Received: 25 July 2018 | Revised: 20 October 2018 | Accepted: 4 December 2018
DOI: 10.1002/rra.3400

WILEY

RESEARCH ARTICLE

Naturalised Atlantic salmon smolts are more likely to reach the sea than wild smolts in a lowland fjord

Hugo Flávio | Kim Aarestrup | Niels Jepsen | Anders Koed

Freshwater Fisheries and Ecology, Danish Technical University, Silkeborg, Denmark

Correspondence
Hugo Flávio, DTU Aqua, Vejlsøvej 39, 8600 Silkeborg, Denmark.
Email: hdmfla@aqua.dtu.dk

Funding information
Danish Rod and net license fund, EU-funded NASCO project "Understanding and comparing early mortality of European salmon populations at sea"

Abstract

The survival rates of three groups of seaward-migrating *Salmo salar* smolts were investigated in 2005, 2016, and 2017 in the River Skjern and River Omme, as well as in the Ringkøbing Fjord using acoustic telemetry. Ringkøbing Fjord extends for approximately 300 km^2, and has a narrow, regulated outlet to the sea. Smolts of three different origins: (a) wild smolts, (b) hatchery-reared smolts previously released at half-year-old, and (c) hatchery-reared smolts previously released at 1-year-old were captured in rotary screw traps and surgically implanted with acoustic transmitters. The progress during seaward migration was monitored with a network of automatic listening stations deployed in the river estuary, fjord mouth and sea opening.

The smolts' probability of survival in the river was related to their length, with larger smolts being more likely to reach the fjord. Once in the fjord, the probability of reaching the sea was related with the smolt's group, with smolts previously released at half-year-old being more likely to succeed than wild smolts. However, none of the biometric or behavioural variables explained the difference between the studied smolt groups, masking the potential reasons behind this difference in survival probability.

Overall, approximately 47% of the tagged smolts were registered at the last array of automatic listening stations (i.e., entered the sea), demonstrating the early migration as a critical bottleneck for the local Atlantic salmon population. Ultimately, this limits the number of Atlantic salmon that survive to adulthood and return to River Skjern and River Omme for spawning.

KEYWORDS
Denmark, hatchery, predation, salmo salar, seaward migration, river restoration

1 | INTRODUCTION

Atlantic salmon (*Salmo salar*) is a species of biological, cultural, and economic importance. Despite various attempts to reduce anthropogenic pressures, salmon populations have been in decline throughout most of the species' geographic range (ICES, 2017). Recent literature points towards limiting factors operating both in the marine and freshwater ecosystems, which are part of the Atlantic salmon's life cycle (e.g., Chaput, 2012; Gibson, 2017). From a management perspective, controlling the factors limiting salmon survival is less costly and more feasible in smaller environments (e.g., rivers and estuaries). Thus, exploring mortality rates at early life stages may provide interesting insights on the bottlenecks for salmon populations (Klemetsen et al., 2003). Furthermore, marine mortality is considered density-independent, implying that an increase in the number of smolts that reach the marine environment will directly translate to an increase in the number of returning spawners (Jonsson, Jonsson, & Hansen, 1998; Milner, Elliott, Armstrong, Gardiner, Welton, & Ladle, 2003). During seaward migration, salmon smolts face unfamiliar habitats and must withstand important physiological changes, which are crucial for survival in a marine environment (Hoar, 1976). During this phase, there is often a strong predation pressure, with high mortality rates caused by different predators (Handeland, Järvi, Fernö, & Stefansson, 1996; Jepsen, Klenke, Sonnesen, & Bregnballe, 2010). Interestingly, although predation might commonly act as a proximal driver for smolt loss, there are multiple factors that might affect the smolts' vulnerability to predation, therefore acting as ultimate drivers for smolt loss. Examples include acidification, chemical pollution, and the presence of physical barriers, which may directly lead to mortality or alternatively hinder the smolts' ability to avoid and survive predator encounters (e.g., Aarestrup & Koed, 2003; Birnie-Gauvin, Candee, Baktoft, Larsen, Koed, & Aarestrup, 2018a; Thorstad, Uglem, Finstad, Kroglund, Einarsdottir, Kristensen, ..., & Økland, 2013).

To assist the Atlantic salmon populations, management plans frequently include the stocking of hatchery-reared fish (Aprahamian, Martin Smith, McGinnity, McKelvey, & Taylor, 2003, 2006). It is highly relevant to optimise stocking techniques to obtain maximum gains and, accordingly, recent literature has worked towards this topic. For example, Roberts, Taylor, Gough, Forman, and Garcia De Leaniz (2014) tested the importance of habitat enrichment for post-release performance and Brunsdon, Fraser, Ardren, and Grant (2017) evaluated the effects of clumped versus dispersed stocking. Adult salmon returning to the target river for spawning are usually stripped of eggs and sperm, which are then used to rear hatchery individuals with indigenous characteristics (Araki, Cooper, & Blouin, 2007). These individuals may then be released to the wild at multiple life-stages (e.g., fry, parr, smolt, and adult) depending on the management options and habitat availability. One critical difference amongst these options is that fish released at earlier life-stages have time to interact with the river environment (henceforth referred to as "naturalised" smolts), whereas fish released at smolt age are expected to immediately attempt to migrate to sea. Interestingly, Birnie-Gauvin, Larsen, Thomassen, and Aarestrup (2018b) report that juveniles released as half-year old were more likely to migrate than those released as one-year old, indicating differences between release ages.

1.1 | Objective

The survival rates of seaward-migrating *Salmo salar* smolts were investigated using acoustic telemetry in 2005, 2016, and 2017. The main objectives of the study are (a) to explore the developments in the proportion of smolts successfully reaching the sea across years, and (b) to explore potential differences in survival and migration behaviour between wild and naturalised smolts. We hypothesise that wild smolts have a higher survival probability during early seaward migration than naturalised ones. This is because wild smolts have been submitted to natural selective pressures for a longer period (e.g., predator–prey interactions), which may provide a better preparation for migration.

2 | METHODS

2.1 | Study area

The Danish River Skjern holds an important Atlantic salmon population (Nielsen, Hansen, & Bach, 2001). This lowland river has a catchment area of 2500 km^2, a mean annual flow of 35 m^3/s, and runs for approximately 95 km before meeting Ringkøbing Fjord and reaching the North Sea (55° 55'N, 8°22'E; Figure 1). After a period of high-anthropogenic impacts (i.e., draining, damming, and channelisation), the River Skjern Nature Project was implemented during 2000–2002, which allowed part of the regulated river to return to its former meandering state (Neilsen, 2002). It also allowed returning salmon spawners to enter River Omme, which was previously barred by a weir. Previous studies in the River Skjern have showed increased salmon smolt riverine mortality postrestoration, as the restoration activities provided suitable habitat for the establishment and/or expansion of predatory species (e.g., cormorants, *Phalacrocorax carbo* and pike, *Esox lucius*; Koed, Baktoft, & Bak, 2006).

The smolt traps were positioned approximately 26.1 and 18.3 km upstream of the river estuary (21.5 and 13.8 km from the first automatic listening station). The Ringkøbing Fjord extends for 284 km^2, and is regulated by a floodgate that is operated by the Danish Coastal Authority.

2.2 | Experimental fish

Wild and hatchery-reared migrating smolts released at half-year-old or one-year-old (W, 1/2Y and 1Y groups, respectively), were captured using two rotary-screw traps (Thedinga, Murphy, Johnson, Lorenz, & Koski, 1994) in 2005, 2016, and 2017. In 2005, smolts were only captured from River Skjern, whereas in 2016 and 2017, both the Skjern and Omme traps were operated. The traps were maintained (i.e., cleaned, emptied, and inspected) every day before midday. At capture, fish were selected for tagging based on morphological indicators (e.g., silvery appearance and enlarged eyes). Total length and weight were measured for the selected smolts (in 2016, only length was measured). Smolts smaller than 14 cm were not considered for tag implementation to ensure a low tag/body–weight ratio. Fish released in September at 1/2Y lack the adipose fin, and fish released in March at 1Y lack adipose fin and have a coded wire nose tag (CWT). The retention of CWT in 1Y Atlantic salmon juveniles released in River Skjern has been estimated to be of approximately 93% (Søren Thomasen, Danmarks Center for Vildlaks, personal communication). Therefore, CWT loss should have a minimal effect on the results presented here. A total of 56, 54, and 215 smolts were tagged in 2005, 2016, and 2017, respectively.

2.3 | Tagging procedure

Smolts were anaesthetised (2–4 min) in a 0.03 gL^{-1} solution of benzocaine until operculum rate became slow and irregular. The fish were then placed on a V-shaped surgical table, and the acoustic transmitter was inserted into the body cavity through a mid-ventral incision, posterior to the pelvic girdle. The incision was closed with one or two separate absorbable (Vicryl) sutures. The duration of the procedure varied between 1 and 2 min. Recovery time was 2-5 min and all tagged fish appeared to be in good health at release. After the tagging procedure, the smolts were released during the day, after showing full recovery from the handling and tagging procedure, approximately 100 m downstream of the trap. The acoustic transmitters used were Thelma 7.3 mm tags, weighing 1.9 g in air and 1.2 g in water. The transmitters had an expected operation time of 150 days. Surgical implantation was performed by an experienced fish surgeon in accordance to the guidelines of the Danish Experimental Animal Committee (2017-15-0201-01164).

2.4 | Fish tracking

Automatic listening stations (ALS, Vemco VR2W) were distributed at strategic points along the study area. ALS were deployed at the river estuary, the fjord mouth, and the sea outlet (Figure 1). This allowed to determine the number of fish that disappeared in the river or in the fjord, as well as to determine how many fish successfully crossed to the sea side. ALS detection efficiency was measured by doing reverse

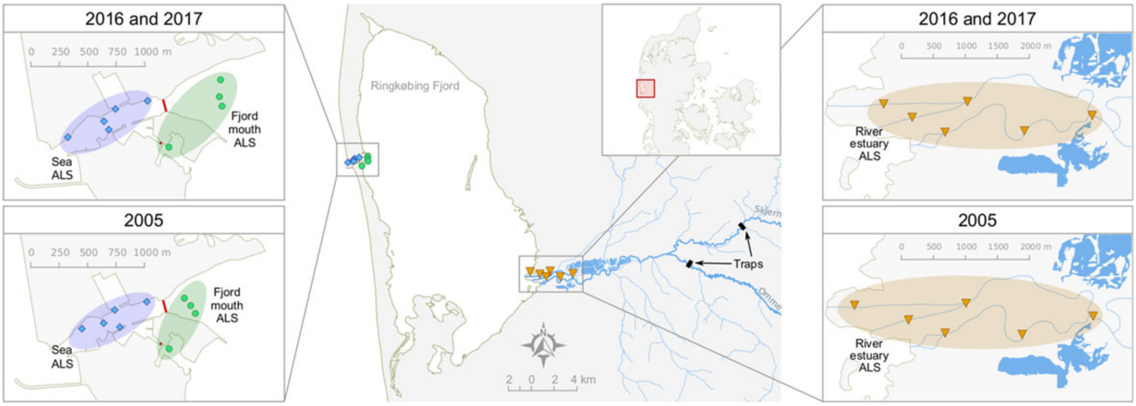

FIGURE 1 The Ringkøbing Fjord and lower River Skjern ecosystems, highlighting the rotary screw trap positions (top: Skjern trap; bottom: Omme trap). Orange triangles represent the river estuary Automatic Listening Stations' (ALS) group, green circles represent the fjord mouth ALS group, and blue diamonds represent the sea ALS group. In the left panels, the red lines represent the sluice gates [Colour figure can be viewed at wileyonlinelibrary.com]

checking of detected fish (Aarestrup, Baktoft, Thorstad, Svendsen, Höjesjö, & Koed, 2015). Specifically, intra-group ALS efficiency was measured by comparing the smolts detected in each ALS with the smolts detected on the remaining ALS within the same group; whereas inter-group ALS efficiency was measured by comparing the smolts detected in a given ALS group with the smolts detected in the group following it. For the sea ALS group, the most westward station was used as a reference for the efficiency of the remaining group.

2.5 | Data analysis

2.5.1 | Potential false detections

Data from acoustic telemetry in 2005, 2016, and 2017 were used to evaluate the factors affecting smolt survival. Raw data were checked for unlikely behaviour, such as skipping ALS groups (e.g., being detected in the river estuary and sea ALS groups but not in the fjord mouth) or unrealistic speeds (e.g., having a single detection in the fjord mouth ALS group in between river estuary detections). These events were analysed in detail so that false detections could be found and removed. After removal of false detections, no smolts were detected which moved back to the river estuary ALS after being detected on a fjord mouth or sea ALS. Rare examples of intersection movements between fjord mouth and sea ALS were found, but these were considered normal given the shifting tides and the short distance between the two ALS groups.

2.5.2 | Biometric analyses

One-way ANOVA and Wilcoxon rank sum tests were applied to test for differences in mean biometric values from different groups, depending on data normality (which was confirmed with previous Shapiro–Wilk testing).

2.5.3 | Survival analyses

After confirming the absence of outliers and collinearity among explanatory variables, two general linear models (GLM) with Bernouli distribution (logit link) were applied for survival analysis:

1. A river model was used to test for effects of studied year, smolt group, smolt length, and release-day-of-year on river survival probability (measured as registration in one of the outermost river estuary ALS);
2. A fjord model was used to test for the effects of the same variables on fjord survival probability (measured as last registration in the sea ALS group).

Step-wise goodness of fit model selection was used on both models to reveal the significant predictor variables.

2.5.4 | Migration timing

Mardia–Watson–Wheeler testing was applied to test for the individual effects of tagging year, smolt group, and migration success in arrival time-of-day at the river estuary, fjord mouth, and sea. These analyses were not performed when the sample size of any group was below 10 to maintain the test's statistical power.

All statistical analyses were performed in R; circular statistics were performed resorting to the "circular" R package (Agostinelli & Lund, 2017).

3 | RESULTS

3.1 | Group biometrics and ALS efficiency

The tagging period extended from April 7th to April 25th in 2005, April 13th to May 8th in 2016, and March 27th to May 22nd in 2017. A total of 122 W, 104 1/2Y, and 99 1Y smolts were tagged during the 3 years. The total length (L_T) of the tagged smolts varied between 14 and 20 cm, averaging at 16.5 cm (detailed values in Table 1). Fulton's condition factor (K) varied between 0.68 and 1.02, averaging at 0.82. K was not calculated for 2016 due to absence of weight data. No significant differences were found among smolt groups on either L_T, weight or K.

Detection efficiency estimates revealed high detection rates in all ALS arrays during the three studied years, with the lowest efficiency estimated at 94% for both the fjord mouth ALS array in 2005 and the sea ALS array in 2016 (Table 2).

TABLE 1 Biometric means for the salmon smolts tagged in the studied years in River Skjern and River Omme. Weight of the tagged smolts was not recorded in 2016

Group	Metric	2005	2016	2017
W	***n***	24	10	88
	L_T (mm)	175	166	164
	Weight (g)	44.8	-	36.5
1/2Y	***n***	10	9	85
	L_T (mm)	175	160	163
	Weight (g)	45.1	-	35.6
1Y	***n***	22	35	42
	L_T (mm)	175	160	161
	Weight (g)	46.6	-	35.3

TABLE 2 Detection efficiency of the ALS groups. Efficiency was calculated by comparing the smolts detected in a given ALS group with the smolts detected in the group following it. For the sea ALS group, the most seaward station was used as a reference for the efficiency of the remaining group

ALS Group	2005	2016	2017
River estuary	100%	100%	100%
Fjord mouth	94%	98%	98%
Sea	100%	94%	97%

TABLE 3 Absolute survival for all of the released Atlantic salmon smolts during the studied years. For each year, a row containing the pooled survival is shown. Data are displayed as 'number of survivors'/'Total'. Overall survival represents the number of smolts that reached the sea by the number of released fish

Year	Group	River survival	Fjord survival	Overall survival
2005	W	22/24	11/22	11/24
	1/2Y	9/10	6/9	6/10
	1Y	21/22	11/21	11/22
	Grouped	52/56	28/52	28/56
2016	W	8/10	5/8	5/10
	1/2Y	7/9	6/7	6/9
	1Y	31/34	17/31	17/34
	Grouped	46/54	28/46	28/54
2017	W	62/86	31/62	31/86
	1/2Y	66/87	45/66	45/87
	1Y	32/42	20/32	20/42
	Grouped	160/215	96/160	96/215

3.2 | Survival rates during seaward migration

The survival probability for smolts descending the river decreased during the three studied years, with an overall mean river survival of 79.4% (258 out of 325 smolts; Figure 2). In 2005, fjord survival was 52.8% (28 out of 52 smolts, Table 3), whereas in 2016 and 2017, approximately 60% of the smolts successfully crossed the fjord (28 out of 46 and 96 out of 160 smolts, respectively, Table 3). The year 2016 had the highest overall survival rates, with 28 out of 54 smolts (51.9%) successfully crossing the study area and reaching the sea (Table 3). In 2005, 28 of 56 released smolts reached the sea (50%), whereas in 2017, overall survival was the lowest at 44.7% (96 out of 215 released smolts).

The river model showed a significant effect of L_T (GLM: $\chi^2 = 5.767$, $p = 0.016$) and a nearly significant effect of year (GLM: $\chi^2 = 3.587$, $p = 0.058$) on river survival probability, with larger smolts appearing more likely to successfully reach the fjord (Figure 3a). The fjord model showed a significant effect of smolt group (Figure 3b; GLM: $\chi^2 = 6.344$, $p = 0.042$) on fjord survival probability, with wild smolts appearing less likely to reach the sea than naturalised smolts. Post hoc testing revealed a significant difference between wild and 1/2Y smolts (GLM, Tuckey's Post hoc Test, $p = 0.038$). Smolts from the 1Y group were not statistically different from the remaining groups during post hoc testing.

3.3 | Arrival time at river estuary, fjord mouth, and sea

Arrival time at the ALS arrays differed between years (Figure 4; test values in Table 4). On average, in 2005, the smolts were first detected at the different ALS arrays between 1 and 2 am, whereas in 2016, they arrived during the afternoon (3 to 8 pm) and in 2017, around 10 to 11 pm. Further analyses of arrival time at the river estuary, fjord mouth, and sea were performed year-by-year.

When comparing smolt groups, significant time differences were only detected at arrival time at sea in 2017 ($\bar{x}_{1Y} = 00{:}57$, $\bar{x}_{1/2Y} = 22{:}31$, $\bar{x}_W = 18{:}43$, $W(4) = 12.802$, $p = 0.012$). No differences were detected in arrival time at the river estuary for smolts originating from River Omme and River Skjern in 2017. Comparing smolts that ultimately disappeared or reached the sea did not reveal any statistical time differences in arrival time at the river estuary or at the fjord mouth.

4 | DISCUSSION

4.1 | Survival in the river

The proportion of smolts disappearing in the river was higher in 2016 and 2017 compared with 2005 (Figure 2). Accordingly, year had a nearly significant effect ($p = 0.058$) on river survival probability (Figure 3a). Koed et al. (2006) reports river mortality rates for radio-tagged salmon smolts of 7.69% and 21.57% for 2000 and 2002, respectively (16.88% on average), for the same river, indicating that river mortality can fluctuate considerably between years. Smolt length had a clear effect on river survival probability, with larger smolts having higher probability of reaching the fjord than smaller smolts. To test for a potential effect of length on migration speed, it would have been interesting to relate these results with the time from release to reaching the fjord. However, Aarestrup, Nielsen, and Koed (2002) reports that length had no effect on net ground speed for Atlantic salmon smolts migrating out of river Lilleaa (Denmark), suggesting that a lower time available to predation might not be the reason behind these differences in survival probability. Alternatively, predators may exhibit a preference for smaller migrating smolts. Jepsen, Aarestrup, Økland, and Rasmussen (1998) found that the mean size for smolts captured in a trap situated upstream of the reservoir Tange (Denmark)

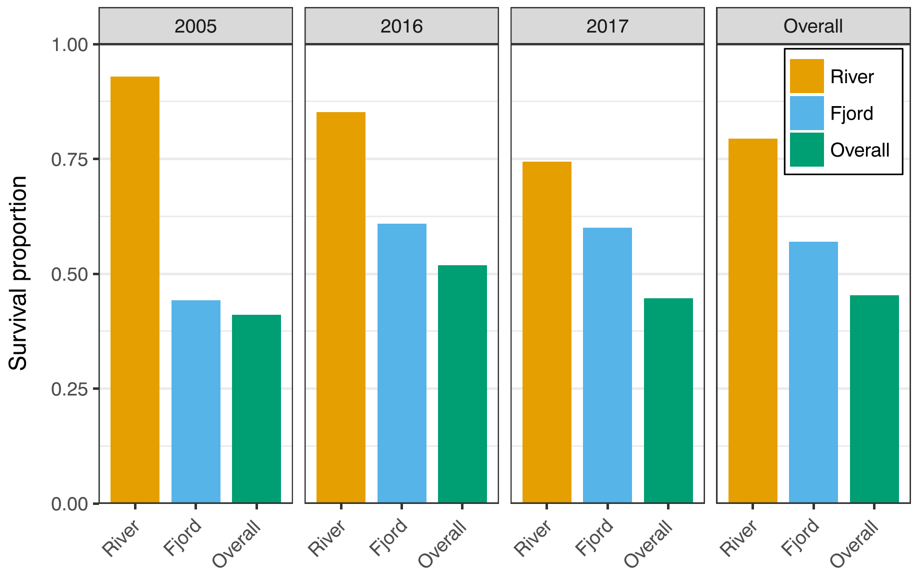

FIGURE 2 Migration fate for the acoustic tagged smolts in the three studied years. Fjord survival was calculated based on the number of smolts that successfully entered the fjord. Overall survival represents the proportion of smolts that reached the sea based on the number of released fish [Colour figure can be viewed at wileyonlinelibrary.com]

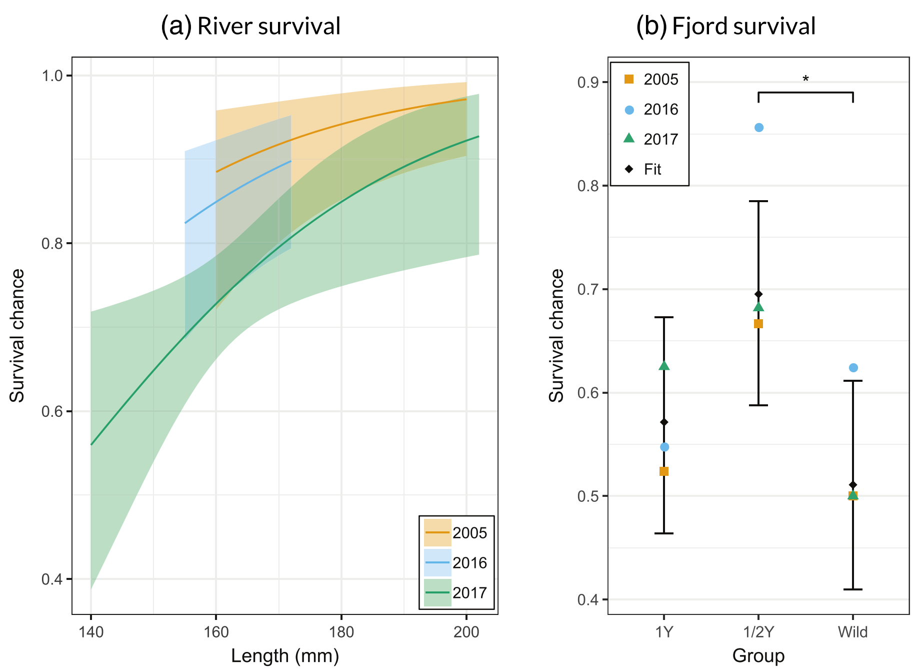

FIGURE 3 (a) River survival probability for smolts of different lengths in the three studied years. (b) Fjord survival probability for smolts of different groups, with the average survival per year represented as well. The interval areas/lines represent the 95% confidence interval around the predicted values [Colour figure can be viewed at wileyonlinelibrary.com]

was of 14.9 cm, whereas the average size for smolts captured in a trap downstream of that reservoir was of 18.4 cm, indicating that smolt survival through the reservoir might be size-dependent. Lastly, it is possible that larger smolts are less impacted by the handling and tagging, leading to an enhanced probability of survival in comparison with smaller smolts. However, Lacroix, Knox, and McCurdy (2004) reports that Atlantic salmon juveniles (13.6–15.5 cm length) did not show negative effects from implanting 24-mm long dummy tags. Considering the smaller size of the tags used in our study, the tagging should have minimum effects.

4.2 | Survival in the fjord

Fjord survival varied between 54% and 61%. These values are consistent with that found in other studies. For example, after releasing hatchery-reared Atlantic salmon smolts at river Eira's estuary, Finstad, Økland, Thorstad, Bjørn, and McKinley (2005) reports 52% of the smolts reaching the last fjord ALS array with full coverage in the Romsdalsfjord (Norway). Later, Thorstad, Økland, Finstad, Sivertsgård, Plantalech, Bjørn, and McKinley (2007) reports survival rates of approximately 35% for hatchery-reared and wild smolts during fjord crossing in the same area.

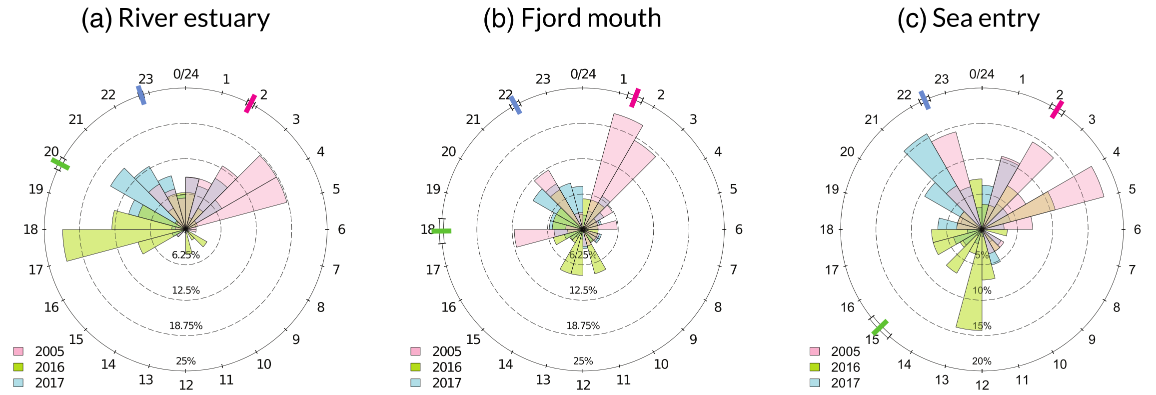

FIGURE 4 Arrival time at different migration points for salmon smolts in the three studied years. Mardia–Watson–Wheeler testing showed significant differences in arrival time between years. Coloured lines on the outer circle indicate the mean value for each year and the respective ranges show the SE. Each year's bars sum to 100% [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Mean arrival time at the river estuary, fjord mouth and sea for salmon smolts in the studied years. Mardia–Watson–Wheeler testing showed significant differences in arrival time between years (W value and p value for each comparison are presented). Further arrival comparisons (e.g., between smolt groups) were performed year-by-year. Times shown in hh:mm

ALS group	Mean 2005 (SE)	Mean 2016 (SE)	Mean 2017 (SE)	W value (df)	p value
River estuary	01:51 (00:05)	19:50 (00:10)	22:50 (00:03)	39.45 (4)	$5.626e^{-8}$
Fjord mouth	01:38 (00:12)	17:57 (00:20)	22:05 (00:07)	15.67 (4)	0.0035
Sea	01:28 (00:12)	15:04 (00:21)	22:24 (00:08)	19.85 (4)	0.0005

The small dimension of Ringkøbing Fjord's outlet, combined with the sluice operations that camouflage the tidal signs, may make it hard for the smolts to find their way out of the ecosystem. In a study in River Dee (North Wales), Gardner, Rees-Jones, Morris, Bryant, and Lucas (2016) noticed a significant decrease in migration speed of wild and naturalised Atlantic salmon smolts during a sluice crossing. The small outlet forces the concentration of migrating fish into a small area, which is heavily populated by avian predators. Predators tend to adapt and aggregate in migration bottlenecks, where the probability of finding prey is highly increased (Holling, 1959). For example, Kennedy, Rosell, Millane, Doherty, and Allen (2018) reports the aggregation of pike *Esox lucius* on bottlenecks for the migration of wild Atlantic salmon smolts in Lough Erne and its tributaries (Northern Ireland). However, Dempson et al. (2011) reports long residence times in the Bay d'Espoir (Newfoundland), which has a larger outlet, indicating that smolts may be reluctant in entering the sea even on unrestricted areas.

Smolts from the 1/2Y group showed a significantly higher probability of successfully crossing the fjord than wild smolts, with 1Y smolts ranking between the two remaining groups (Figure 3b). Interestingly, Larsen, Hingst, Aarestrup, Holdensgaard, Thomassen, Larsen, and Koed (2016) found that, in River Skjern, Atlantic salmon adults originating from 1/2Y releases had a significantly higher return rate (0.17%) than adults that had been released as 1Y (0.09%); a result that is in accordance with our own and points towards a better performance of fish stocked earlier.

There is a variety of studies in literature comparing hatchery-reared smolts and wild smolts (e.g., Kallio-Nyberg, Romakkaniemi, Jokikokko, Saloniemi, & Jutila, 2015; Thorstad et al., 2007). However, the performance of naturalised smolts has received less attention. Jokikokko, Kallio-Nyberg, Saloniemi, and Jutila (2006) studied the differences between the survival of migrating hatchery-reared, wild, and naturalised Atlantic salmon smolts through Carlin-tagging and adult recapturing in River Simojoki (Finland). Jokikokko et al. (2006) reports that wild salmon showed a similar probability of recapture to that of the naturalised smolt group, whereas hatchery-reared smolts performed significantly worse. In contrast to the present study, Jokikokko et al. (2006) study encompasses a broader range of the Atlantic salmon's life cycle, collectively analysing group performance both during early seaward migration and also during growth at sea.

On the other hand, in a study comparing multiple stocking ages for Atlantic salmon in river Kymijoki (Finland), Salminen, Alapassi, and Ikonen (2007) found that releasing older, smoltified individuals was more profitable than releasing both younger smolts or parr of different ages. However, Salminen et al.'s (2007) study results encompasses the survival from release to capture as adults (i.e., including the selection pressure from juvenile release to smoltification), whereas both our study and Jokikokko et al. (2006) do not include the parr-to-smolt phase of the life cycle. It is important to note that salmon juveniles at different stages have different habitat requirements. Thus, the survival of stocked juveniles in the wild varies depending on the habitat availability/quality and stocking density (e.g., Finstad, Armstrong, & Nislow, 2010). Results relating to stocking success may provide advice for managers searching for the best compromise between the number of stocked juveniles and the cost of up-keeping them until release in their home river.

Interestingly, no biometric nor behavioural pattern clearly distinguished wild smolts from naturalised smolts, offering no explanation of the underlying reasons behind the larger success of the naturalised smolts compared with wild smolts during seaward migration.

4.3 | Behavioural patterns

In accordance with known literature (e.g., Thorstad, Whoriskey, Uglem, Moore, Rikardsen, & Finstad, 2012), the studied smolts showed a clear tendency to arrive at the river estuary in the later part of the day and throughout the night. The lack of differences between migration patterns in smolts with a wild or naturalised origin seems to indicate that all smolt groups were similarly receptive to migration cues and that these were not affected (or equally affected) by the handling and tagging processes.

4.4 | Considerations

When performing telemetry studies, there is a risk that the recorded behaviour might not be that of the target animal, but of a predator having eaten the first (Gibson, Halfyard, Bradford, Stokesbury, & Redden, 2015). For the particular case of River Skjern and Ringkøbing Fjord, Koed et al. (2006) reports finding radio tags inside pike and in cormorant and heron nests in the river's vicinity. Interestingly, Koed et al. (2006) reports that tags ingested by pike stood out due to altered behaviour that indicated the migration of the predated smolt had been stopped. In our study, accurately pinpointing tags by manually tracking was not possible due to the technological differences between acoustic and radio telemetry. However, it is not likely for a pike to move close to the fjord mouth. For the case of avian predators, particularly cormorants, it is possible for the predator to move within range of one or more of the ALS arrays after predating a smolt, leading to flawed detections. However, predators mimicking smolt behaviour and going through all the ALS arrays before shedding is not likely and, thus, we expect that the recorded data truly represent the smolt fates.

It is also important to note that our study had a small sample size both in 2005 and in 2016. This may influence the percentage survivals for these years and, as such, we looked into these results with care. However, the fact that the results from 2017 point in the same direction, with a larger sample size, ensures a bigger confidence to the overall survival trends recorded. Undergoing more studies with larger sample sizes per year would prove useful to confirm the present findings.

5 | CONCLUSION

Overall, only approximately 47% of the smolts tagged in the three studied years successfully crossed the study area and reached the outer marine environment (Figure 2). Combining the specific survival rates of each studied year and river with the corresponding estimated smolt runs for those years (Koed, unpublished), the total number of smolts lost during seaward migration is estimated to be approximately 13,600, 11,300, and 19,600 smolts in 2005, 2016, and 2017, respectively. This represents an important bottleneck that ultimately limits the number of Atlantic salmon that survive to adulthood and return to River Skjern and River Omme for spawning.

Contrary to our initial expectation, wild smolts proved less likely to survive the fjord crossing than naturalised smolts. The optimal feeding conditions provided to these hatchery-reared fish, combined with the adaptation time they have between being released as juveniles and their smoltification, may provide good conditions for the fish to grow and successfully prepare for migration. However, given the low sample size in some of the studied years, it is important to run further tests with larger sample sizes to confirm the present findings. Future work on the survival and success of these naturalised individuals during the remaining life stages (i.e., from release to smoltification, during growth at sea and during the spawning migration) is important to consolidate the scientific knowledge and provide managers with well-informed options.

Interestingly, our data shows that, during fjord crossing, smolts stocked as 1/2Y had a marginally higher survival than those stocked at 1Y. This result is in accordance with Birnie-Gauvin et al. (2018b), which argue that the stocking of half-year old Atlantic salmon may be more rewarding than the release of other year classes.

Our study adds to the growing evidence base indicating that freshwater survival plays a main role in regulating Atlantic salmon populations, which is in turn likely to influence the spawning run (e.g., Halfyard, Gibson, Ruzzante, Stokesbury, & Whoriskey, 2012; Jonsson et al., 1998). Therefore, future work on how to improve survival of smolts during seaward migration may prove essential to increase the populations of Atlantic salmon native to River Skjern and River Omme and potentially apply to other rivers elsewhere.

ACKNOWLEDGEMENTS

This project was funded by the Danish Rod and Net License Fund and the EU-funded NASCO Project "Understanding and comparing early mortality of European salmon populations at sea".

ORCID

Hugo Flávio https://orcid.org/0000-0002-5174-1197
Kim Aarestrup https://orcid.org/0000-0001-8521-6270
Niels Jepsen https://orcid.org/0000-0003-0927-6823
Anders Koed https://orcid.org/0000-0002-2163-0955

REFERENCES

Aarestrup, K., Baktoft, H., Thorstad, E., Svendsen, J., Höjesjö, J., & Koed, A. (2015). Survival and progression rates of anadromous brown trout kelts Salmo trutta during downstream migration in freshwater and at sea. *Marine Ecology Progress Series*, *535*, 185–195.

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*, 169–176.

Aarestrup, K., Nielsen, C., & Koed, A. (2002). Net ground speed of downstream migrating radio-tagged Atlantic salmon (Salmo salar L.) and brown trout (Salmo trutta L.) smolts in relation to environmental factors. *Hydrobiologia*, *483*, 95–102.

Agostinelli, C., & Lund, U. (2017). R package circular: Circular statistics. (version 0.4-93). https://doi.org/r-forge.r-project.org/projects/circular/

Aprahamian, M., Martin Smith, K., McGinnity, P., McKelvey, S., & Taylor, J. (2003). Restocking of salmonids–opportunities and limitations. *Fisheries Research*, *62*, 211–227.

Aprahamian, M. W., Wyatt, R. J., & Shields, B. A. (2006). Use of biological reference points for the conservation of Atlantic salmon, Salmo salar, in the River Lune, North West England. *Fisheries Management and Ecology*, *13*, 21–30.

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science*, *318*, 100–103.

Birnie-Gauvin, K., Candee, M., Baktoft, H., Larsen, M., Koed, A., & Aarestrup, K. (2018a). River connectivity reestablished: Effects and implications of six weir removals on brown trout smolt migration. *River Research and Applications*, *34*, 548–554.

Birnie-Gauvin, K., Larsen, M. H., Thomassen, S. T., & Aarestrup, K. (2018b). Testing three common stocking methods: Differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (Salmo salar). *Aquaculture*, *483*, 163–168.

Brunsdon, E. B., Fraser, D. J., Ardren, W. R., & Grant, J. W. A. (2017). Dispersal and density-dependent growth of Atlantic salmon (Salmo salar) juveniles: Clumped versus dispersed stocking. *Canadian Journal of Fisheries and Aquatic Sciences*, 1337–1347.

Chaput, G. (2012). Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, *69*, 1538–1548.

Dempson, J. B., Robertson, M. J., Pennell, C. J., Furey, G., Bloom, M., Shears, M., Ollerhead, L. M. N., Clarke, K. D., Hinks, R., & Robertson, G. J. (2011). Residency time, migration route and survival of Atlantic salmon Salmo salar smolts in a Canadian fjord. *Journal of Fish Biology*, *78*, 1976–1992.

Finstad, A. G., Armstrong, J. D., & Nislow, K. H. (2010). Freshwater habitat requirements of Atlantic salmon, *Atlantic Salmon Ecology*. Oxford, UK: Wiley-Blackwell, pp. 67–87.

Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A., & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, *66*, 86–96.

Gardner, C. J., Rees-Jones, J., Morris, G., Bryant, P. G., & Lucas, M. C. (2016). The influence of sluice gate operation on the migratory behaviour of Atlantic salmon Salmo salar (L.) smolts. *Journal of Ecohydraulics*, *1*, 90–101.

Gibson, R. J. (2017). Salient needs for conservation of atlantic salmon. *Fisheries*, *42*, 163–174.

Gibson, A. J. F., Halfyard, E. A., Bradford, R. G., Stokesbury, M. J., & Redden, A. M. (2015). Effects of predation on telemetry-based survival estimates: Insights from a study on endangered Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 728–741.

Halfyard, E. A., Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W., & Whoriskey, F. G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon Salmo salar smolts. *Journal of Fish Biology*, *81*, 1626–1645.

Handeland, S. O., Järvi, T., Fernö, A., & Stefansson, S. O. (1996). Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (Salmo salar) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 2673–2680.

Hoar, W. S. (1976). Smolt transformation: Evolution, behavior, and physiology. *Journal of the Fisheries Research Board of Canada*, *33*, 1233–1252.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, *91*, 385–398.

ICES (2017). Report of the Working Group on North Atlantic Salmon (WGNAS). (*Tech. Rep.*) Copenhagen, Denmark: ICES CM 2017/ACOM:20.

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (Salmo salar L.) and trout (Salmo trutta L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, *371/372*, 347–353.

Jepsen, N., Klenke, R., Sonnesen, P., & Bregnballe, T. (2010). The use of coded wire tags to estimate cormorant predation on fish stocks in an estuary. *Marine and Freshwater Research*, *61*, 320–329.

Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., & Jutila, E. (2006). The survival of semi-wild, wild, and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. *Journal of Fish Biology*, *68*, 430–442.

Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon Salmo salar. *Journal of Animal Ecology*, *67*, 751–762.

Kallio-Nyberg, I., Romakkaniemi, A., Jokikokko, E., Saloniemi, I., & Jutila, E. (2015). Differences between wild and reared Salmo salar stocks of two northern Baltic Sea rivers. *Fisheries Research*, *165*, 85–95.

Kennedy, R. J., Rosell, R., Millane, M., Doherty, D., & Allen, M. (2018). Migration and survival of Atlantic salmon Salmo salar smolts in a large natural lake. *Journal of Fish Biology*, *93*, 134–137.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr Salvelinus alpinus (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*, 1–59.

Koed, A., Baktoft, H., & Bak, B. D. (2006). Causes of mortality of Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) smolts in a restored river and its estuary. *River Research and Applications*, *22*, 69–78.

Lacroix, G. L., Knox, D., & McCurdy, P. (2004). Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. *Transactions of the American Fisheries Society*, *133*, 211–220.

Larsen, M. H., Hingst, B. O., Aarestrup, K., Holdensgaard, G., Thomassen, S. T., Larsen, S., & Koed, A. (2016). Udbytte af udsatte 1/2;- og 1-å rs laks (Salmo salar) i Skjern Å. (*Tech. rep.*): DTU Aqua-rapport nr.

Milner, N., Elliott, J., Armstrong, J., Gardiner, R., Welton, J., & Ladle, M (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, *62*, 111–125.

Neilsen, M. (2002). Lowland stream restoration in Denmark: Background and examples. *Journal of the Chartered Institution of Water and Environmental Management*, *16*, 189–193.

Nielsen, E. E., Hansen, M. M., & Bach, L. A. (2001). Looking for a needle in a haystack: Discovery of indigenous Atlantic salmon (Salmo salar L.) in stocked populations. *Conservation Genetics*, *2*, 219–232.

Roberts, L. J., Taylor, J., Gough, P. J., Forman, D. W., & Garcia De Leaniz, C. (2014). Silver spoons in the rough: Can environmental enrichment improve survival of hatchery Atlantic salmon Salmo salar in the wild? *Journal of Fish Biology*, *85*, 1972–1991.

Salminen, M., Alapassi, T., & Ikonen, E. (2007). The importance of stocking age in the enhancement of River Kymijoki salmon (Salmo salar). *Journal of Applied Ichthyology*, *23*, 46–52.

Thedinga, J. F., Murphy, M. L., Johnson, S. W., Lorenz, J. M., & Koski, K. V. (1994). Determination of salmonid smolt yield with rotary-screw traps in the Situk River, Alaska, to predict effects of glacial flooding. *North American Journal of Fisheries Management*, *14*, 837–851.

Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P. A., & McKinley, R. S. (2007). Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Hydrobiologia*, *582*, 99–107.

Thorstad, E. B., Uglem, I., Finstad, B., Kroglund, F., Einarsdottir, I. E., Kristensen, T., ..., & Økland, F. (2013). Reduced marine survival of hatchery-reared Atlantic salmon post-smolts exposed to aluminium and moderate acidification in freshwater. *Estuarine, Coastal and Shelf Science*, *124*, 34–43.

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*, 500–542.

How to cite this article: Flávio H, Aarestrup K, Jepsen N, Koed A. Naturalised Atlantic salmon smolts are more likely to reach the sea than wild smolts in a lowland fjord. *River Res Applic*. 2019;35:216–223. https://doi.org/10.1002/rra.3400