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Timing of Atlantic salmon *Salmo salar* smolt migration predicts successful passage through a reservoir

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Running Headline: Timing predicts successful smolt migration

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Around 30% of Atlantic salmon *Salmo salar* smolts successfully survived passage through Loch Meig, a reservoir in the north of Scotland, en route to the sea. However, this survival rate was in turn dependent on the timing of migration, with the earliest migrants in the spring having the best chance of survival. This could have implication for fisheries management, since the estimation of smolt downstream survival may be influenced by which time period of the smolt run is analysed.

Key-words: phenology; predation; salmonid; Scotland; temporal.

Migration confers many benefits, such as better feeding opportunities and associated greater growth and reproductive potential, but it can also be energetically demanding and a cause of significant mortality (Dingle, 2014). The anadromous Atlantic salmon *Salmo salar* L. 1758 spends its first years in fresh water, before transforming into the smolt stage and migrating to sea. Mortality during the marine phase of the lifecycle is high: for instance, only around 6% of Scottish smolts survive to return to home waters (prior to coastal fisheries) (ICES, 2015). There are numerous factors that may influence the probability of salmon successfully completing a marine migration and returning home to spawn in their natal river, including the degree of predator swamping during the downstream river migration (Furey *et al.*, 2016), as well as the ocean temperature at the time of sea entry (Friedland, 1998; Friedland *et al.*, 2000).

A recent, separate study on *S. salar* smolt survival found a temporal effect *within* the typical spring period of outward migration, with the smolts migrating earliest in the spring having the highest probability of return (McLennan *et al.*, 2017). There are several potential explanations for these temporal effects, but analyses such as these, which are based on return rates of adults, cannot separate out effects operating on the downstream migration from those acting on the fish when they reach the sea. What is therefore needed are measurements of survival rates of smolts migrating downstream at different times – an approach adopted by Schwinn *et al.* (2017) who showed that the survival rate of brown trout *Salmo trutta* L. 1758 smolts migrating through an artificial shallow coastal wetland declined over the course of the spring migration period.

This study examines the temporal pattern of survival rates of *S. salar* smolts crossing a potentially significant obstacle – a large reservoir - during their seaward migration. Lakes and reservoirs may reduce smolt survival for two reasons: they are a challenge to downstream navigation, and they may contain significant numbers of predators (which may be unfamiliar to fish that have spent their previous life in shallow streams).

The study was conducted in northern Scotland at Loch Meig, a reservoir 2.7 km long and a maximum of 350 m wide, which was created by damming the River Meig in the 1960s as part of the River Conon hydropower scheme (Fig. 1). The Meig Dam is a diversion dam, with a proportion of water being diverted to the nearby Luichart Power Station. The diversion tunnel is screened with a 12mm square mesh that is specifically designed to prevent *S. salar* smolts from entering (Environment.Agency, 2016). A Borland fish lift within the dam allows adult *S. salar* to ascend the dam, enter the reservoir and continue their return migration up the River Meig. Likewise, seaward migratory *S. salar* smolts are able to pass through the same fish lift. Because the diversion tunnel is screened, the lift is the only feasible downstream exit from the reservoir. The reservoir contains a population of wild *S. trutta*, and is stocked several times per year with triploid *S. trutta* as part of a recreational fishery. The extent of smolt predation in Loch Meig is not currently known. The wild and triploid *S. trutta* are the most likely piscivorous threat (since the reservoir contains no pike *Esox lucius* L. 1978), with personal observations of wild *S. trutta* as small as 23 cm predating on smolts. The stocked triploid *S. trutta* tend to weigh between 0.5-1 kg. Avian predators, such as goosander *Mergus merganser* and red-breasted merganser *Mergus serrator* are also present. No fishing of *S. salar* is permitted.

In May 2015, wild *S. salar* smolts were captured in the river flowing into Loch Meig during their seaward migration, using a temporary rotary screw trap (*e.g.* Thedinga *et al.*, 1994), which was positioned ~1 km upriver from the head of the reservoir. While some of the smolts entering Loch Meig may have been stocked in upstream tributaries as eggs as part of the local fishery management programme, all of these eggs would have arisen from *in vitro* fertilization using sperm and eggs from wild adult salmon returning to the River Conon to spawn. The trap was checked regularly between 04 May and 25 May and any captured smolts were removed. Five smolts were captured on 04 May, indicating that the smolt run was just beginning at that time. The trap was lifted on 25 May, partly because the smolt run had begun to slow down by that point (24 smolts were trapped on the last day of capture) but also because the start of poor weather conditions would have made the trap inoperable from that point onwards. Captured smolts (n = 638) were individually removed from the trap, immediately anaesthetised in an MS222 solution (80 ppm) and measured (fork length, L_F, mm: body mass, to 0.1 g). A passive integrated transponder (PIT) tag, each with a unique code, was then inserted into the abdominal cavity of each smolt. Tagged fish were placed in a recovery tank containing fresh water that was regularly replenished (for a maximum of 3 h) and then released on the same day back into the river, approximately 150 m downstream of the rotary screw trap; all fish captured on a given day were released at the same time and no mortality occurred prior to release. A permanent PIT tag decoder in place at the Borland fish lift (within the dam at the downstream end of the reservoir, ~3.8 km downstream from the release site) recorded the identity of all the tagged smolts that survived the passage through the reservoir. The PIT detector is a swim-through loop and is annually range tested. The last migrant was recorded on 07 June 2015 and it is unlikely that any smolts remained in the reservoir after this point, since the PIT tag decoder (active all year) did not record any further fish, even during the following year's spring smolt migration. An introduction of triploid *S. trutta* occurred during the smolt run, on 19 May 2015. This study was conducted as part of routine fisheries management by the local fisheries trust, and so ethical permission was not considered necessary.

The probability of a smolt successfully passing through the reservoir (subsequently referred to as *smolt survival*) was analysed in relation to the following independent variables: the Julian date on which an individual was captured and PIT tagged in the river at the upstream end of the reservoir (*timing of smolt migration*), the time of day that the smolt was released back into the river after tagging (*time of day*, nearest h), the body mass of the smolt (*smolt mass* g), the L_F of the smolt (*smolt length*, mm), and the number of smolts that were captured and released on a given day, as an indicator of the size of the cohort that the smolt was in (*cohort size*). Including a covariate that indicated the rate of water flow through the reservoir was also considered, measured as the average width of the dam gate opening - based on 24 hourly measurements (*flow*). However, this measurement of *flow* was incidentally, and potentially problematically, collinear with *time of day* (Pearson r = -0.60, $P < 0.001$, n = 638). For the final analysis, *time of day* was included as a covariate over *flow* (see Table I for final model); however, even when an alternative model was run, which included *flow* but excluded *time of day*, the likelihood of successful passage through the reservoir was not significantly associated with *flow* (Wald Z = -0.51, $P > 0.5$, n = 638). A Pearson's correlation coefficient matrix of the variables also showed that smolt mass and smolt L_F were highly collinear (Pearson r = 0.92, $P < 0.001$, n = 638), therefore only smolt mass was used in the analyses.

Statistical analyses were carried out using R version 3.4.0 software. Factors affecting smolt survival were assessed by a binary logistic regression analysis, using the glm function with a binomial distribution. Significance was evaluated using the Wald Z statistic (distributed as chi-squared). See Table I for an outline of the full model.

In total, 191 tagged *S. salar* smolts (~30%) successfully passed through Loch Meig, and the average passage time was 100.4 h. The likelihood of successful passage was not significantly affected by the mass of the smolt (range 8.2 - 61.8 g), the time of day that it was released back into the river at the head of the loch (range 11.00 - 15.00 hours), or the size of the cohort that the smolt was in (1 – 140). However, it was significantly influenced by the timing of migration: migration earlier in the spring was associated with an increased likelihood of successfully passing through the reservoir (see Table I and Fig. 2).

A similarly poor survival was found for *S. trutta* smolts migrating through both a reservoir and a wetland (Jepsen *et al.*, 2000; Schwinn *et al.*, 2017), although in these cases the water bodies were relatively shallow (1.7 m and <0.8 m deep respectively, in comparison with the sometimes >20 m depth of Loch Meig). However, in all three situations, there would have likely been a delay in migration due to the artificial nature of these water bodies: Jepsen *et al*. (2000) found that many smolts reached the far end of the shallow reservoir, but then initially failed to pass through the outlet sluice; a delay that increased their exposure to predators. Aarestrup and Koed (2003) also found increased mortality of *S. salar* and *S. trutta* smolts during weir passage, which again may be due to migration delay and subsequent increased predation pressure. Predation is known to be the one of the biggest natural causes of *S. salar* smolt mortality during downstream freshwater migration (Jepsen *et al.*, 1998; Jepsen *et al.*, 2000; Thorstad *et al.*, 2012). In this study, the wild and triploid *S. trutta* are the most likely piscivorous threat, with personal observations of *S. trutta* predation on *S. salar* smolts in Loch Meig. It is also possible that the triploid *S. trutta* introduced during this particular smolt run would have contributed to the predation pressure; however, these newly introduced fish would not be familiar with *S. salar* smolts, unlike the more established triploid *S. trutta* from previous introductions. The temporal effect identified in this study may arise, in part, because predators (both avian and piscivorous) may take time to cue in on the arrival of the smolts or to increase their attack success through experience (*e.g.* Reid *et al.*, 2010), thus giving an advantage to early migrants. Schwinn *et al.* (2017) suggests that temperature may also play a role, since higher temperatures (usually found towards the end of the smolt run) result in higher energetic requirements of piscivorous predators, and hence higher attack rates (Öhlund *et al.*, 2015). However, Haraldstad *et al.* (2017) argue that warmer water may also confer advantages to the smolts, since a higher metabolic rate may increase the probability of a successful escape. In support of this, they found that smolts were more likely to migrate at night (thought to be a predator avoidance behavior) when the water was relatively cooler. It may be the case that some mortality occurred as a result of the reservoir infrastructure, or that a small proportion of the smolts were able to pass through the 12mm square mesh that screens the diversion tunnel at the dam. While this may contribute to the calculation of overall mortality, it is unlikely that this would affect the temporal effect identified in this study. A final possibility is that the earliest fish to start the migration may be phenotypically of higher quality than those that come later, although in this study there was no indication that body mass or body length changed over the course of the migration period; moreover, Schwinn *et al.* (2017) found the same temporal effect in hatchery *S. trutta* smolts, which would have been more uniform in phenotypic quality across time.

This study monitored a population of *S. salar* smolts that had been captured between 04 May and 25 May 2015. While on average around 30% of *S. salar* smolts successfully passed through the reservoir, the survival rate was over 70% at the start of the smolt run, but only 10% towards the end. This temporal change could have implication for fisheries management, since the estimation of smolt survival may be highly influenced by which period of the smolt run is analysed (making it important to base survival estimates on as full a period of the smolt run as possible). The relatively poor survival found in smolts migrating through impounded water bodies (Jepsen *et al.*, 2000; Schwinn *et al.*, 2017; this study) is clearly of concern, and similar studies should now be conducted in natural lakes, to see if this also applies when there are fewer barriers to fish attempting to exit downstream. Doing so will allow more accurate assessment of the factors influencing smolt survival during seaward migration, including whether this will be influenced by the gradual shift towards earlier dates of migration in a warming world (Otero *et al.*, 2012).

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Table 1. Summary of the full model explaining variation in *Salmo salar* smolt survival. Significance was evaluated using the Wald Z statistic (distributed as chi-squared). N = 638.

	Parameter Estimate	SE	Z	p
Intercept	23.55	4.08	5.78	<0.001
Timing of smolt migration	-0.18	0.03	-7.11	<0.001
Time of day	0.02	0.10	0.25	>0.50
Smolt weight	0.01	0.02	0.62	>0.50
Cohort size	<0.01	<0.01	-0.18	>0.50

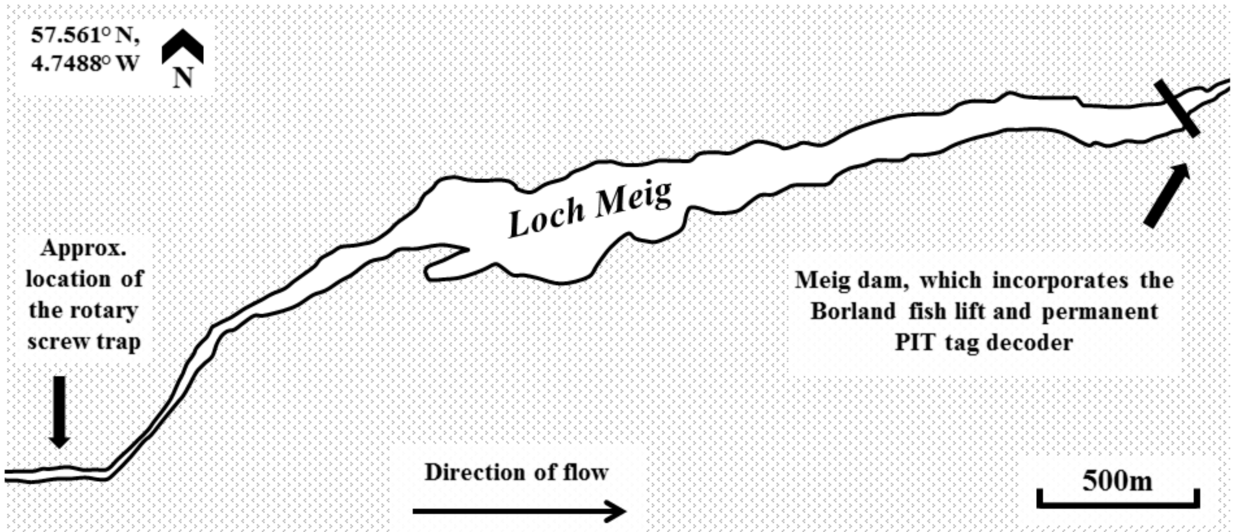

Fig. 1. Diagrammatic outline of Loch Meig, Scotland.

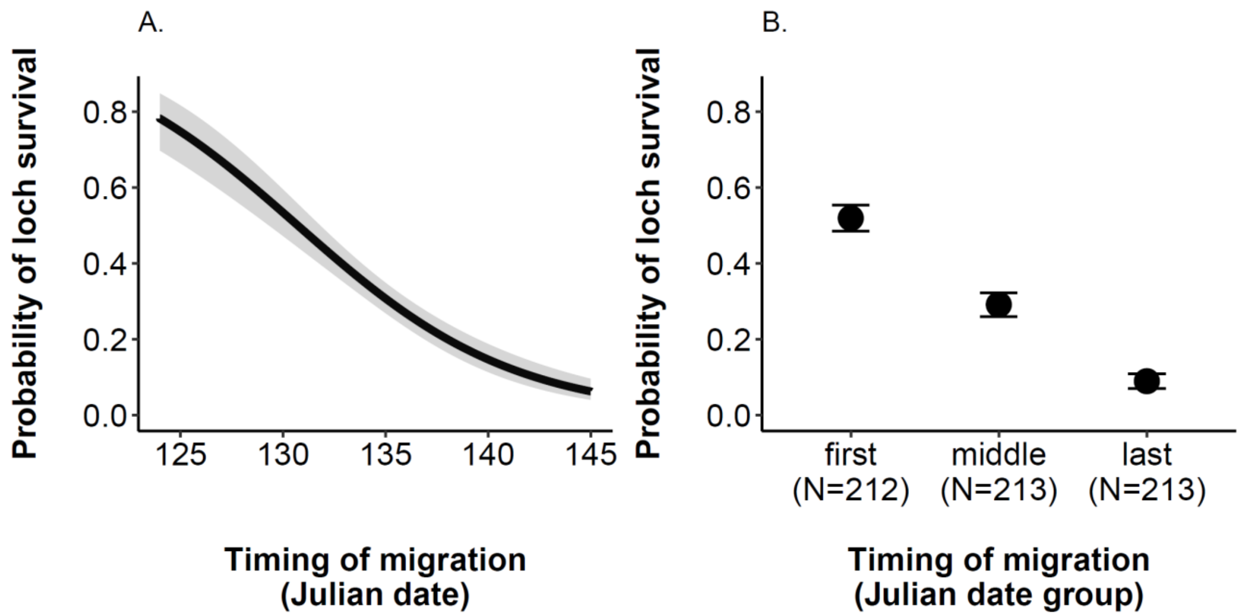

Fig. 2. The relationship between the timing of seaward migration of a *Salmo salar* smolt and the probability of it successfully passing through Loch Meig during the course of that migration. The logistic regression curve in (A) is from the binary logistic regression analysis (with 95% confidence bands), while in (B) the data are shown for presentation purposes as mean probabilities +/- SE in three Julian date categories of equal sample size: the first (N = 212), middle (N=213) and last third (N=213) of smolts tagged. Total N = 638.