Received: 12 February 2021 | Revised: 22 April 2021 | Accepted: 24 April 2021

DOI: 10.1111/fme.12495

ORIGINAL ARTICLE

Fisheries Management and Ecology WILEY

Validating timing of salmon smolt runs obtained by telemetry studies

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Abstract

Telemetry tags are increasingly used in management to monitor the migration timing of Atlantic salmon smolts (*Salmo salar* L.). It has been postulated that (1) effects from tagging and handling may alter migration behaviour, and (2) that the selection of fish during sampling is not representative of all migrating smolts, yielding bias in migration timing estimates. In the River Dale (Vestland, Norway), five groups of wild Atlantic salmon smolts (N = 385) were tagged in April–May and recaptured in a wolf trap. Migration timing was then compared to the untagged population. Migration timing differed between tagged (12 mm PIT) and untagged fish for 4/5 groups. Only fish tagged at the first time point did not have significantly different timing of migration from untagged counterparts. The relationship between length and the timing of migration was different for initial length and length at recapture; initial length suggested earlier migration of longer fish, but the extra time spent in the river prior to migrating for smolts that were initially smaller compensated for the size difference. The tagging protocol is crucial to obtaining representative migration timing results. Smolts should be tagged as early as possible and include the entire size distribution.

KEYWORDS
acoustic telemetry, Atlantic salmon, ecology, migration, PIT tag, wolf trap

1 | INTRODUCTION

Knowledge regarding the timing of salmon smolt migration is needed for the understanding of the ecology and recent declines of Atlantic salmon, *Salmo salar* L., because it determines how and when a smolt encounters natural and anthropogenic threats during its migration to feeding grounds (Myksvoll et al., 2020). Warming water temperature (Jonsson & Ruud-Hansen, 1985; Jutila et al., 2005; Whalen et al., 1999) and flashier discharge (Hesthagen & Garnås, 1986; Hvidsten & Johnsen, 1993) are regarded as the proximate cues for migration (Jonsson & Jonsson, 2009). However, populations may respond differently to these environmental cues (Thorstad et al., 2011). Along the Norwegian coast, smolts enter the sea at different times of the year (Rikardsen et al., 2004), and even within the same watershed, it has been found that smolts in the upper tributary migrate earlier than those from the lower tributary (Stewart et al., 2006). This local adaptation results in a simultaneous sea entry from the entire watershed (River Tay, Scotland; Stewart et al., 2006). Ultimately, smolts may attempt to synchronize their migration to reach the ocean at a specific time when conditions are favourable for growth and survival (Hvidsten et al., 2009; Rikardsen & Dempson, 2010).

Several methods have been used for monitoring the timing of smolt migration (e.g. video surveillance, traps, telemetry). Results from these studies indicate that the majority of smolts in southern Norway migrate out in May, while some start already from mid-April. For some of the rivers in southern Norway, data show considerable among-year variation (up to a month) in migration timing (measured as median day of migration) from the same river (Ugedal et al., 2014). These variations are likely caused by climatic differences, where a cold winter and spring result in a later migration. Electronic tags are increasingly used to monitor seaward migration in populations of wild Atlantic salmon (Barlaup et al., 2018). Normal practice has been to capture smolts once during spring, before smolt migration, and tag a random sample of the population. The tagged smolts are registered on antennas or acoustic receivers further downstream. It is then assumed that the tagged group is representative of the entire population in terms of outwards migration to estimate the timing and synchronicity with environmental cues. However, the selection of fish for tagging, handling and tag effects can alter migration and survival of smolts, and thus biasing the dataset used for estimating the time of migration. This is supported by recent findings suggesting that tagged fish consistently migrate earlier than fish monitored using other methods, such as video surveillance and traps (Vollset et al., 2021).

Migration timing estimates have large implications for the understanding of Atlantic salmon ecology and for successful management and regulation of industry operations. There is a need for an unbiased method for estimating the timing of smolt migration. This will be needed for optimal timing of the delousing in the aquaculture farms, thus reducing the contact rate between out-migrating smolts and salmon-louse. In this study, the hypothesis that migration of wild Atlantic salmon smolts is independent of handling, fish length and timing of capture/release was tested. This was investigated by capturing, tagging and releasing groups of Atlantic salmon smolts with 12-mm HDX PIT-tags at five different time points throughout April and May and recapturing them in a wolf trap downstream, which is used to monitor the abundance and timing of the smolt migration. Individual probability of migration and migration timing were tested using recapture data in the wolf trap and validated with gill ATPase data to evaluate the performance of electronic tags for monitoring out-migration of salmon smolts.

2 | METHODS

2.1 | Study site

The study took place during spring 2019 and was conducted in the River Dale (60°35′N, 5°49′E) on the west coast of Norway (Figure 1). The River Dale is regulated by four hydropower plants. These hydropower plants are supplied by water from two reservoirs and several impoundments (Sauterleute et al., 2016). The River Dale is inhabited by populations of both *Salmo salar* and anadromous trout, *Salmo trutta* L., within 4.7 km from the river mouth up to a waterfall, Storefossen, acting as a natural barrier (Sauterleute et al., 2016). The river has a catchment area of 249 km^2 and a mean annual discharge of 21 m^3/s (Vollset et al., 2016). Water temperature and discharge measurements were taken throughout the year. Temperature measurements were taken hourly in the wolf trap using an Orpheus Mini Logger. Water discharge data were obtained from the power plant and collected using a SonTek FlowTracker2.

Electrofishing of wild Atlantic salmon smolts was carried out in a ~380-m river stretch, 500 m upstream of the wolf trap and lowermost power plant (Figure 1). The river reach where smolts were captured is a residual flow area that includes sandbanks, gravel and boulders known to be suitable and frequently used spawning grounds for salmonids. A standardised procedure for capture and PIT-tagging of wild smolts was conducted at five-time points in April and May.

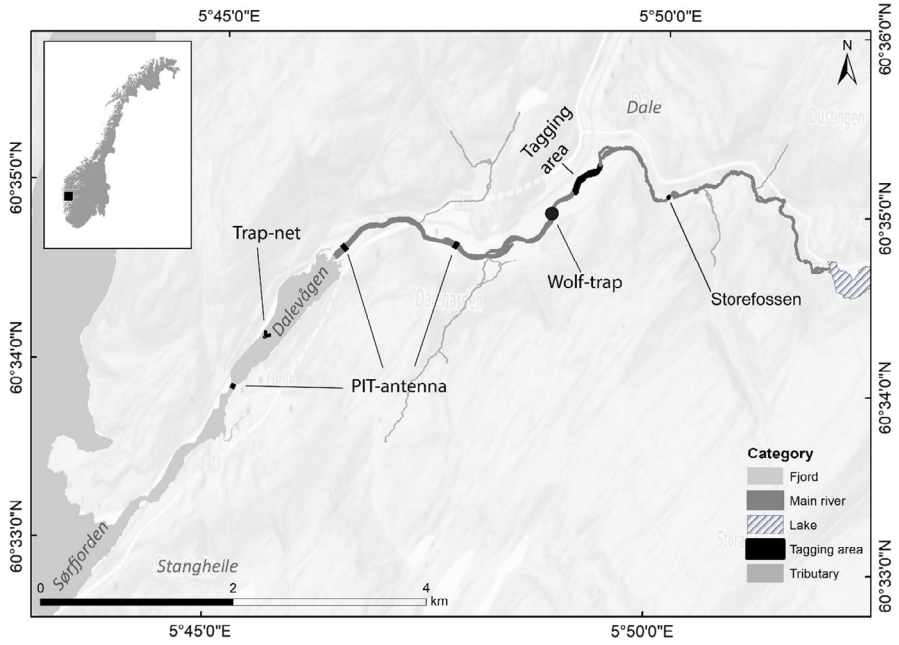

FIGURE 1 Map of the Dale River tagging site. The Dale River empties into the Dalevagen, a brackish embayment that meets the Osterfjord system and the North Sea

2.2 | Smolt capture

Electrofishing of wild Atlantic salmon smolts was conducted in accordance with the method described by Bohlin et al. (1989). The study followed a batch sampling design such that fish were captured, held and then tagged. Batch sampling is the standard protocol for tagging studies as opposed to individual sampling. Holding may be stressful for fish, but short durations (<1 day) in flowing water should not be a severe stressor. Fish were electrofished and retrieved from the water using a hand net and visually identified as either salmon smolts or trout based on morphological characteristics. Fish that were silver in colouration were determined to be likely smolts, distinguished from counterparts that still had colourful parr markings. Only smolts of total length (TL) ≥ 100 mm were captured. The fish were then transferred to a bucket with fresh water. Captured fish were regularly transferred to a keep-net to avoid crowding in the bucket. The keep-net was positioned in an area with intermediate flow and shade. Fish were held in the keep nets until electrofishing of the river stretch was finished after 0.25–2 h, and all fish were then tagged and released together.

Before PIT-tag implantation, fish were transferred in small batches (~10 fish per batch) from the keep-net to anaesthetic solution containing Tricaine methanesulfonate (MS-222) and sodium bicarbonate ($NaHCO_3$) as a buffer, both with a final concentration of 100 mg/L. After approximately two minutes in the anaesthetic solution, the fish reached light anaesthesia with partial loss of equilibrium. Each individual was surgically implanted with a 100 mg HDX PIT-tag (12 mm long 2.12 mm wide; www.biomark.com). A ~5-mm incision was made between the posterior ends of pectoral fins on the side of the midventral line (see Prentice et al., 1990). Next, the PIT-tag was inserted with the tip first in a vertical position. Once the tip was inside the abdomen, the tag was tilted horizontally and pushed posteriorly (see Gries & Letcher, 2002). Afterwards, the fish was registered on a PIT-tag scanner (Biomark) and total length (TL, mm) measured on an attached electronic length measuring board. The tagging procedure took ~10–20 s per fish. All tagged smolts were released during daytime.

2.3 | Registration of recaptures

A wolf trap was positioned ~325 m downstream (60°34′54.2″N, 5°48′46.0″E) of the tagging area (Figure 1). The trap covered the entire river, assuming it would capture all passing fish including the recapture of the different PIT-tagged smolt groups. It was deployed prior to, and operative throughout, the entire migration period. Every morning, the wolf trap was emptied. The fish caught were scanned for PIT-tags, measured (TL) and registered on that date as either recaptures or untagged smolts. During the summer, two bottom-mounted PIT-antennas were active at the river mouth and at the end of the Dalevagen embayment (Figure 1). A trap-net was also operated to capture migrating smolts in Dalevagen where all captured smolts were scanned for PIT-tags (Figure 1).

2.4 | Gill ATPase sampling

To validate that the wolf trap was capturing migrating Atlantic salmon, gill samples for measurements of Na^+K^+-ATPase activity were taken from smolts at four different occasions throughout May (3 May: N = 10, 16 May: N = 5, 24 May: N = 10, 21 May: N = 10). Approximately, ten PIT-tagged wild smolts captured in the wolf trap were chosen for each gill sampling. If the trap captures contained zero or few tagged individuals, the sample was supplemented with untagged smolts. Fish were euthanized by cranial percussion. Gill sampling was standardised and involved heart puncture to cease blood circulation before removal of the entire second-gill arch. Each gill arch was placed in a tube containing SEI-buffer (250 mM sucrose, 10 mM Na_2EDTA, 50 mM imidazole, pH 7.3) for conservation. Tubes were refrigerated before and after insertion of the gill arch, then put in the freezer as soon as possible.

Gill Na^+K^+-ATPase activity was analysed according to the method described in McCormick (1993). The gill filaments obtained from fish from the wolf trap were thawed before assemblage of the kinetic assay. The production of adenosine diphosphate (ADP) in the presence of Na^+K^+-ATPase is ouabain-sensitive (ouabain inhibits Na^+K^+-ATPase). The reaction is enzymatically coupled to the oxidation of nicotinamide adenine dinucleotide (NADH) by pyruvate kinase and lactic dehydrogenase, which could be directly measured on a Spark multicode microplate reader at 340 nm (25°C, 60 cycles, 10 min). Protein in the homogenate was determined by bicinchoninic acid method according to Smith et al. (1985). The Na^+K^+-ATPase activity was measured as the difference in activity, with and without ouabain present as an inhibitor, expressed as µmol ADP mg/protein/h.

2.5 | Analysis

All data analyses were conducted in R, version 4.0.3 (R Core Team, 2019, https://www.r-project.org/). Visualizations were drawn with ggplot2 (Wickham, 2017).

2.5.1 | Capture efficiency of the wolf trap

Although the wolf trap was assumed to capture all fish passing it, a proportion of the tagged smolts were detected on bottom-mounted PIT-antennas (usually used for monitoring adult returns) or in a trap-net downstream without being captured in the wolf trap first. Assuming the likelihood of being observed downstream of the wolf trap is the same for all individuals, it is possible to estimate the total number of tagged smolts that were able to cross the wolf trap without being captured by Lincoln-Peterson mark-recapture estimation (Peterson, 1896).

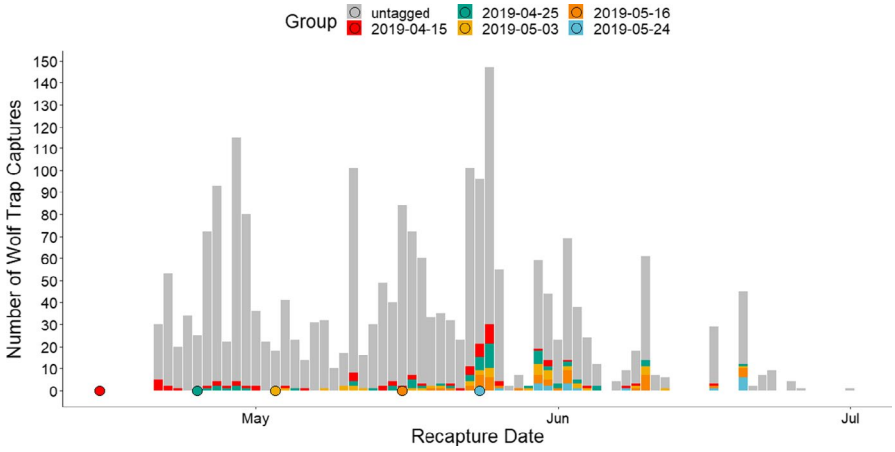

FIGURE 2 Overall distribution of Atlantic salmon smolts captured in the Dale River wolf trap in 2019

2.5.2 | Compensatory growth

To test for growth among smolts to offset small size early in the migration window, a simple linear regression was run with the days between release and capture in the wolf trap as the dependent variable. This is referred to as compensatory growth (i.e. growth that compensates for small size early in the season), but it is expected to follow the regular growth rate. The ratio between recapture length and initial length was the only independent variable to test whether fish were exhibiting compensatory growth between tagging and migration. A flat slope would indicate no growth whereas a significant positive slope would suggest that longer time between tagging and recapture was conferring compensatory growth to the smolts.

2.5.3 | Probability of migrating

Logistic regression (*glm* function in R) was used to investigate if the time of tagging during the season and the length of a smolt at tagging affected the probability that a smolt would migrate. Length and tagging group (five dates) were considered; two models were compared by AIC, one with an interaction and one without.

2.5.4 | Tag effects

To test if there was a temporal difference in out-migration between a PIT-tagged group and the untagged population, a two-sided Kolmogorov–Smirnov test (KS-test) was performed to compare the distributions of tagged and untagged fish captured in the wolf trap. Because it was not possible to compare the timing of tagged fish migrating to untagged fish captured in the wolf trap prior to those fish being tagged, untagged fish for each tagging group was sub-divided and separate KS-tests were run for each tagging group. Figures were illustrated by calculating the cumulative proportion of captures in treatment and control groups for each release group, such that the control group for each treatment group only included fish passing the Wolf trap on days equal to or after the treatment group was tagged.

2.5.5 | Na^+K^+-ATPase activity

A linear model was used to compare gill Na^+K^+-ATPase activity (measured as µmol ADP mg/protein/h) between migrating smolts captured in the wolf trap at four different sampling dates in May, and to investigate if length affected Na^+K^+-ATPase activity.

3 | RESULTS

During the five capture trials in April–May 2019, 385 Atlantic salmon smolts were PIT-tagged, of which 231 were recaptured in the wolf trap (Figure 2). In addition, 1964 untagged smolts were captured in the wolf trap.

3.1 | Capture efficiency of the wolf trap

The wolf trap was assumed to capture all fish passing it, but 10 tagged smolts were detected downstream that had not been registered at the wolf trap. Seven were detected on downstream PIT-antennas and three captured in the trap-net. From the 154 tagged smolts that were not recaptured in the wolf trap, an estimated 45 individuals (29%) had passed the wolf trap based on Lincoln-Peterson estimation. This results in an estimated 109 tagged smolts left upstream of the wolf trap (28%), whereas an estimated 276 (231 ± 45) tagged smolts migrated (72%).

3.2 | Compensatory growth

The total length of PIT-tagged smolts (N = 231) at the time of out-migration (wolf trap capture) ranged from 115 to 164 mm, while that of the untagged population (N = 1964) ranged from 106 to 199 mm. The 231 smolts had grown up to 21 mm in length, with a mean increase of 6 ± 5 mm. Percentage growth was up to 18% of the initial body length for one fish, with a mean of 5 ± 4%. The time it took from tagging to capture in the wolf trap was related to the ratio of recapture length to initial length (t = 14.14, p < 0.01), suggesting that

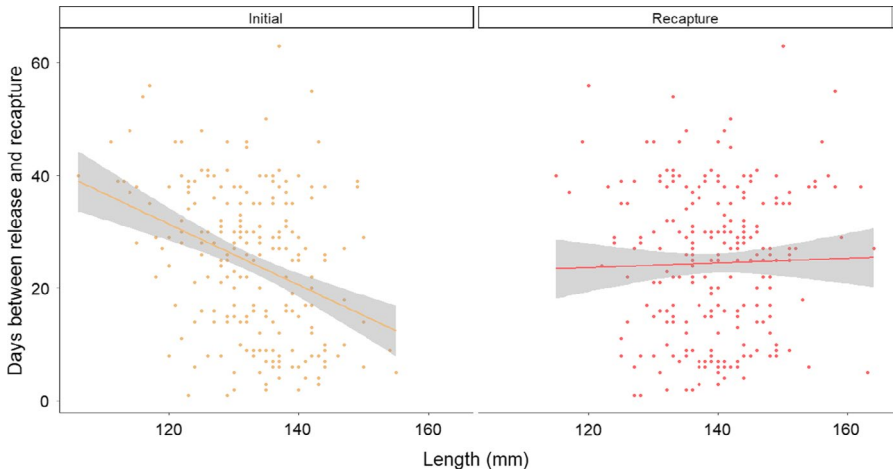

FIGURE 3 Response of migration timing to length at capture and upon recapture. Fish that were initially longer migrated earlier; however, the relationship did not hold upon recapture. Size at recapture had a comparatively flat slope, suggesting that smaller fish that delayed migration were growing while waiting to migrate, ultimately attaining similar size at the onset of migration

smolts that delayed migration were also growing, compensating for their smaller size at tagging in so delaying (Figure 3).

3.3 | Probability of migrating

For all capture groups except the last (May 24; 42%), the majority of tagged fish were recaptured in the wolf trap (56%–64%). The model without the interaction between group and length was the better model (ΔAIC = 4). The model suggested that the migrants from the 24 May tagging group were the group that was significantly different from the others, such that fewer fish migrated ($z = -2.54$, $p = 0.01$). Whether a fish was recaptured in the wolf trap was not related to the initial length ($t = 1.43$, $p = 0.15$).

3.4 | Tag effects

Two-sided KS-tests suggested that the tagged smolts were migrating significantly later than the untagged population for tagging groups on 25 April, 3 May, 16 May and 24 May (all $D > 0.27$, all $p < 0.03$; Figure 4). However, smolts tagged in the earliest group, 15 April, did not have a significantly different distribution than the untagged population ($D = 0.12$, $p = 0.36$). The difference in median out-migration timing (50% of the group) for tagged smolts was 8, 7, 4 and 3 days for the four last tagging groups, respectively. Note that, at the time of tagging for Group 5 (24 May), 74% of the untagged population had already emigrated.

3.5 | Na^+K^+-ATPase activity

No explanatory variables were included in the best linear model (lowest AICc), indicating that date of gill sampling and length of smolts did not affect Na^+K^+-ATPase activity in wild Atlantic salmon smolts captured in the wolf trap. Na^+K^+-ATPase activity ranged from 5.0 to 16.4 (mean 11.2 ± 3.1 SD μmol ADP mg/protein/h).

4 | DISCUSSION

It was hypothesised that tagged smolts were not representative of all out-migrating smolts due to effects from tagging and handling, with the rationale that this may affect survival, fitness or behaviour of the smolts. After all, smolts are exposed to multiple stressors including electrofishing, time out of water, anaesthesia, handling, confinement and internal implantation of the tag. In general, tagged smolts were migrating later than the temporal distribution of untagged fish, unless they were tagged at the earliest time point. Exactly why most groups were migrating later is not known. Although mortality rates after tagging can be affected by the tag-to-size ratio (Lacroix et al., 2004; Larsen et al., 2013; Sigourney et al., 2005), they are generally considered negligible (Gries & Letcher, 2002; Larsen et al., 2013; Prentice et al., 1990). Tag loss rates are also minor (Gries & Letcher, 2002; Larsen et al., 2013), and repetitive electrofishing exposure does not affect growth or survival in smolts (Sigourney et al., 2005). Knowledge about potential adverse, indirect effects from tagging is scarce although some studies suggest that swimming capacity (Lacroix et al., 2004; Larsen et al., 2013), buoyancy regulation (Macaulay et al., 2020) and growth rate (Lacroix et al., 2004; Prentice et al., 1990; Sigourney et al., 2005) can all be depressed after tagging, especially short-term. Consequently, such tagging effects may alter survival rates (e.g. predation-induced mortality) or migration behaviour, although Jepsen et al. (2008) observed no difference in predation of tagged *Salmo trutta* compared with controls. The results indicate that an early tagging date (before the migration has started), produces the most representative sample in terms of migration timing by tagged fish.

Early tagging may be ideal for tagged fish to be representative of the untagged population, but tagging early will exclude the smallest individuals due to tagging restrictions. Indeed, small individuals in the study migrated later, and grew longer in this intervening time, compensating for the smaller size at tagging. Early tagging will therefore over-represent large, early migrating smolts and the results of telemetry data will predict an earlier onset and completion of migration as a consequence. Size-dependent migration phenology has been documented in the River Imsa (Norway), where

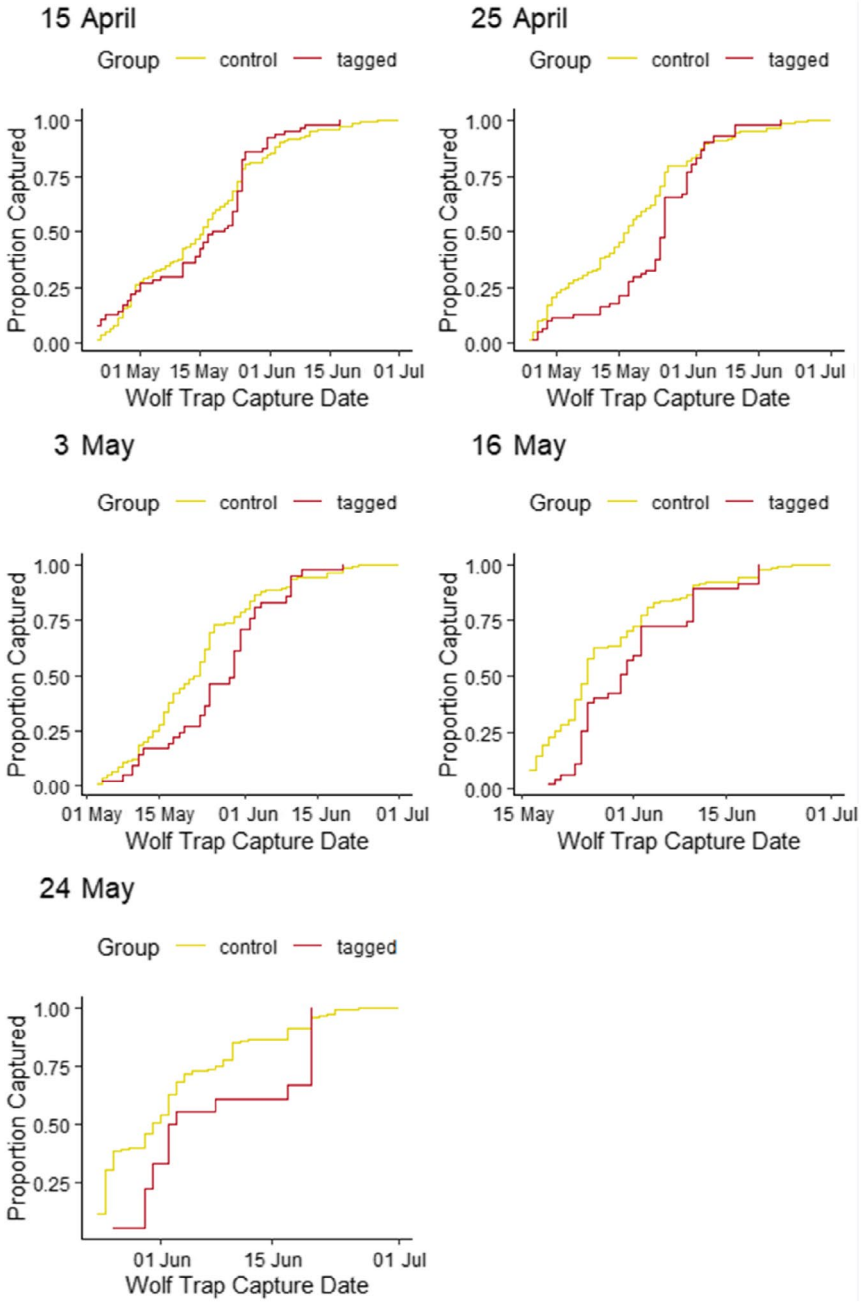

FIGURE 4 Cumulative plots of the proportion of Atlantic salmon smolts captured in the wolf trap in the Dale River, Norway for the tagged and untagged populations. Distributions were tested by the two-sided Kolmogorov–Smirnov test. Note that proportions refer to the number of fish detected

especially small (<13 cm) and large (>20 cm) fish migrated outside the regular smolt migration period (April–June), in October–March and July–September, respectively (Jonsson et al., 2017). Diel migration patterns also seem to be size dependent (Haraldstad et al., 2017; Ibbotson et al., 2011). A possible explanation for the observed pattern could be that size-selective predation is reduced by synchronising the migration with conspecifics of equal size. Although small individuals have more potential piscivorous fish predators (Parker, 1971; Poe et al., 1991), it has been proposed that large individuals may also be targeted to maximise the cost/benefit ratio for predators (Mather, 1998). Thus, intermediate size may be advantageous. Investigators should be cognisant of compensatory growth of small individuals such that small individuals will continue to grow between tagging and onset of migration.

One of the questions to answer was whether fish captured in the wolf trap positioned ~2–3 km upstream of the estuary, was due to within-river movements rather than actual migrating smolts. To investigate this, gill Na^+K^+-ATPase activity (NKA) was used as an indicator for smoltification of smolts (n = 35) captured in the wolf trap at four different time points during May. NKA activity was not affected by the length of smolts, did not differ between sampling dates, and that the overall average NKA activity was 11.2 µmol ADP/mg protein/h (±3.1 SD). It may be argued that the reason why NKA levels were similar in all groups could have been due to the sampling procedure during the fieldwork differed slightly from the procedures described in McCormick (1993). Even though the gill sample tubes were put in a temporary freezer within 0.5 h, they were not frozen (and only cold) during transportation (~2 h) to −20°C where they

were stored for four months, whereas the recommended storage temperature in McCormick (1993) is −80°C for up to 3 months. This could have caused sample degradation, further reducing observable levels of NKA activity. Nevertheless, except for the two outliers potentially representing pre-smolts or within-river movements, the overall average NKA activity was comparable or higher than observed as common levels for smolt in other studies (Stefansson et al., 2012; Strand et al., 2011).

Tagged smolts covered 97.8% of the length distribution of untagged smolts, missing a marginal 0.92% at the lower tail and 1.27% at the upper tail. Although the overlap was substantial, it was not evidenced that the length distribution was identical at the time of tagging due to compensatory growth. Growth rates in tagged smolts can be slower than in untagged smolts for ~1–3 months after tagging (Vollset et al., 2021), which could have shifted the length distribution between the time points. Handling stress, tag burden and auxiliary factors associated with telemetry tagging may affect growth of treated fish (Wargo Rub et al., 2014). Growth was measured up to 18% of the initial body length among tagged smolts, suggesting that growth was not substantially impacted. The effects of excluding some size classes can be estimated by down-sampling the data; for example, if fish <140 mm had been omitted from group 1 (tagged 15 April) migration timing would have differed by 16 days between tagged and untagged animals. Future studies may consider using visible implant elastomer tags for marking the smallest size classes that are not eligible for implantation with electronic tags. Visible implant elastomer tags are, however, easy to overlook when monitoring thousands of smolts and they were not practical in the present study design. Nevertheless, the results should be interpreted in the light of that part of the size distribution being omitted due to regulatory restrictions.

The wolf trap did not capture all migrating fish, which was unexpected. Two hundred and 31 (60%) of the tagged smolts were captured in the wolf trap, but an estimated 45 out of the remaining 154 tagged smolts were able to pass the trap without being captured. It is unknown when exactly this occurred, and this prevents the possibility to compare temporal migration patterns in these individuals to the untagged population. During high discharge, the catchability of wolf traps can decrease (Ugedal et al., 2014), and this may explain the pattern observed in this study. Nevertheless, the wolf trap captured the majority of migrating smolts enabling comparisons in migration timing to the untagged population. Because there is limited fishable reach above the study site up to the waterfall that marks the end of the anadromous part of the river, the sampling population is representative of the smolt run from the river at large.

4.1 | Applications

The present results show that there is a size-dependency on migration timing, an observation that may explain why telemetry studies have shown earlier migration estimates than video counts (Vollset et al., 2021). Whereas the smolts in this study were implanted with the smallest PIT-tag (12 mm), other telemetry studies conducted in Norway, such as Urke et al. (2019) in the River Eio, have primarily used longer acoustic tags (18–22 mm) with correspondingly longer smolts (approximately 140 mm TL). Consequently, this could explain why median migration in 2018 was early (17 May) using acoustic telemetry (Urke et al., 2019), compared with previous studies in the same system, using video surveillance and trap-nets (~29 May; Skoglund et al., 2012). Having said that, between year variations in migration timing can be up to one month (Ugedal et al., 2014), and thus cannot be neglected as a possible explanation. All monitoring methods have potential biases, and the extent of these may vary throughout the migration period (e.g. avoid traps as day-length increases). Unfortunately, few rivers have more than one monitoring method (Vollset et al., 2021). Therefore, to further investigate the effect of these biases on migration timing estimates, several methods should be compared within the same river system (Vollset et al., 2021).

Migration timing estimates that are either too early or too late may have large implications for management and the understanding of post-smolt survival of Atlantic salmon. For example, lice-induced mortalities in post-smolts depend on both migration timing and residency through fjords and coastal areas (Kristoffersen et al., 2018; Nilsen et al., 2017). Bøhn et al. (2020) found that control smolts had 50 times higher mortality risk than smolts treated with lice prophylaxis when migration timing was late (June) and infestation pressure high. By contrast, control fish that migrated during lower infestation pressures (May) did not have a lower likelihood of survival than treated fish (Bøhn et al., 2020). Accordingly, migration timing is crucial and one of the most sensitive parameters when modelling parasite-induced mortalities (Kristoffersen et al., 2018). The accuracy of these models can be improved by monitoring more rivers and quantifying the uncertainties in methods used to estimate migration timing. Although more research is needed in other rivers, the results if this study enlightens some of the potential biases produced in telemetry studies, a method that is increasingly used to monitor populations.

5 | CONCLUSION

The findings advocate that future telemetry studies must consider that the size distribution of the sample (affected by, for example, tagging-size restrictions) may cause a bias in migration timing estimates, which in some cases can be considerable. Additionally, the results showed that tagging of smolts late in the season will yield delayed estimates of migration timing for the tagged smolts compared with the untagged population. These findings will contribute to management practices and the use of telemetry, further enhancing the accuracy of migration timing estimates.

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How to cite this article: Hulbak M, Hanssen EM, Lennox RJ, et al. Validating timing of salmon smolt runs obtained by telemetry studies. *Fish Manag Ecol.* 2021;00:1–9. https://doi.org/10.1111/fme.12495