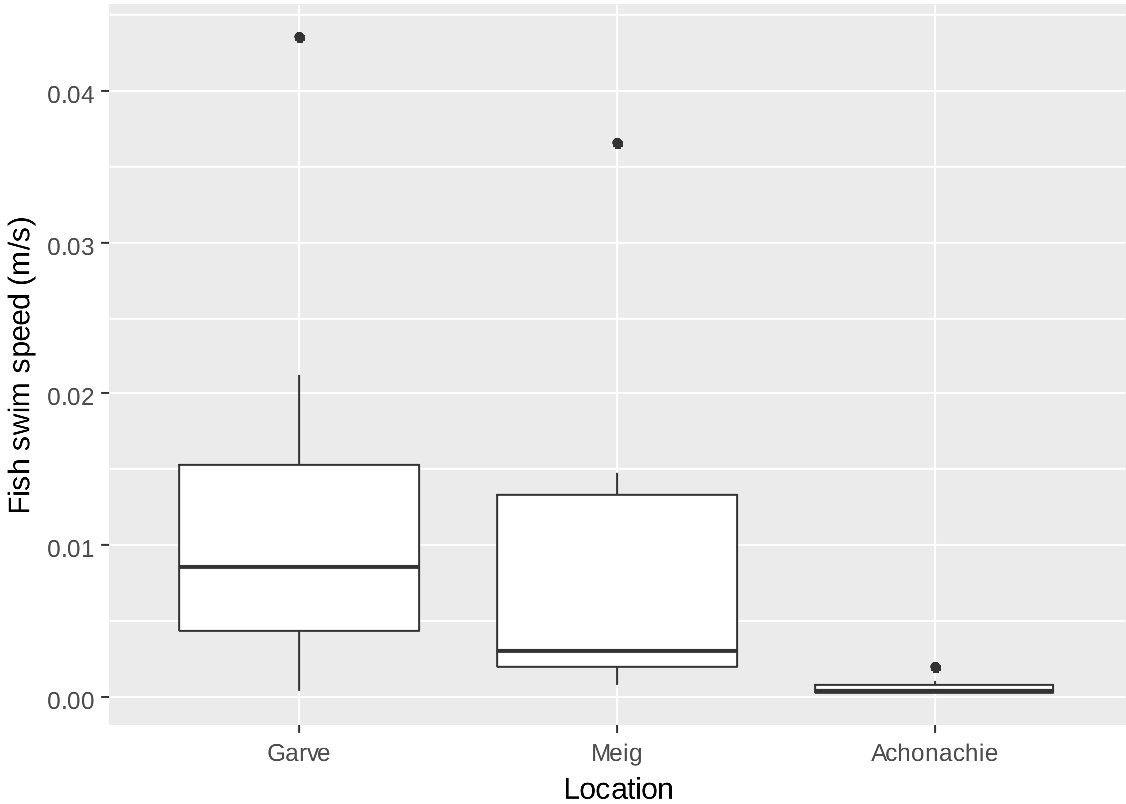


Fig. 9. The absolute minimum lake transit speed of fish successfully exiting their respective lakes in metres per second (m/s).

### 3.4.3 Total distance

There was a significant difference in the total distance travelled by fish in the three different lakes (ANOVA, $F_{2, 50} = 6.11$, $P = 0.004$). A post-hoc Tukey test found a significant difference in distance travelled by fish in Loch Garve and Loch Meig ($P = 0.011$), and Loch Garve and Loch Achonachie ($P = 0.015$), but not between the two impounded lakes, Loch Meig and Loch Achonachie ($P = 0.996$). This result is also supported by an analysis of variance test which found a significant difference in the total distance travelled by fish in impounded and not impounded lakes (ANOVA, $F_{1, 51} = 12.46$, $P < 0.001$). There was no significant difference in the distance travelled by smolts that exited a lake and those that did not in Loch Garve (ANOVA, $F_{1,19} = 2.11$, $P = 0.163$) and Loch Meig (ANOVA, $F_{1, 14} =$

0.726). But there was a significant difference in the distance travelled by smolts that exited Loch Achonachie, and those that did not (ANOVA, $F_{1, 14} = 5.26$, $P < 0.05$).

Tagged smolts that successfully and unsuccessfully exited Loch Garve travelled the smallest total distance during the entire study period, with a total distance of 912 km travelled (*N* = 21): 521 km by successful fish (*N* = 15, mean distance per fish = 35 ± 3 SD km), 391 km by unsuccessful fish (*N* = 6, mean distance per fish = 65 ± 8 km SD) (Fig. 10). Tagged smolts in Loch Meig (*N* = 16) travelled the greatest cumulative distance at 3 084 km travelled during the entire study period; with 967 km travelled by fish that successfully exited the lake (*N* = 7, mean distance per fish = 138 ± 19 km SD), and 2116 km travelled by those that did not (*N* = 9, mean distance per fish = 235 ± 30 km SD). Tagged smolts in Loch Achonachie travelled, with a total distance of 2 987 km (*N* = 16): 700 km by successful fish (*N* = 9, mean distance per fish = 78 ± 7.69 km SD), and 2 288 km by unsuccessful fish (*N* = 7, mean distance per fish = 327 ± 23.34 km SD).

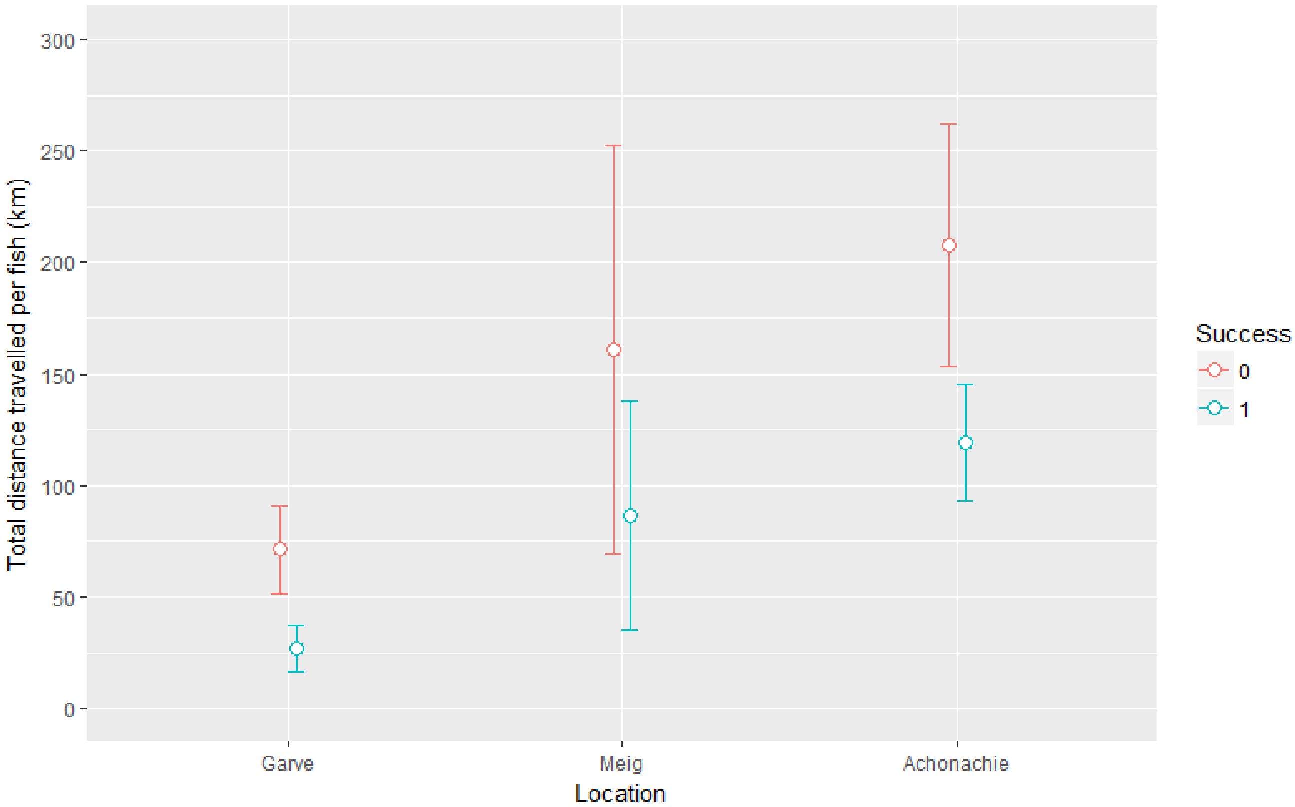


Fig. 10. Median total distance travelled km ± SE per tagged fish that unsuccessfully (0) and successfully (1) exited each lake during the study period.

### 3.4.4 Fish swim speed

There was no significant difference in the mean swim speed during the study period of tagged fish in the three lakes (ANOVA, $F_{2,50}$ = 2.381, P = 0.103), or between impounded and not impounded lakes (ANOVA, $F_{1,51}$ = 0.898, P = 0.348). There was also no significant difference in mean swim speed of smolts that exited a lake, and those that did not in the three lakes during the study period (ANOVA, $F_{1,51}$ = 1.559, P = 0.218). There was no significant difference in mean swim speed in relation to fish length (ANOVA, $F_{17,11}$ = 1.109, P = 0.345).

Smolts that exited Loch Meig had the fastest mean swim speed of 0.24 m/s (range = 0.03 – 0.387 m/s) (Fig. 8; Table 6), and smolts that exited Loch Achonachie had the slowest mean swim speed of 0.053 m/s (range 0.007 – 0.116 m/s).

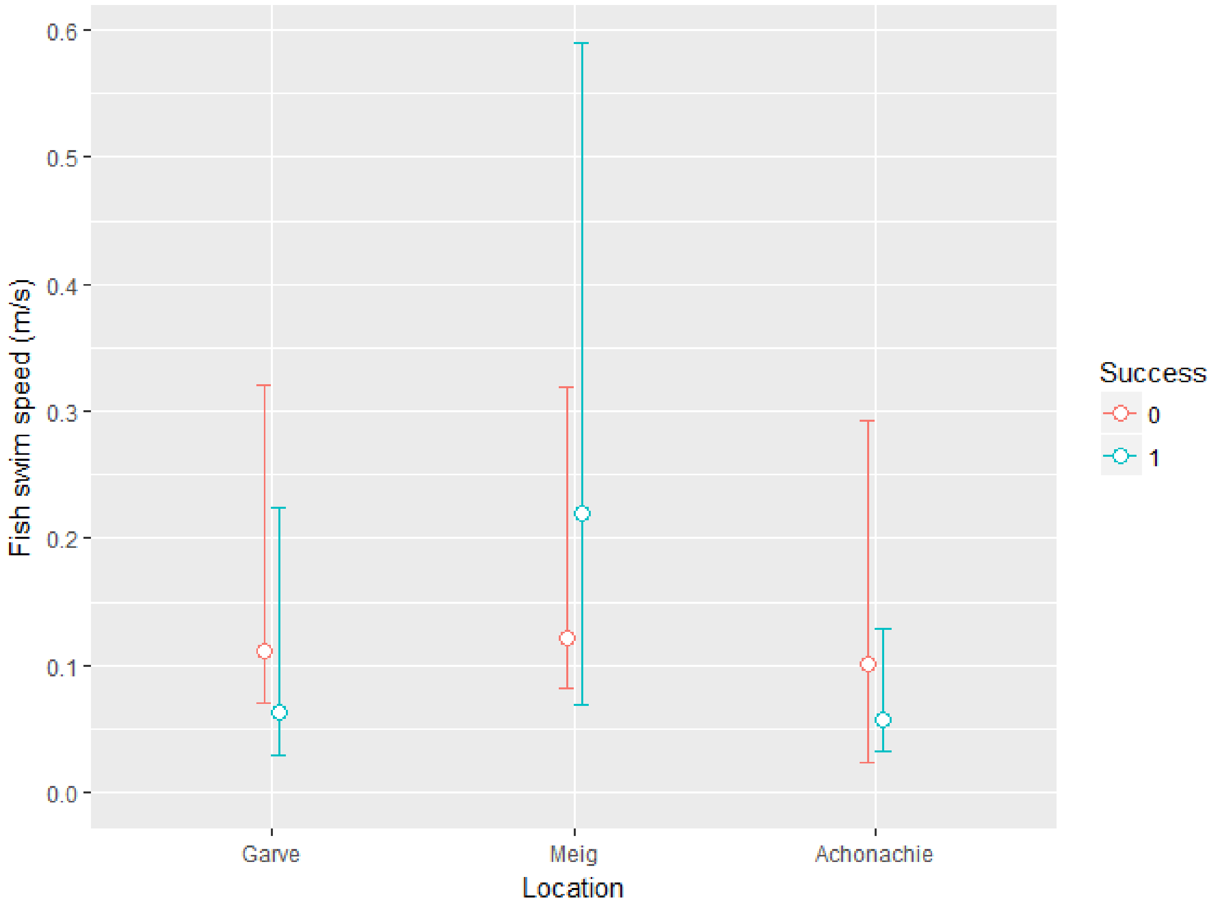


Fig. 11. Median fish swim speed (m/s), 75% quantile (upper limit), and 25% quantile (lower limit) are indicated of tagged fish that successfully (1) and unsuccessfully (0) exited each lake during the study

period. There was no significant difference in fish swim speed of fish that successfully exited a lake and those that did not.

Table 6. The number of tagged fish that successfully (1) or unsuccessfully (0) exited their respective lake. The detection time describes the time window of study of that respective group, for example for successful fish this is the time difference between the first detection on the first AMR gate and the last detection on the last AMR gate in the lake. For unsuccessful fish, this is the total time for which they were detected.

| | | | Lake detection time (days) | | | Swim speed (m/s) | | | |
|---|---|---|---|---|---|---|---|---|---|
| Location | No. fish | Success | Min. | Max. | Mean | Min. | Max. | Mean | Median |
| Garve | 15 | 1 | 0.5 | 30.2 | 6.0 | 0.018 | 0.261 | 0.096 | 0.063 |
| | 6 | 0 | 0.1 | 16.4 | 7.9 | 0.015 | 0.574 | 0.032 | 0.112 |
| Meig | 7 | 1 | 0.2 | 14.6 | 9.2 | 0.030 | 0.387 | 0.240 | 0.220 |
| | 9 | 0 | 1.3 | 47.2 | 15.9 | 0.020 | 1.028 | 0.209 | 0.121 |
| Achonachie | 7 | 1 | 8.3 | 34.3 | 21.8 | 0.007 | 0.116 | 0.033 | 0.058 |
| | 9 | 0 | 8.7 | 43.0 | 23.9 | 0.041 | 0.316 | 0.150 | 0.101 |

### 3.4.5 Directional movement

Movement analysis only included tagged fish detected in the three lakes ($N$ = 55). Overall, tagged smolts ($N$ = 55) carried out 26% more recorded upstream movement than recorded downstream movements (across all sites) (Fig. 12a). Tagged smolts in impounded lakes ($N$ = 34) carried out 28% more total grecorded upstream than downstream movements, and tagged smolts in a non-impounded lake (natural standing water) carried out 9% more total recorded downstream than upstream movements (Fig. 12b). Tagged fish in Loch Garve *(*$N$ = 21) and Loch Meig ($N$ = 17) carried out proportionally more total recorded movements downstream than upstream, however, tagged fish in Loch Achonachie ($N$ = 17) carried out 82% more total recorded movements upstream than downstream (Fig. 12c).

Tagged fish that successfully exited a lake (*N* = 30) carried out 34% more total recorded upstream movement than downstream, and those that did not exit a lake (*N* = 25) carried out 21% more total recorded upstream than downstream movement (Fig. 13a). However, the proportion of downstream to upstream movements by tagged *S. salar* that exited a lake, and those that did not differed between the three studied lakes (Fig 13b; Fig 13c; Fig 13d).

There was a significant difference in the total number of recorded downstream and upstream directional movements of smolts in the three respective lakes, $x^2(2, N = 55) = 419.61, P < 0.001)$, and between impounded and natural lakes, $x^2(1, N = 55) = 66.50, P = < 0.001)$. There was also a significant difference in the total number of recorded downstream and upstream directional movements of smolts that successfully exited a lake, and those that did not, across the three lakes, $x^2(1, N = 55) = 34.31, P < 0.001)$.

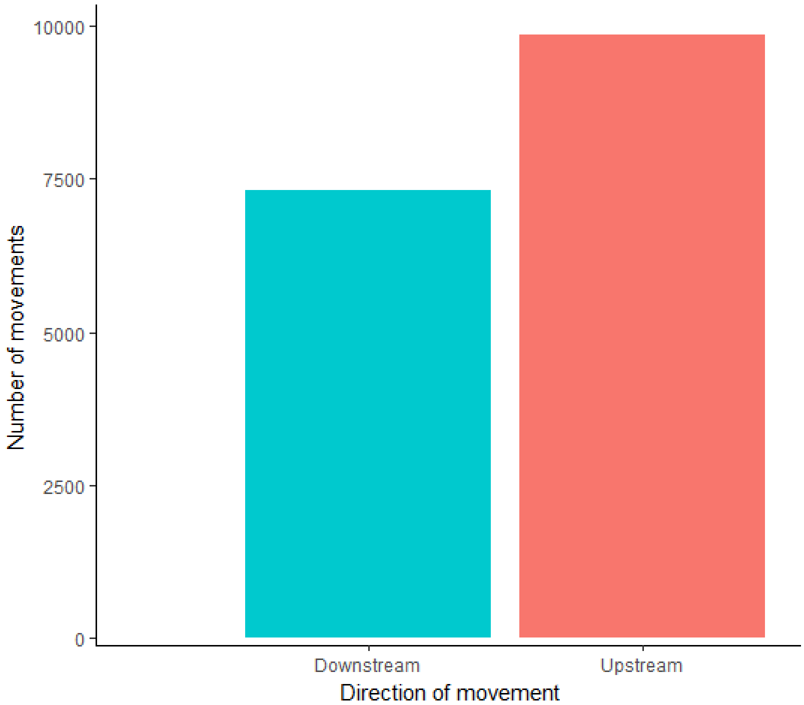


Fig. 12a. Total number of recorded downstream and upstream movements by tagged *S. salar* (*N* = 55) smolts across the three lakes.

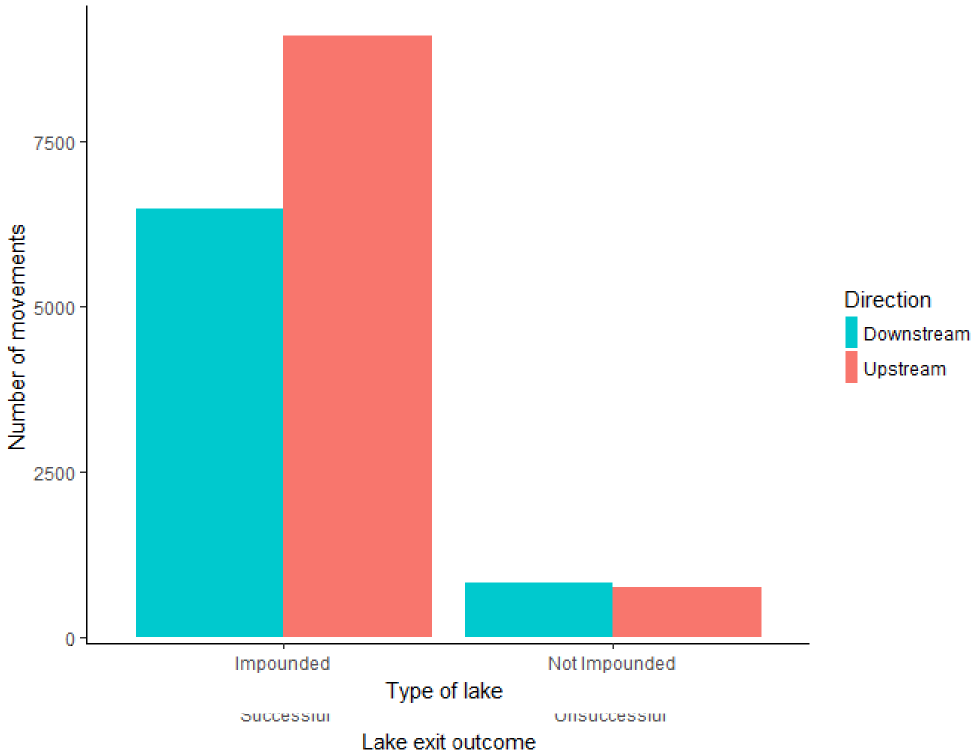


Fig 12b. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts in impounded (*N* = 34) and not impounded lakes (*N* = 21).

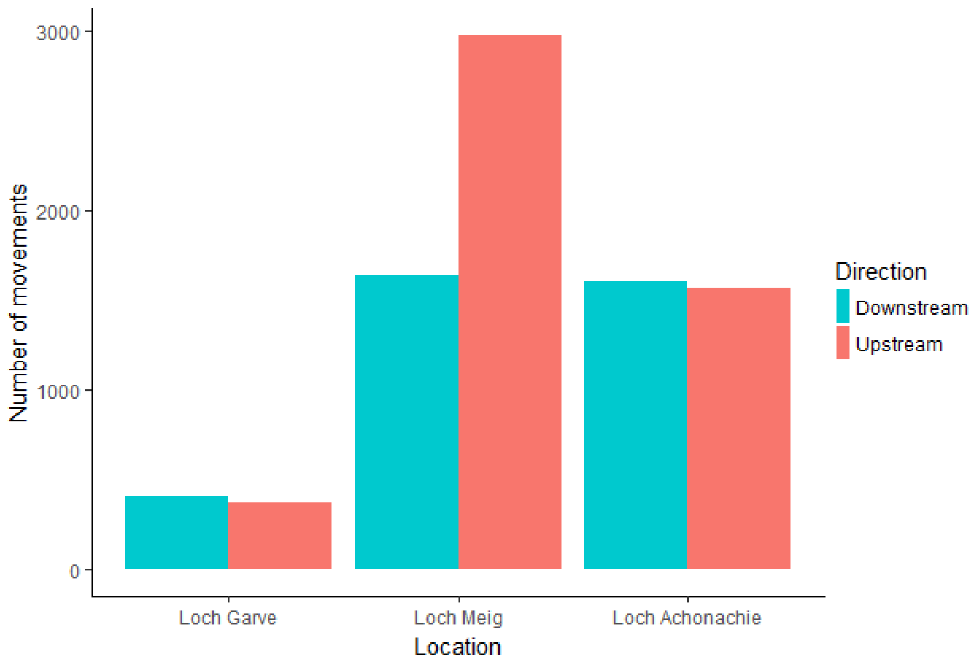


Fig. 12c. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts in Loch Garve ($N$ = 21), Loch Meig ($N$ = 17), and Loch Achonachie ($N$ = 17).

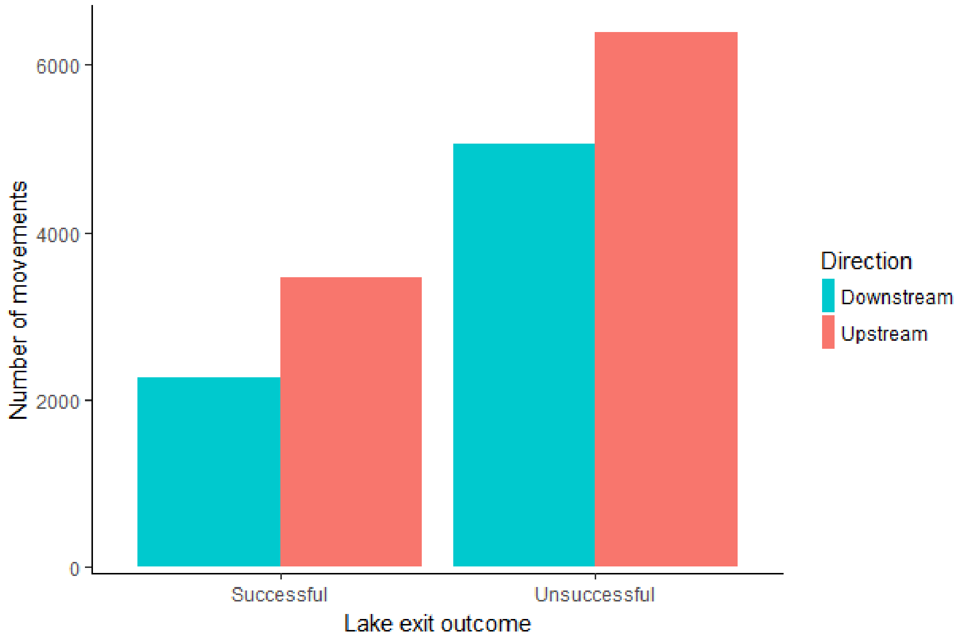


Fig. 13a. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts that successfully ($N$ = 30), and unsuccessfully ($N$ = 25) exited a lake.

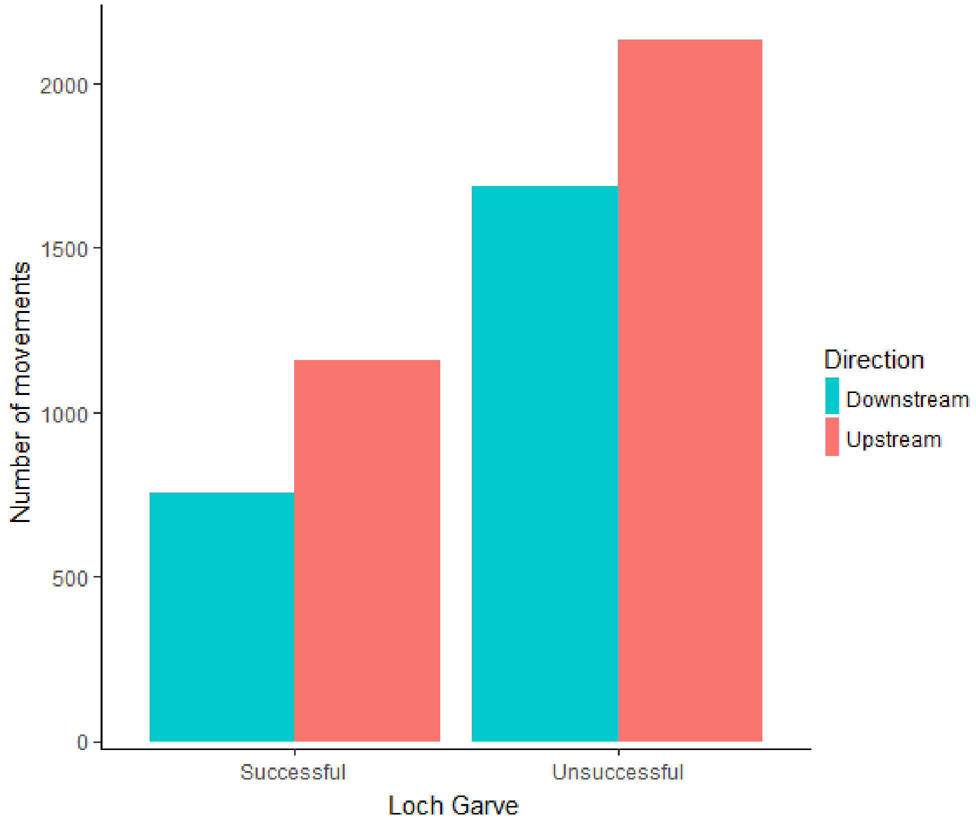


Fig. 13b. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts in Loch Garve (*N* = 21), that exited the lake (successful; *N* = 15) and those that did not (unsuccessful; *N* = 6).

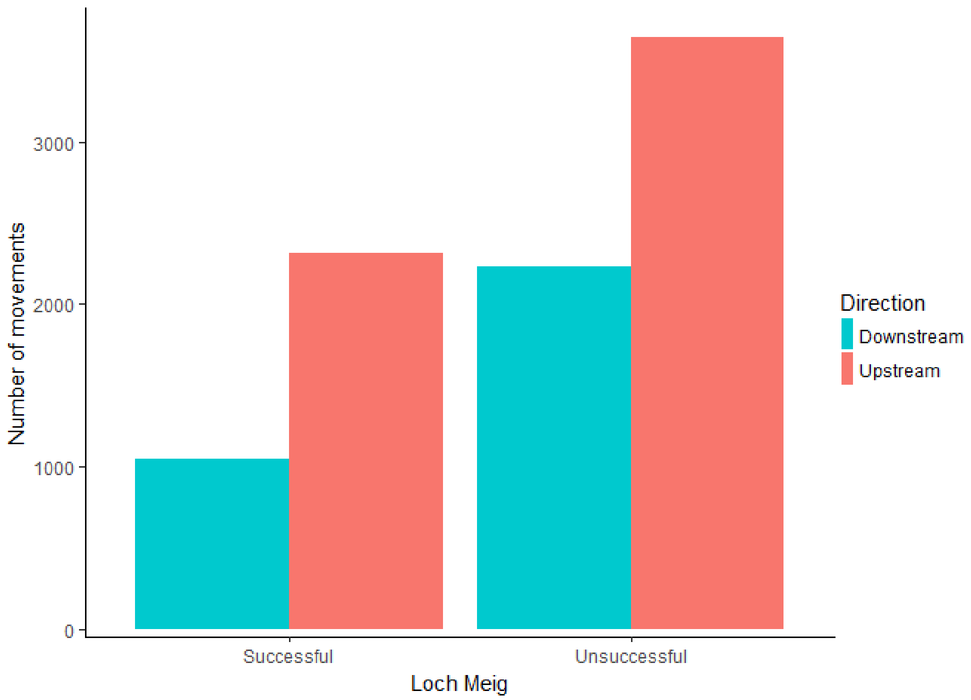


Fig. 13c. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts in Loch Meig (*N* = 17), that exited the lake (successful; *N* = 8) and those that did not (unsuccessful; *N* = 9).

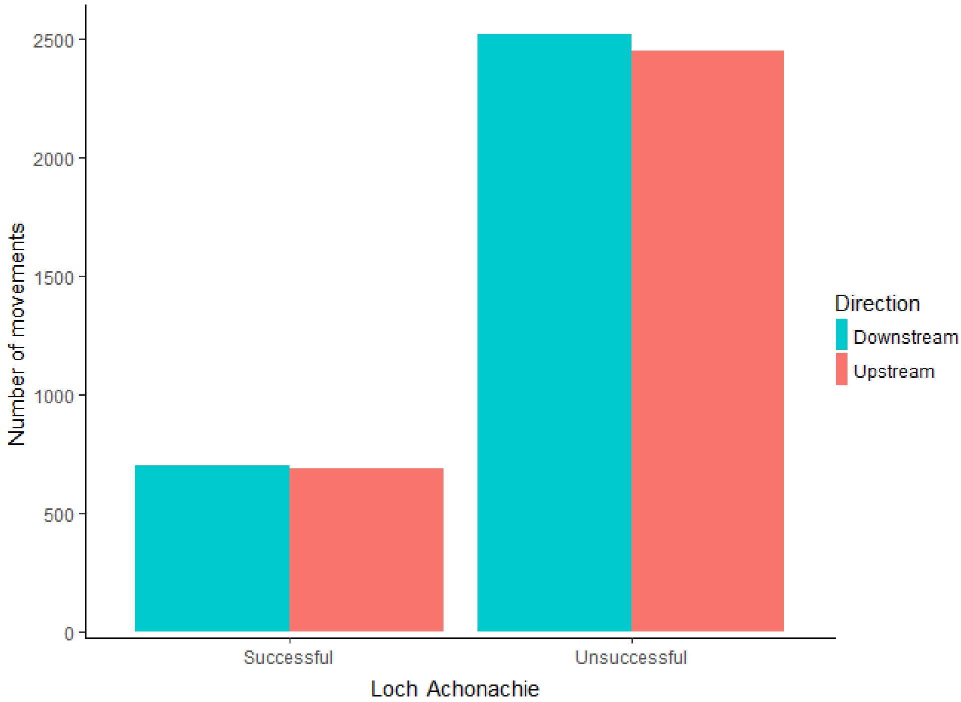


Fig. 13d. Total number of recorded downstream and upstream movements by tagged *S. salar* smolts in Loch Achonachie (*N* = 16), that exited the lake (successful; *N* = 7) and those that did not (unsuccessful; *N* = 10).

Table 6. The total number of recorded downstream (D) and upstream (U) movements (no. moves) made by tagged *S. salar* smolts that successfully and unsuccessfully exited their respective lake during the entire study period. Includes the total recorded distance travelled across all smolts of a given category (e.g. successful fish travelling downstream). Of the fish released in Loch Garve two made no recorded upstream movements (*).

| Location | Success | No. fish | Direction | No. moves | Total (km) | Dist. per fish (km) |
|---|---|---|---|---|---|---|
| Garve | Yes | 14* | U | 465 | 207 | 16 |
| | | 15 | D | 524 | 237 | 16 |
| | No | 5* | U | 293 | 193 | 33 |
| | | 6 | D | 306 | 198 | 33 |
| Meig | Yes | 7 | U | 2 316 | 591 | 84 |
| | | 7 | D | 1 046 | 377 | 54 |
| | No | 9 | U | 3 644 | 1 192 | 132 |
| | | 9 | D | 2 230 | 924 | 103 |
| Achonachie | Yes | 9 | U | 688 | 355 | 51 |
| | | 9 | D | 699 | 344 | 49 |
| | No | 7 | U | 2 452 | 1 150 | 128 |
| | | 7 | D | 2 519 | 1 138 | 126 |

# 4. Discussion

***Survivorship***

*Lake migration survivorship*

This study has shown that survivorship in lakes is generally low, with an average mortality rate of 16% km$^{-1}$ in natural standing waters and 32% km$^{-1}$ in impounded waters. This is higher than the reported mortality rate of downstream riverine smolt migration. Thorstad *et al.* (2012) summarised the reported natural mortality rates of *S. salar* smolts as ranging between 0.3-7.0 % (median 2.3 % km$^{-1}$; averaged between 8 studies) during downstream river migration. As hypothesised, it was found that survivorship decreases with impoundment. Existing research suggests that reservoirs are a favourable habitat for predatory fish species due to the creation of large areas of slack water, this in combination with potential delays in fish migration posed by large hydropower dams, may lead to increased predation (Jepsen et al. 1998; Aarestrup et al. 1999).The effect of impoundment on survival was not the same across all the studied lakes. Acoustic tagged fish at Loch Meig experienced a mortality rate of 16% km$^{-1}$, similar to that seen in a natural standing water (Loch Garve). In contrast, Loch Achonachie had a mortality rate of 25.7% km$^{-1}$.

These estimates of acoustic tagged *S. salar* smolt survivorship are supported by PIT tag data also collected during this study. PIT tagged fish at Loch Garve had a mortality rate of 16% km$^{-1}$ between the river release site and 4.16 km downstream (recapture in a RST 0.29 km downstream of Loch Garve). Similar results were found for Loch Meig, with a calculated rate of 16% km$^{-1}$ between the river release site and Meig dam (redetection at the dam's integrated PIT loop).

*Riverine migration survivorship*

High mortality rates were also found between the river release location and the three lakes; Loch Garve (25% km$^{-1}$), Loch Meig (28% km$^{-1}$) and Loch Achonachie (10% km$^{-1}$). While the reason for this mortality is not certain, Thorstad *et al.* (2012) suggested the that high observed mortality observed at river mouths and estuaries is due to increased predation. While tagging mortality may play a part in observed mortality between the release site of tagged fish and the lake entrance in our study, it would be expected that if this mortality was due to tagging alone, the frequency of mortality would be roughly uniform across the three sites. Reported predatory species of *S. salar* smolts includes but is not limited to: the Eurasian otter (*Lutra lutra;* Carrs, Kruuk and Connroy, 1990), herons (*Ardea cinereal* L.; Jepsen *et al.*, 1998; Koed, Baktoft and Bak, 2006), and cormorants (*Phalocrocorax* carbo; Kennedy and Greer, 1988; Koed, Baktoft and Bak, 2006). Predation from avian or mammalian predators would prevent downstream detection as acoustic signals attenuate in air (Michelson 1978). Predation by predatory fish including brown trout (*Salmo trutta)* and pike (*Esox lucius*) may also account for the observed mortality (Piggins 1959; Hvidsten & Mokkelgjerd 1987). Loch Garve and Loch Meig are known by anglers as good lakes for both pike and brown trout. Thus, it is likely that smolts in this area were consumed by predators.

***What makes a successful lake migrant?***

*Total distance travelled and time taken to exit*

This study found that the total recorded distance travelled by a smolts that exited a lake (successful smolts) was on average 95km less than those that did not (unsuccessful smolts). This difference in distance is likely due to the difference in time that successful and unsuccessful fish were detected in a lake for, with unsuccessful fish detected on average 3.6 days longer. The total distance travelled by smolts in impounded lakes was greater on average (181 km per fish) than fish travelling through natural standing waters (49 km per fish). This difference may be best explained by the time taken for smolts to exit an impounded lake, which on average took 2.8 times longer (21 days) than it did for fish in natural standing waters (7.8 days). However, the effect of impoundment on lake exit time was not the same across both impounded lakes. Tagged fish in Loch Meig took on average 14.5 days to exit the lake, whereas smolts in Loch Achonachie took 29 days to exit. Although exit time through Loch Garve was faster compared to the other lakes, no information was obtained to determine whether this was movement was active or passive. Balchen (1976) hypothesised that fish migration represents a ‘simpleminded process of maximising comfort’. It may be the case, similar to that which has been reported during downstream riverine *S. salar* smolt migration (Tytler et al. 1978; Thorpe et al. 1981; Greenstreet 1992; Hansen et al. 1984), that smolts are simply travelling in the direction of the water’s flow. Impounded lakes could have experienced greater variance in the direction of the water’s flow due to differences in exposure to wind buffering, or associated regular fluctuations of water height due to hydropower generation.

*Swim speed*

This study has shown that the mean swim speed of *S. salar* smolts migrating through a Scottish lake is 0.035 m $s^{-1}$ or 0.24 bl $s^{-1}$ (averaged across all tagged fish, mean tagged smolt length = 148 mm). This result is similar to that reported in existing literature. Thorpe *et al.* (1981) found that the swimming velocity of *S. salar* smolts migrating through a Scottish lake to be 0.05-0.22 body lengths (bl) $s^{-1}$. Similarly, Hansen, Jonsson and Doving (1984) reported swim speeds of 0.05 to 0.24 bl $s^{-1}$ of wild and reared smolts through lakes in Norway. In lakes with low water velocities, the smolts may be unable to detect a current and therefore swim actively to find an outlet leading to higher average swim speeds than if movement were passive (Aarestrup et al. 1999).

*Factors driving successful lake migration*

Day of year of release was a significant predictor of lake exit success of acoustic tagged fish, with earlier migrants more likely to exit a lake. A previous study on the River Conon found that the success of smolts migrating across Loch Meig depended on timing of entry to the lake’s upstream entrance, with those migrating earlier having the best chance of success (E. Rush & S. McKelvey, unpubl. data), which matches the result of our mixed effect modelling. It may be that predators may take time to cue on the arrival of smolts, therefore giving early migrants an advantage (McLennan 2016).

When riverine and lake survival were looked at together, *S. salar* smolts released in larger groups were found to have increased survivorship (for both PIT and acoustic tagged fish). Smolts have been found to often migrate downstream in groups, or shoals (Hvidsten et al. 1995; Riley 2007). Existing behavioural research on teleost fish suggests that shoals form synchronised and polarised swimming groups (Pitcher & Parrish 1993). Benefits of forming shoals may include improving exit searching efficiency and an increased ability or detect and mitigate a predatory threat (Pitcher & Parrish 1993). While extensive literature exists to describe migratory patterns in herds of mammals and flocks of birds, fish schooling behaviour in wild fish remains poorly understood due to the difficulties associated with monitoring wild fish movements (Parrish & Hamner 1997). It not known whether smolts travelled downstream in their release groups. Further analysis of this data could assess the precise time that acoustic tagged fish passed receivers and match similar readings so to assess the possibility of group swimming behaviour.

While there was no significant difference in the number of successful migrants through an impounded lake in relation to experience (whether they had successfully passed a dam previously e.g. fish that had crossed Loch Meig dam and subsequently passed the dam at Loch Achonachie) this may be due to small sample sizes. Existing research has focussed largely on the cumulative effect of barriers on reduced survival, rather than the role of experience (Gowans et al. 2003; Lucas et al. 2009; Roscoe et al. 2011). However, the finding that 66% of fish (2 of 3 fish) that entered Loch Meig with prior experience of crossing a dam did so again compared to 42% (7 of 17 fish) that exited Meig dam with no prior experience indicates an interesting relationship may be present. Existing research suggests that fish can detect environmental modifications (Welker & Welker 1958) and show an organised pattern of exploration behaviour when introduced into a novel environment (Kleerekoper et al. 1974) which in turn suggest some degree of spatial memory (Odling-Smee & Braithwaite 2003). Future studies should account for mortality between hydropower dams to ensure adequate sample sizes to assess this potential relationship.

*Direction of movement*

This study also found that on average smolts that successfully exit a lake follow a more linear downstream migration trajectory than those that do not. However, the proportion of total (recorded) upstream to downstream movement carried out by successful fish differs significantly between natural standing waters (lake average: 12% more upstream than downstream movement), and impounded waters (combined lake average: 58% more upstream than downstream movement). This is the first study to compare directional movement of *S. salar* smolts migrating through natural and impounded lakes. A study of *S. salar* smolts migrating through two impounded lakes by Aarestrup, Jepsen and Rasmussen (1999) also found that on average 16% of total (recorded) migration was directed upstream. In this study it is uncertain whether smolts simply moved in the direction of strong winds, which created surface water currents as found by Aarestrup, Jepsen and Rasmussen (1999) and Thorpe *et al.* (1981). Further analysis could assess the effects of environmental factors including wind and water velocity on smolt directionality and rate of movement.

The effect of impoundment on the direction of total recorded movement of smolts that exited a lake was not the same across the two studied impounded lakes. While smolts that exited Loch Meig carried out on average 2% more total recorded downstream than upstream movements, smolts that exited Loch Achonachie carried out 220% more upstream than downstream movements. Unidirectional flow in rivers has been found to provide a strong orientational cue to migrating fish, with narrow channels providing fixed reference points for migrants (Northcote 1984). Damming interrupts the linearity of a channel by posing a physical barrier, and also alters the natural flow regime (Ugedal et al. 2008). The effect of damming on directional flow may have been compounded by the larger dam wall at Loch Achonachie (184 m) which could require a greater degree of searching behaviour to find the exit compared to the dam at Loch Meig (76 m).

***Study limitations and assumptions***

*The effect of tagging on natural behaviour*

A key assumption of telemetry studies is that the movement, behaviour and mortality of tagged fish will not significantly differ to that seen in the natural environment (Zale et al. 2005; Drenner et al. 2012). In fish telemetry, to limit the risk of tagging causing the observed behaviour the '2% rule' (the tag used should not exceed 1.25% in water, or 2% in air of the fish's body weight out of water) has been accepted as a benchmark for the maximum tag mass to body mass ratio (Winter 1996). Empirical studies have supported this rule by showing negative effects of tag burden above 2% (McCleave & Stred 1975; Ross & McCormick 1981; Adams et al. 1998). However, studies have challenged this rule by assessing the effect of surgically intracoelomic implanted transmitters across a variety of fish species including: Pacific salmon (*Onchorhynchus* spp.: Brown *et al.*, 1999), cutthroat trout (*Oncorhynchus clarkii*: Zale, Brooke and Fraser, 2005), and Atlantic salmon (*S. salar*: Newton *et al.*, 2016). Newton *et al.*, 2016 tested the effect of transmitter burden on mortality probability of downstream migrating wild *S. salar* smolts and found that a tag burden of > 12.7% had no effect on the short term (~ 40 day) mortality. Similarly, Brown *et al.*, 1999 found swimming performance in juvenile rainbow trout (*Oncorhynchus mykiss*) was not affected by the presence of transmitter or the operation, and hypothesised that this should be extended to a 6 to 12% ratio. The difficulty of comparing the effects of intracoelomic insertion are outlined by Cooke *et al.*, 2011, whereby a review of 108 peer-reviewed published studies found most studies took place in laboratory environments, or other pseudo-field settings such as mesocosms or experimental ponds. These studies also often opted for different measures of effect which makes the ability to cross-compare results limited. Furthermore, these studies did not investigate the effects of different surgical techniques and tools on the tagged fish fitness under the differing conditions.

In our study, the calculated average tag burden for acoustically tagged fish was 4.3% (tag weight in air to fish body weight), and 0.6% for PIT tagged fish. While this tag burden is above that suggested by Winter (1996) we believe that existing research supports the hypothesis that this ratio is low enough to not significantly affect the mortality, behaviour and natural movement of migrating *S. salar* smolts.

*Survivorship*

Survivorship statistics were based off the assumption that tagged *S. salar* smolts that did not exit out of a lake died. Of the fish that remained in the lake all were deemed to have died. This deduction was made following the rule that if a fish had not moved from a single AMR gate for more than 7 days then it had died due to natural causes. Inference of mortality was made difficult in some cases by simultaneous detections across a number of gates which was thought to be a result of detection range overlap and favourable conditions (reduced turbidity, low levels of boat traffic etc.). The case for fish mortality could be further supported by analysis of the depth sensor data recorded by the tags were used in this study. The cause for mortality remains uncertain, however, this study found that smolts that did not exit a lake travelled greater recorded distances, this is likely to equate to a reduction in energy reserves, which may turn may lead them to be vulnerable to predation or death due to fatigue.

The true fate of tagged fish that did not make it to the first lake AMR gate is speculative, and there is no clear answer. There is the possibility of utilising manual tracking to scan the rivers for transmitters. If the transmitters remain in the river then this may suggest riverine predation, whereas tag disappearance could be due to mammalian or avian predators (Halfyard et al. 2012). Time constrains made this not possible during this study.

*Movement and behaviour*

While our estimates of average swim speed were similar to that reported there may be inaccuracy in this estimate due to the proximity of the two detection ranges of adjacent AMR gates within each lake. A acoustic tagged fish may have only swum a few metres between one position and another, but if this was enough to register its presence on both receivers this would be stored as a unique movement event. Therefore, this may lead to an overcalculation of the distance travelled by tagged fish, and subsequently a miscalculation in the average swim speed. The average swim speed calculated also assumes equal rate of movement during night and day. Existing research suggests that downstream smolt migration is nocturnal and limited to the surface layer (Thorpe & Morgan 1978; Moore et al. 1995; Greenstreet 1992), therefore calculation of an average swim speed may lead to an overestimation of daytime swim speed, and an underestimation of swim speed at night.

Error may have also been introduced by close proximity detection interference (CPDI). CPDI is a phenomenon whereby echoes off reflective surfaces such as dam walls or the lake basin which may lead to the interruption of a transmission sequence of a transmitter in relative close proximity to a receiver (Kessel et al. 2014). This leads to the signal colliding with itself, and thus it may not be properly decoded and logged by that receiver. CPDI may also occur when a large number of tagged individuals are released at the same time, which may lead to decreased positioning probability. However, the small group sizes of acoustic tagged individuals released at one time in this study may minimise its occurrence due to this contributor in this case. However, Binder *et al.* (2016) found that the probability of code collisions can be quite high even at relatively low transmitter densities if the nominal delay of the transmitters (i.e., period between successive transmission) is fairly low. The transmission delay of 25 seconds in this study may be low enough, given that tagged fish were travelling through an enclosed environment, to propagate a large number of collisions. One way that this could have been reduced is the use of stationary receivers ('sync tags'). Binder *et al*. (2016) used sync tags synchronize clocks among receivers and evaluate array performance to identify periods of poor positioning possibility e.g. due to unfavourable environmental conditions (boat noise, high water velocity etc.). The risk of CPDI is that this may lead to a misrepresentation of data as transmissions may be false, or assumptions that an unusual detection (a tagged fish in Loch Garve appearing in Loch Meig) is due to misdetection rather than removal and relocation of a tagged fish by an avian predator.

Acoustic tags continue to transmit when inside a predator, therefore estimations of fish movement also rely on the assumption that tagged individual are alive. Thorstad, Uglem, et al. (2012) found that acoustic transmitters may remain in fish predators for up to 47 days before being dispelled. To accurately track smolt movement it is important to isolate the timing that a predation event occurs. This can be done by assuming a tagged fish if it makes no movements between receiver gates for a long period of time e.g. 7 days (like in this study), or using ancillary sensor data including depth and temperature recorded by the acoustic tag. Conclusions drawn from this data may also be supported through the use of cluster analyses or mixture models to analyse fish movement patterns and identify movement patterns which deviate from the norm (Romine et al. 2014; Gibson et al. 2015).

## 5. Conclusion

This study has compared mortality and movement behaviour of *S.salar* smolts through a natural standing water, and two sites impounded by large hydropower dams. Using acoustic telemetry, it was found that smolts in impounded lakes take longer to exit, and smolts migrating earlier are more likely to exit a lake. Overall survivorship from river release to the estuary of PIT and acoustic tagged fish was also predicted by size of the release group, with fish belonging to larger group sizes more likely to reach the estuary. This study found high and variable mortality rates in the riverine environments preceding lake entry, which supports the idea that impoundment creates areas of slack water which in turn are favourable habitat for predatory species. The proportion of total recorded downstream and upstream directed movement differed significantly between impounded and natural standing waters, with *S. salar* in impounded lakes travelling predominantly upstream. This finding supports the hypothesis that impoundment promotes more variable movement patterns which may in turn reduce the number of individuals that successfully migrate downstream. This information is vital for expanding our limited understanding of juvenile Atlantic salmon movements through lakes, without a base line for comparison the effects of hydropower dams cannot be accurately determined.

## 6. Acknowledgements

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