Doogan *et al. Animal Biotelemetry* (2023) 11:39
https://doi.org/10.1186/s40317-023-00352-z

Animal Biotelemetry

RESEARCH **Open Access**

Partitioning survival during early marine migration of wild and hatchery-reared Atlantic salmon (*Salmo salar* L.) smolts using acoustic telemetry

Aisling Doogan[1,2*], Deirdre Cotter[2], Nigel Bond[2], Niall Ó'Maoiléidigh[2] and Deirdre Brophy[1]

Abstract

The marine migration of Atlantic salmon (*Salmo salar*) has been prioritised for research internationally as populations of *S. salar* have declined significantly throughout the species' range. The main objectives of this study were to use acoustic telemetry to partition survival during the early migration phase, investigate potential causes of mortality and establish diurnal and tidal influences on movements. In 2017 and 2018 wild ($n=49$) and hatchery ($n=81$) *S. salar* smolts were tagged with acoustic transmitters. Migration was monitored through a brackish tidal lake, which discharges through a short estuary into northeast Clew Bay in Ireland situated in the northeast Atlantic. Partitioned survival through each area was similar for both wild and hatchery smolts and both groups followed the same migration routes, travelling along the main current out of Clew Bay. Total survival was high within the brackish lake (wild = 98% ± 1.21 and hatchery = 100%) and estuary (wild = 98% ± 1.01 and hatchery = 89% ± 9.28) compared to the marine environment (wild = 67% ± 4.39 and hatchery = 66% ± 7.91). Leaving the brackish lake during an ebb tide and entering the marine environment during daylight increased the probability of survival through the early marine period. The majority of smolts transited through the study area during ebb tides. Migration of hatchery smolts occurred mainly during hours of daylight while wild smolt migration showed no diel patterns. High mortality rates during the initial stages of the marine migration have consequences for the persistence of salmon populations and should be addressed through regionally tailored management measures and conservation efforts aimed at increasing the resilience of salmon stocks.

Keywords Atlantic salmon, Smolt, Wild, Hatchery, Acoustic telemetry, Migration, Survival

Introduction

The Atlantic salmon (*Salmo salar*) is listed as vulnerable under the IUCN Red List of Threatened Species due to decreasing numbers throughout the species range [28]. In the Northeast Atlantic, marine survival has been in decline since 1980 and return rates of some Atlantic salmon stocks are currently at their lowest in recent years [31, 45]. Due to the particularly high rates of mortality that occur during the marine migration [91], it is recommended that research efforts focus on partitioning mortality of salmon among phases of the marine migration ([43], NASCO 2018). Recent research has focussed on identifying how barriers impact on migration [6, 37, 52, 88], while the release of tagged hatchery fish provides detailed information on survival rates [8], Ó'Maoiléidigh

---

*Correspondence:
Aisling Doogan
aisling.doogan@research.atu.ie
[1] Marine and Freshwater Research Centre, ATU Galway City, Dublin Road, Co, Galway, Ireland
[2] Marine Institute, Furnace, Newport, Co, Mayo, Ireland

et al. [73], [16, 77] and helps to identify potential causes of declining survival [35, 74, 87].

Evidence shows that migratory behaviours influence survival [32, 91]. Important factors include migration speed on approaching the marine environment [21, 58] and the timing of migration in relation to the tide [21, 38, 61, 65] and level of daylight [21, 53, 58]. When they reach marine habitats salmon encounter human activities such as fishing, shipping and aquaculture [53] and are exposed to novel predators, disease and parasites, competition for food and physiological stress [10, 75, 83, 91]. Such pressures may produce a bottleneck in survival of migrating salmon as they pass through unfamiliar coastal environments to feeding grounds in the North Atlantic [18, 40, 79, 86].

Acoustic telemetry provides a means of tracking Atlantic salmon during the early part of their migration and partitioning survival between different habitats (e.g. [13, 21, 32, 53, 58]), which can inform the design of targeted conservation measures. Telemetry has proven useful for determining the influence of temperature, time of day and tidal patterns on the timing and direction of fish movements [21, 36, 42, 61, 65].

Tagging studies frequently use hatchery-reared *S. salar* which are produced for restocking purposes to describe migration behaviour and pathways and to monitor survival [34, 51, 67, 77]. However, it has been shown that wild salmon generally survive better than their hatchery-reared counterparts [55, 80, 84]. Differences in the timing of smoltification and smolt migration between hatchery and wild fish are reported [3, 63, 84], which could contribute to differences in survival. In addition, anti-predator behaviours are less well developed in hatchery-reared smolts compared to wild smolts [30, 81, 85]. Given the reliance on data from hatchery-reared populations for monitoring survival, it is important to understand how both hatchery and wild smolts move and survive throughout the early seaward migration and to consider how release conditions may affect recruitment of both stocks, within the context of climate change [87]. Detailed knowledge of movements and survival can inform improvements to smolt trap management during the downstream run to enhance the downstream survival rates, thereby potentially increasing the number of successful returns [49].

The Burrishoole catchment, on the West coast of Ireland supports a wild Atlantic salmon population. In this catchment, upstream and downstream migrating salmon, trout and eels are monitored, and between approximately 9000 and 41,000 hatchery-reared salmon smolts have been released into the catchment yearly since the 1960s [16]. This extensive monitoring has made the Burrishoole an important index site for monitoring salmon stocks [45]. This study used acoustic telemetry to partition survival and examine migration behaviour of Atlantic salmon smolts through a brackish lake, estuarine and early marine phases of the seaward migration in the Burrishoole catchment. Migration behaviour and survival were compared between wild and hatchery-reared smolts. The influence of tidal cycle, time of day and smolt behaviour on survival and migration of both groups were also investigated. The Burrishoole system is one of 21 national index rivers in the Northeast Atlantic that are used by the International Council for the Exploration of the Sea (ICES) to monitor trends in survival of Atlantic salmon [45]. The overall goal of the study was to provide insight into how Burrishoole smolts migrate between freshwater and marine environments and thereby inform future management and conservation efforts.

Materials and methods

Experimental site

The Burrishoole catchment is located on the west coast of Ireland (53° 55′ N, 9° 34′ W) and covers an area of 90 km^2 which is primarily used for forestry and hillside subsistence farming. Rivers in the catchment flow into a deep, oligotrophic freshwater lake, Lough Feeagh (4.1km^2) which is connected to the brackish lake, Lough Furnace (1.4 km^2) by two streams on which upstream and downstream traps are located. The total trapping facilities on the catchment allow for an annual census on abundance of anadromous fish species in the area. Lough Furnace is a brackish tidal lake with a permanent halocline, which produces anoxic conditions in the deeper areas of the lake. The lake discharges through a short estuary (3.3 km) into northeast Clew Bay which is situated in the Northeast Atlantic and is approximately 27 km long (Fig. 1).

Smolt trapping, tagging and release

The wild smolts used in this study originated from naturally spawned salmon from rivers in the Burrishoole catchment, and generally migrate to the ocean at age 2+. Hatchery-reared smolts were derived from a line-bred ranching stock of local Burrishoole origin (see [16] for more detail), which are released for migration at age 1+. From here on smolts will be referred to as wild or hatchery smolts. During early May 2017 and 2018, hatchery smolts were provided by the fish rearing facility and migrating wild smolts were collected from the downstream traps. A total of 55 hatchery and 25 wild smolts were tagged in 2017 and 26 hatchery and 24 wild smolts were tagged in 2018. Wild smolts were tagged when fish of an appropriate size (i.e. fork length > 14 cm in order to maintain a low tag-body mass percentage) entered the traps; this produced some between year variation in the date of tagging. Due to

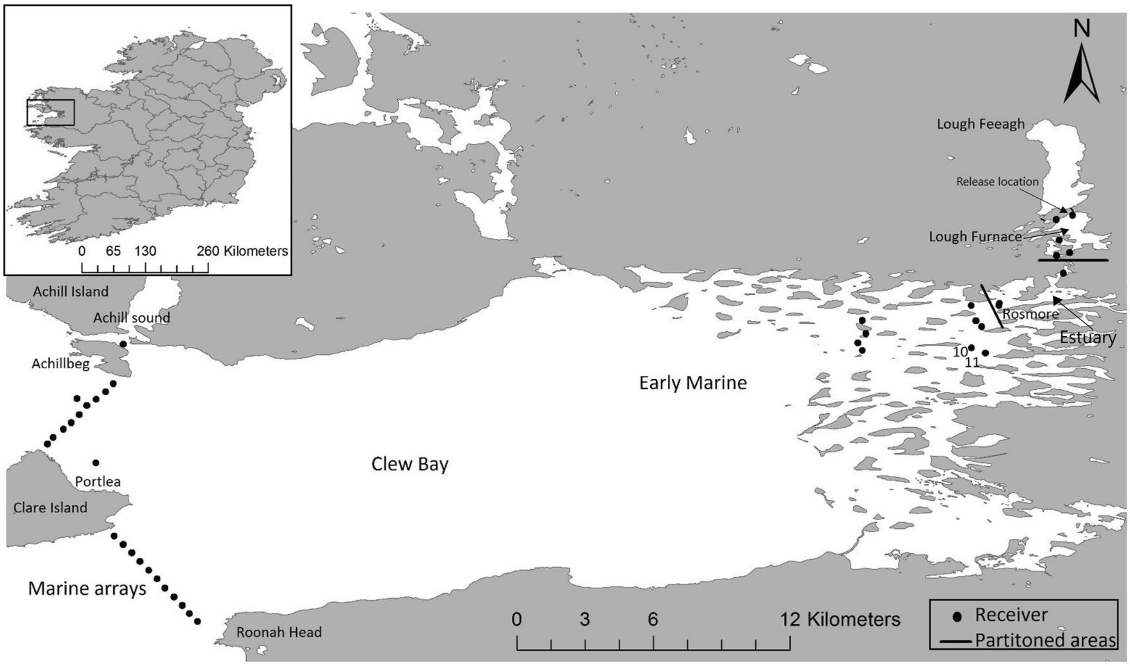

Fig. 1 Map of Clew Bay displaying receiver locations and partitioned areas referred to as the lake (Lough Furnace), the estuary (between Furnace and Rosmore) and the marine (between Rosmore and Clare Island). In 2017 the 180-kHz system was positioned in the lake and estuary only. Two additional receivers (10 and 11) were placed in the inner bay in 2018. Receivers in the Clare Island arrays are numbered North 1–9 (from north to south) with North 10 sitting behind the array, and South 1–11 (from north to south)

low water levels during April and early May in 2017, the movement of wild smolts was delayed and they did not enter the downstream traps in high numbers until mid-May (Marine [60]. In 2018 smolts arrived at the traps in a series of pulses rather than a single discrete peak (Marine [60]. See Table 1 for information on release dates and length/weights for each group.

Three models of Innovasea, (Nova Scotia, Canada) acoustic transmitters and receivers were used during the study: V5 coded tags (signal delay 15 ± 0.1 s), requiring a VR2W 180 kHz receiver for detection, V7 coded tags (signal delay 15 ± 0.1 s) and V7P depth sensor tags (signal delay 20 ± 0.1 s) requiring VR2W and VR2Tx 69 kHz receivers for detection (see Table 1 for tag details and fish numbers). The V5 tag was the smallest but had a reduced detection range compared to the V7 and V7P. The three tag types were included in the tagging operations in 2017 and the range and survival rates associated with each were compared. Survival rates were similar in the fish tagged with the V5 and V7/V7P tags (Table 1) while the range of the smaller V5 tag was 30% lower (see later). Therefore, the V5 tags were not used in 2018. The smaller tag may be useful in future studies for tagging smaller wild smolts (< 14 cm) and so the data collected from the V5 tags in 2017 are presented here.

Before tagging, salmon smolts were transferred from the hatchery ponds and fish traps to the surgical area and held in containers with aerated water. Fish were anesthetised in 2-phenoxyethanol (0.7 ml L^{-1}) and positioned ventral side up on a sterile surgical table. Surgery was carried out by the same two individuals throughout the study. An incision was made between the pectoral and pelvic fins and an acoustic transmitter was implanted into the peritoneal cavity. The incision was closed with two simple interrupted suture knots (Ethicon Vicryl 4–0 Polyglactin 910 absorbable suture, Johnson and Johnson Intl., Brussels, Belgium) and fish were transferred to recovery tanks. Prior to release into Lough Furnace, smolts were held overnight to ensure full recovery from the procedure. Smolts less than 14 cm were not tagged but were held overnight with tagged fish. Fish that were unresponsive to stimuli (a shadow/ripple over the water using a small net) or dead were removed from the study group and transmitters were redeployed. Smolts were released directly into Lough Furnace (Fig. 1) during the wild smolt run between 4 and 16 May 2017 and 10–17 May 2018 (Table 1).

Range testing and acoustic monitoring system

Range testing of tags was conducted in the lake and inner bay to determine the detection range of receivers

Table 1 Summary information and estimated survival for Atlantic salmon (*Salmo salar*) smolts tagged in 2017 and 2018

Release dates	Fish type	Mean length (cm)	Mean weight (g)	Tag type	Tag weight in air (g)	Tag frequency (kHz)	Mean tag:body mass %	Tagged (N)	Released (N)	Survival brackish lake (%)	Survival estuary (%)	Survival early marine (%)	Overall survival (%)	Detection period (days)	Mean daily mortality (%)
2017															
04/05 & 16/05	Hatchery	19.2	76.2	V7	1.6	69	2.2	45	41	100	95	62	59	8.8	5.8
16/05	Wild	16.6	40.7	V7	1.6	69	4	15	12	100	92	73	67	5.1	7.6
12/05	Hatchery	19.5	80.3	V5	0.65	180	0.8	10	9	100	100	–			
04/05 & 12/05	Wild	16.7	40.8	V5	0.65	180	1.6	10	9	100	100	–			
2018															
11/05	Hatchery	19.2	83.7	V7P	1.7	69	2.2	6	6	100	67	75	50	8	9.6
10/05–17/05	Wild	16.8	46.7	V7P	1.7	69	3.7	4	3	67	100	50	33	3.9	67.4
11/05 & 12/05	Hatchery	19.6	85.3	V7	1.6	69	1.9	20	20	100	95	63	60	6.3	4.2
10/05–12/05	Wild	15.4	34	V7	1.6	69	4.8	20	20	100	100	65	65	10.2	3.3
2017 & 2018 combined															
	Hatchery			V5/V7/ V7P		69/180		81	76	100	89	66	58*		
	Wild			V5/V7/ V7P		69/180		49	44	98	98	67	63*		

Survival is partitioned through three key sites: the brackish lake (Lough Furnace), estuary (Rosmore) and early marine (to Clare Island arrays). Number released is the number of fish included in survival estimates after potential tag mortalities were removed (i.e. continuous tag detections at the receivers located at the release location). The detection period is the maximum number of days between the release and the last detection at the marine array. V5 tags were only tracked to the exit from the estuary therefore values marked with '*' include V7 and V7P tags only and to establish the optimal spacing between receivers. A VR2W receiver was deployed in a fixed location at approximately 1 m depth, representing the approx. depth at which receivers within the monitoring system were deployed. Using a GPS, the boat was moved 50 m from the receiver where the anchor was dropped, the engine turned off and the tag deployed for a period of 15 min.; this process was repeated up to approximately 300 m distance. The distance at which detections dropped to 70% was considered to be the tag detection limit. This was the higher limit recommended by the manufacturer to account for reductions in detection during poor weather conditions (Innovasea Range Test Manual). The V7 and V7P tags had a detection limit of approximately 250 m and approximately 175 m for the V5 tag. In order to reduce the probability of a fish passing through the array undetected these receivers were spaced approximately 400 m apart. Detection efficiency was calculated based on range testing; at 200 m the rate of detection was 0.76. The probability of detection by at least one receiver (P_{min}) for a fish passing through the array was calculated as follows:

$$P_{min} = P_a + P_b - P_a * P_b,$$

where P_a is the probability of detection at receiver a, P_b is the probability of detection at receiver b and $P_a * P_b$ is the probability of detection by both receivers. P_{min} was calculated as 94%.

Based on range testing, smolt migration was monitored at 37 stations in 2017 using receiver models VR2W (69 and 180 kHz, Innovasea, Nova Scotia, Canada) and VR2Tx (69 kHz, Innovasea, Nova Scotia, Canada) and 40 stations (VR2W and VR2Tx 69 kHz) in 2018 (Fig. 1). Receivers were located in the brackish lake (five stations), estuary (three stations) and initial coastal waters in the inner Bay in the most direct migration pathways (seven in 2017 and nine in 2018, Fig. 1). At the exit of the bay there were two arrays, one north of Clare Island (comprising nine receivers in 2017 and ten in 2018) and one south (11 receivers) of the island. In addition, a receiver was located near Portlea fish farm site and also between Achillbeg Island and the mainland (Achill sound, Fig. 1). Receivers were placed at these locations to determine if smolts were drawn towards the fish farm or migrated north through Achill Sound. In 2017, nine 180 kHz VR2W receivers were located between lower Lough Furnace and inner Clew Bay. Three were deployed at the southern end of the brackish lake, three in the estuary and three in the inner Bay. The 180-kHz receivers were deployed on the same moorings as the 69-kHz receivers. Due to the reduced detection limit and limited availability of the 180-kHz receivers, fish tagged with V5 tags were only tracked to the exit point of the estuary at Rosmore. Therefore, in 2017 20 fish (10 hatchery and 10 wild) were not tracked through the marine phase. Partitioned areas (as shown in Fig. 1) are hereon referred to as the brackish lake (Lough Furnace), the estuary (between Lough Furnace and Rosmore), and marine (between Rosmore and the Clare Island arrays).

Environmental variables

In 2017 and 2018 water temperature and salinity profiles in the brackish lake were gathered from an Automatic Water Quality Monitoring Station located at the deepest point in the lake (data downloaded from: http://burrishoole.marine.ie/FurnaceLake.aspx). Lake data were taken from the surface to 2.5 m depth. In 2017, temperature and salinity parameters were measured at the exit of the estuary by handheld meters during site visits. In 2018 Star-Oddi temperature and salinity recorders were located at the exit of the estuary at 1 m and 3 m depth. Temperature and environmental noise levels were recorded at the marine arrays by the VR2Tx receivers in both years. Measures of salinity at the marine arrays were taken by handheld meters on site visits. These data were used to describe environmental conditions during the study period (Table 2).

Times of sunrise, sunset and civil twilight for the study area were obtained from the Astronomical Applications Department of the US Naval Observatory. (https://aa.usno.navy.mil/data/RS_OneYear) The period between civil twilight (sun 6° below horizon) in the morning and the end of civil twilight in the evening was defined as day (when there was daylight). Night was defined as the period between civil twilight in the evening and the start of civil twilight in the morning. Tidal state was predicted using local tide tables (computed by the Centre for Coastal and Marine Sciences, Proudman Oceanographic Laboratory). These data were used to link diel and tidal cycles with smolt migration through the study area.

Statistical analysis

All analyses were run in the R programming environment [78] using packages 'car' [27], 'circular' [1] and 'lmtest' (Zeileis and Horthron 2002). GLM models were run using the glm() function in the r package 'stats' [78]. Likelihood ratio tests were run using the lrtest() function from the 'lmtest' package [97].

Partitioned survival

Detections at each receiver were used to generate a binary response variable that provided an estimate of survival (positive detection = 1; negative detection = 0). Survival was partitioned through the brackish lake, the estuary and the marine (Fig. 1). Smolts are known to be particularly sensitive to stress [4, 11], and any estimates

Table 2 Mean temperature and salinity data throughout the study area

	Lake		Estuary		Marine arrays	
Date	Temperature (°C)	Salinity (psu)	Temperature (°C)	Salinity (psu)	Temperature (°C)	Salinity (psu)
2017						
01–07 May	12.8	14.1			11.1	
08–14 May	14.6	15.2	13.5[a]	33.8[a]	11.8	
15–21 May	14.5	12.8			12.5	34.7[a]
22–28 May	15.8	11.9	15 [a]	32.9[a]	13.3	34.5[a]
2018						
01–06 May	10.9	8.2	11.2	29.2	10.4[b]	
07–13 May	11.9	7.3	12.8	28.3	10.9	
14–20 May	13.3	8.4	12.9	30.3	11.4	34.8[a]
21–27 May	14.4	9.6	13.6	31.3	12.2	34.6[a]
28–30 May	17.1	9.1	15	31.3	13.4	35.2[a]

[a] Indicates that mean temperature or salinity was taken on one day only using a handheld meter

[b] Indicates that mean temperature was taken between 4 and 6 May

of survival obtained from tagging studies are subject to biases due to tagging-related mortalities and tag expulsion [2, 53]. In a previous study, Atlantic salmon post-smolts of 14.5–16.5 cm carrying internally implanted acoustic tags greater than 7.5% of their body mass showed tagging-related mortality rates of 0.132% per day over 97 days and tag expulsion in the first 25 days after tagging was negligible [9]. In this study, every effort was made to minimise handling and maintain a low tag-to-body mass ratio of less than 5.8% (Table 1). Those fish that were not detected beyond the receivers closest to the release location were categorised as tagging mortalities and were excluded from the dataset before estimating overall survival. Bias in the survival estimates due to tagging-related mortality or tag expulsion after the fish passed the first receiver is likely to be minimal.

Overall survival was estimated for each group by expressing the numbers detected at each point on the migration as a percentage of the numbers released (minus the tagging mortalities). Chi-square tests were used to compare survival rates between hatchery and wild groups and between years. The instantaneous daily mortality rate (z) and the finite percentage daily mortality rates (M) were calculated for each group as follows:

$$z = \frac{\ln(S)}{D}$$

$$M = \left(1 - e^{z}\right) * 100,$$

where S is the proportion of the tagged fish (excluding suspected tagging mortalities) that were detected at the marine array and D is the number of days between the release and the last detection at the marine array.

Effect of tagging on survival

A GLM (generalised linear model) with a binomial distribution was used to examine the impact of the tagging procedure on survival through each partitioned area. Survival was modelled as a function of time in anaesthetic, time in surgery, fish type (two-level factor; wild and hatchery) and tag-to-body mass ratio expressed as a percentage. Surgeon effects were not considered as a variable in this analysis as surgeon was not recorded for every fish tagged. To test if tagging influenced survival, all fish tagged including fish categorised as tagging mortalities were included in this analysis.

Effect of behaviour on survival

A binomial GLM was used to establish relationships between migration behaviour and survival through each partitioned area; survival (minus tagging mortalities) was modelled as a function of lake, estuary and marine residence times (continuous variables) and the categorical variables diel (day or night) and tidal (ebb or flood) state.

During GLM model selection the drop1() function was used to determine the best fitting model. This function estimates the overall model and a series of alternative models, each with one additional explanatory variable excluded. On each iteration the predictor with the largest p-value above alpha level is excluded from the model and the process repeated. Akaike's information criterion (AIC) values were compared between models and the highest-ranked model with the lowest AIC value was considered to be the best fit model for the data. Likelihood ratio tests were run, and the final best fitting model was the one with the lowest AIC value and with all explanatory variables statistically significant.

Migration behaviour

Residence times in the brackish lake, estuary and marine were calculated using the first and last detections in each area. Again, the potential tagging mortalities were removed from this analysis. GLMs were fitted to test whether residence times in each partitioned area differed between years and fish type (hatchery and wild), with residence time as the response variable and the interaction term year*fish type as the predictor. We tested for significant variation using the Anova() function. Average swimming speeds were measured through each partitioned area based on the shortest available migration route (e.g. swimming speeds in the estuary were calculated using direct distance between the last receiver in the brackish lake and last receiver in the estuary divided by the time between the two detections). An ANOVA, followed by Tukey's post hoc tests, was used to compare the mean occupied depth between the brackish lake, estuary and marine areas. Chi-square tests were used to determine if smolts followed a specific exit route from the bay.

Circular statistics were used to determine the distribution of migration movements in relation to diel and tidal cycles. First, we examined density plots to determine unimodal or multimodal departures from normality, then tested the data for the von Mises distribution (circular equivalent to a Gaussian distribution) using Watson's U^2 test for circular uniformity with a significance level of 0.05. Watson's U^2 tested whether the timing of detection was random or directed towards a specific time of day or tidal state. Time of detection was converted to circular degree angles for analyses, with 0° indicating midnight and 180° indicating noon. For tidal cycle analysis, 0° indicated low tide and 180° indicated high tide. Movements and mean times of departure and arrival were calculated and represented on circular plots.

Results

Environmental variables

In 2017, salinity and temperature levels in the brackish lake were higher than in 2018 (two-way ANOVA $p < 0.001$, Table 2). Environmental variables were not recorded consistently in the estuary in 2017. At the marine arrays, temperature levels in early May were also higher in 2017 compared to 2018 (Table 2).

Effect of tagging on survival

The effects of time in anaesthetic, time in surgery, fish type and tag-to-body mass ratio on survival through each area were non-significant (GLM likelihood ratio tests; brackish lake: $\chi^2 = 5.59$, $p = 0.35$, estuary: $\chi^2 = 5.02$, $p = 0.41$ and marine: $\chi^2 = 2.48$, $p = 0.78$). Mean fork length of hatchery fish (19.3 cm ± 0.9 cm) was significantly higher than that of wild fish (16.1 cm ± 0.9 cm) (Mann–Whitney U test, $z = 9.32$, $p < 0.05$), however this size range is representative of the hatchery fish that are typically released.

Partitioned survival

A total of 8% of all smolts tagged and released did not move beyond the first two receivers in the brackish lake (10 fish). Although there was no statistically significant effect of the tagging procedure on survival through the brackish lake, handling and tagging cannot be completely ruled out as the cause of these mortalities. These 10 fish were marked as potential tagging mortalities and were removed before estimating percentage survival.

Ambient noise levels were low throughout the study; average noise level levels were 197 mV in 2017 and 199 mV in 2018. The range test results indicated that a smolt passing through the marine array at a maximum distance of 200 m from a receiver had a minimum probability of detection of 94%. Therefore, survival may be underestimated by up to 6% and overall survival should be considered as a minimum estimate. Survival of smolts from release to the marine arrays was similar between years (Pearson's χ^2 tests; $p > 0.05$). There was no significant difference in overall survival between hatchery and wild smolts (2017; Pearson's $\chi^2 = 0.03$, $p = 0.86$ and 2018; Pearson's $\chi^2 = 0$, $p = 1$). Overall percentage survival was 63% (± 4.78) for wild smolts and 58% (± 7.21) for hatchery smolts. There were also no differences in partitioned survival rates between hatchery and wild smolts through the brackish lake, the estuary or to the marine arrays (Pearson's χ^2 tests; $p > 0.05$). Mortality was highest in the early marine environment between the estuary and Clare Island (Table 1). Percentage daily mortality varied between release groups; in 2017 wild smolts had a higher daily mortality rate compared to hatchery smolts but in 2018 wild smolts had a slightly lower daily mortality rate compared to hatchery smolts (Table 1).

Detections from eight hatchery smolts in 2017 and eight hatchery smolts in 2018 indicated that fish were moving back and forth between receivers situated in the brackish lake, estuary and inner bay. Days later, nine of these tags (seven in 2017 and two in 2018) were only detected at a single receiver for an extended period of time (range; 2.93–50.57 days) which was indicative of a mortality event or possibly the expulsion of a tag digested by a predator. None of the remaining eight fish were detected at the marine arrays. Data were included for these fish up to the point at which they made their first reversal, detections following this were removed from further analysis of migration behaviour. The smolts were considered to have survived the migration up to the point

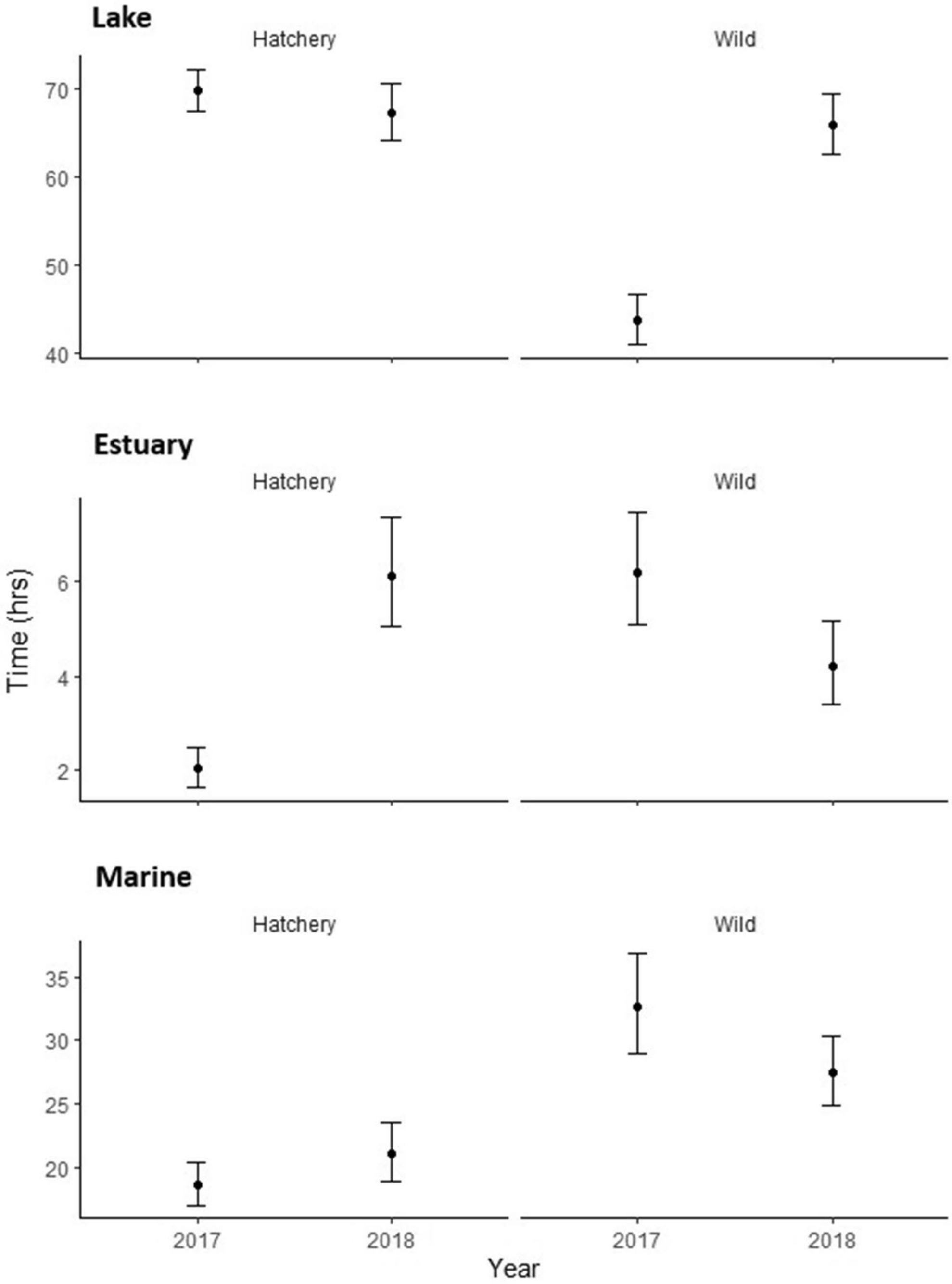

Fig. 2 Predicted mean residence time Atlantic salmon (*Salmo salar*) smolts spent in the brackish lake, estuary and marine (i.e. last detection in the estuary to first detection at the Clare Island arrays). Vertical bars represent 95% confidence intervals. The effects of year and fish type on residence times were estimated from the GLM

at which the reversal occurred. At the marine arrays, seven hatchery smolts that passed through the marine arrays were detected again at the arrays one to three days later.

Migration behaviour

Residence times in each partitioned area differed with fish type and year (GLM likelihood ratio tests, brackish lake: $\chi^2 = 180.3$, $p < 0.001$, estuary: χ^2 88.27, $p < 0.001$, marine:

Table 3 Watson's U^2 values measuring for circular uniformity around 24 h

	Fish type	Time			Test statistic	*P*-value	*n*
		Mean	CI	Median	U^2		
Lake	Hatchery	**12:24**	08:43–16:45	12:05	**0.26**	**< 0.03**	75
	Wild	Random	05:21–19:49	11:09	0.11	> 0.1	43
Estuary	Hatchery	Random	11:38–19:37	15:25	0.16	< 0.1	63
	Wild	Random	13:08 – 22:22	19:52	0.16	< 0.1	38
Marine arrays	Hatchery	**13:32**	10:59–16:29	13:31	**0.3**	**< 0.01**	39
	Wild	Random	07:43–14:57	09:54	0.19	< 0.1	22

Times presented in UTC + 1. Data in bold indicate departure from circular uniformity, i.e. Atlantic salmon (*Salmo salar*) smolt movements were more likely to occur at a specific time of day. 'Random' means the data follow a uniform distribution around the 24-h clock and '*n*' is the total number of fish detected passing the receivers at each section. Mean and median times at which smolts left the lake, left the estuary and arrived at the final marine arrays are presented. Confidence intervals (CI) for the population mean time were calculated using a bootstrapping approach assuming an underlying von Mises distribution. Watson's critical value is 0.19 for all sample sizes

χ^2 64.02, $p < 0{,}001$). Predicted lake residence times were significantly lower in 2017 for wild smolts (43.86 ± 1.45 h) compared to hatchery smolts (69.8 ± 1.19 h, Fig. 2). There were no differences in lake residence times between fish types in 2018. The lake residence times were also significantly different between years for the wild smolts (2018 predicted residence time: 65.86 ± 1.73 h). Residence times within the estuary varied depending on fish type and year, predicted mean residence time for hatchery smolts was 2.02 ± 0.21 h in 2017 and 6.11 ± 0.58 h in 2018 and for wild smolts was 6.18 ± 0.6 h in 2017 and 4.19 ± 0.45 h in 2018. The model also predicted variation in marine residence times, but the means were not significantly different between years (GLM Analysis of deviance $\chi^2 = 0.03$, p = 0.84). Hatchery smolts spent significantly less time (2017: 18.58 ± 0.88 h, 2018: 21.07 ± 1.19 h) in the early marine compared to wild smolts (2017: 32.63 ± 2.02 h, 2018: 27.43 ± 1.4 h, Fig. 2).

Wild smolts migrated through the estuary at a mean swimming speed of 1.86 bl s^{-1} and through the early marine at 1.74 bl s^{-1}. Hatchery smolts migrated through the estuary at 2.29 bl s^{-1} and through the early marine at 1.94 bl s^{-1} on average. In two cases, the average swimming speed of a smolt that displayed reversal behaviour increased to 6.85 and 6.38 bl s^{-1}.

Migration of hatchery smolts occurred mainly during hours of daylight throughout the study area, however diel cycle had no significant effect on migration of wild smolts (Table 3 and Fig. 3). The timing of smolt migration was significantly correlated with the tidal cycle; the distribution of detections departed from circular uniformity (Watson's U^2 test statistic > critical value 0.19 in all cases). Both hatchery and wild smolts migrated through each section predominantly during ebb tides (Table 4 and Fig. 4). Overall, the mean time of migration movement was 09 h 54 min after low water.

Smolts carrying V7P sensor tags migrated within the top four meters of the water column throughout the study area. The deepest recording was within the estuary at 4.5 m. The mean depths occupied by smolts differed significantly between areas (ANOVA F = 133.9, $p < 0.05$, Table 5); Tukey's post hoc analysis showed that all pairwise comparisons were statistically significant ($p < 0.05$). On average smolts were migrating at shallower depths in the lake compared to the estuary and in the estuary compared to the marine array, with the exception of the inner bay where smolts also migrated at shallow depths (Table 5).

Most of the smolts that passed through the marine arrays were detected on the northern array at Clare Island; 91% in 2017 and 100% in 2018. On the receivers in the marine arrays that had detections there was no significant difference in the number of fish detected on each receiver (2017; $\chi^2 = 10.6$, p = 0.56 and 2018; $\chi^2 = 4.32$, $p = 0.93$). There were smolt detections on every receiver in the northern array in both years and on three receivers in the southern array in 2017 (South 2, 3 and 4 Fig. 1). No smolts were detected on the receiver located at Achillbeg. In 2017, two hatchery fish were detected on the Portlea fish farm receiver, one fish subsequently migrated through the northern array and the second fish was not detected again. In 2018, two hatchery smolts and one wild were detected on the Portlea receiver, both hatchery and the one wild fish were later detected at the northern array. The wild smolt was then detected back on the Portlea receiver and was not detected again following this event.

Effect of behaviour on survival

The behaviour of smolts migrating through the brackish lake (i.e. residence time, time of day and tidal cycle when exiting the lake) had no significant influence on survival

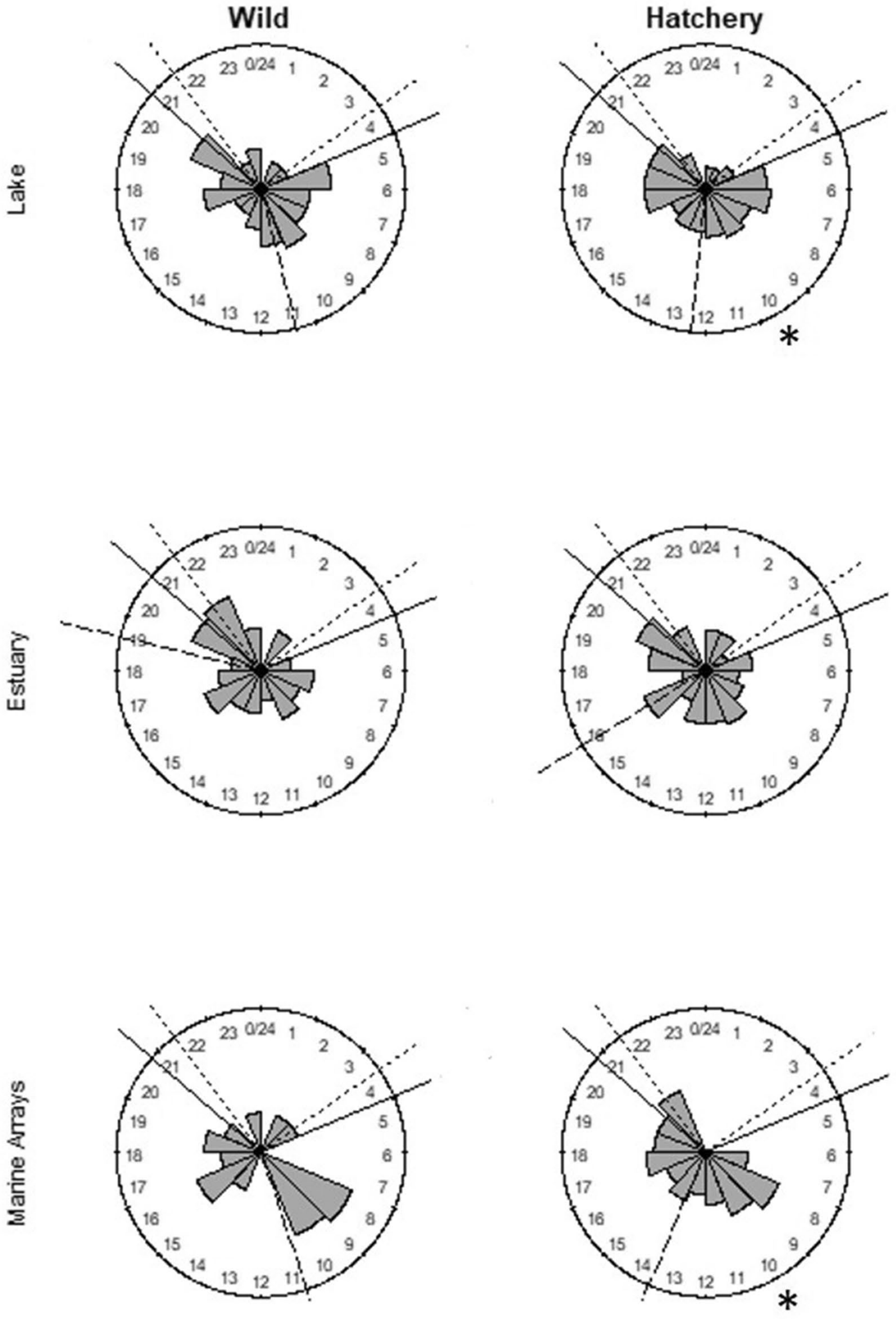

Fig. 3 Circular plots displaying time of day (UTC + 1) when Atlantic salmon (*Salmo salar*) smolts left the lake (top panel), left the estuary (middle panel) and arrived at the marine arrays (bottom panel) as indicated by the detections on each receiver. Time of civil twilight in the morning and evening is denoted by the dotted line. The solid lines represent sunrise and sunset and the long-dashed line represents mean movement time. The * indicates where movements were significantly related to time of day

Table 4 Watson's U^2 values measuring for circular uniformity around a tidal cycle

	Fish type	Time from first low (h)			Test statistic	*P*-value	*n*
		Mean	CI	Median	U^2		
Lake	Hatchery	**9.57**	9.03–10.20	09.15	**1.16**	**< 0.01**	**75**
	Wild	**10.85**	09.63–10.48	10.85	**0.27**	**< 0.01**	**43**
Estuary	Hatchery	**10.50**	09.17–11.77	10.63	**0.35**	**< 0.01**	**63**
	Wild	**07.90**	06.67–09.40	07.67	**0.31**	**< 0.05**	**38**
Marine arrays	Hatchery	**09.85**	08.88–10.82	10.02	**0.44**	**< 0.01**	**39**
	Wild	**10.77**	08.97–12.00	10.73	**0.19**	**< 0.05**	**22**

Data in bold indicate departure from circular uniformity, i.e. Atlantic salmon (*Salmo salar*) smolt movements were more likely to occur at a specific tidal time. *n* is the total number of fish detected passing the receivers at each section. Mean and median times are hours since low tide at which smolts left the lake, left the estuary and arrived at the final marine array. Confidence intervals (CI) for the population mean time were calculated using a bootstrapping approach assuming an underlying von Mises distribution. Watson's critical value is 0.19 for all sample sizes

through the estuary (GLM Likelihood ratio test $\chi^2 = 4.56$, $p = 0.3$). Tidal state when smolts left the brackish lake and time of day when smolts left the estuary had a significant effect on survival to the marine arrays (GLM Likelihood ratio test $\chi^2 = 20.99$, $p < 0.05$, Table 6). Smolts leaving the brackish lake during ebb tides had a higher probability of survival to the marine arrays (ANOVA $\chi^2 = 10.95$, $p < 0.05$) while migration into the marine environment during hours of daylight increased the probability of survival to the marine arrays (ANOVA $\chi^2 = 14.12$, $p < 0.05$). Model predicted probability of survival was highest for fish leaving the brackish lake during ebb tides and leaving the estuary at daytime (0.88) and lowest for fish leaving the lake on a flood tide and leaving the estuary during night (0.12; Table 6).

Discussion

The results of this acoustic tagging study provide estimates of survival for Atlantic salmon smolts from the Burrishoole for each phase of the early marine migration (lake, estuary and early marine). Survival was highest through the brackish lake and estuarine areas, although these habitats are often identified as areas of low survival [21, 25, 35, 57]. Survival of both wild and hatchery smolts was particularly low within the early marine environment. The mean daily mortality rate averaged across the three phases was 10.2% for wild and 26.1% for hatchery smolts. This compares to an overall mean daily mortality rate of 0.56% and 0.73% across the whole marine migration, based on mean percentage return rates of 8.1% and 3.7% for wild and ranched grilse, respectively [44]. Considering the long-range migrations undertaken by Atlantic salmon, the high overall mortality observed through the early migration period in this study (wild mean 37% and hatchery mean 42%) indicate that there is a major survival bottleneck during this phase.

In this study, smolts of hatchery and wild origin had similar survival rates. Previous studies report lower survival of hatchery-reared salmon in the natural environment compared to wild salmon [48, 50, 55, 64, 80, 84]. This may be explained by the fact that wild salmon are more experienced at hunting prey and avoiding predators [23]. The hatchery-reared smolts used in this study are derived from a line-bred ranching stock that are ranched on an annual basis and their return rates to rivers as adults are invariably lower than that of wild smolts [44]. The differences in survival between the hatchery reared and wild stocks may therefore arise later in the migration and there may be further survival bottlenecks in the open marine environment. Marine survival of salmon has been shown to be affected by growth [17, 76], disease and parasites [83, 91], environmental conditions [29, 46, 93] and the availability or distribution of food [5, 29, 75]. Hatchery-reared salmon may be more vulnerable to these effects. Long range tracking of migrating smolts of hatchery and wild origin could help to confirm when in the life cycle the differences emerge.

In any tagging study, the possible influence of the handling and tagging procedure on estimated survival rates must be considered. We used the smallest available tags with sufficient detection range to ensure that the tag-body mass percentage was sufficiently low to minimise their effects on the fish [7, 15]. The maximum tag–body mass was 5.8%, which is below that considered for good survival in recent telemetry studies (< 8% [54], 7% [14]. The analysis showed no evidence that variables associated with the tagging procedure caused variation in survival. We are confident that tagging-related mortalities were minimised. However, we cannot rule out the possibility that some of the mortalities were due to the procedure itself. Tagging and handling procedures can contribute to mortality shortly after tagging [19, 21, 32, 39]. The interaction of handling and osmotic stress is likely to

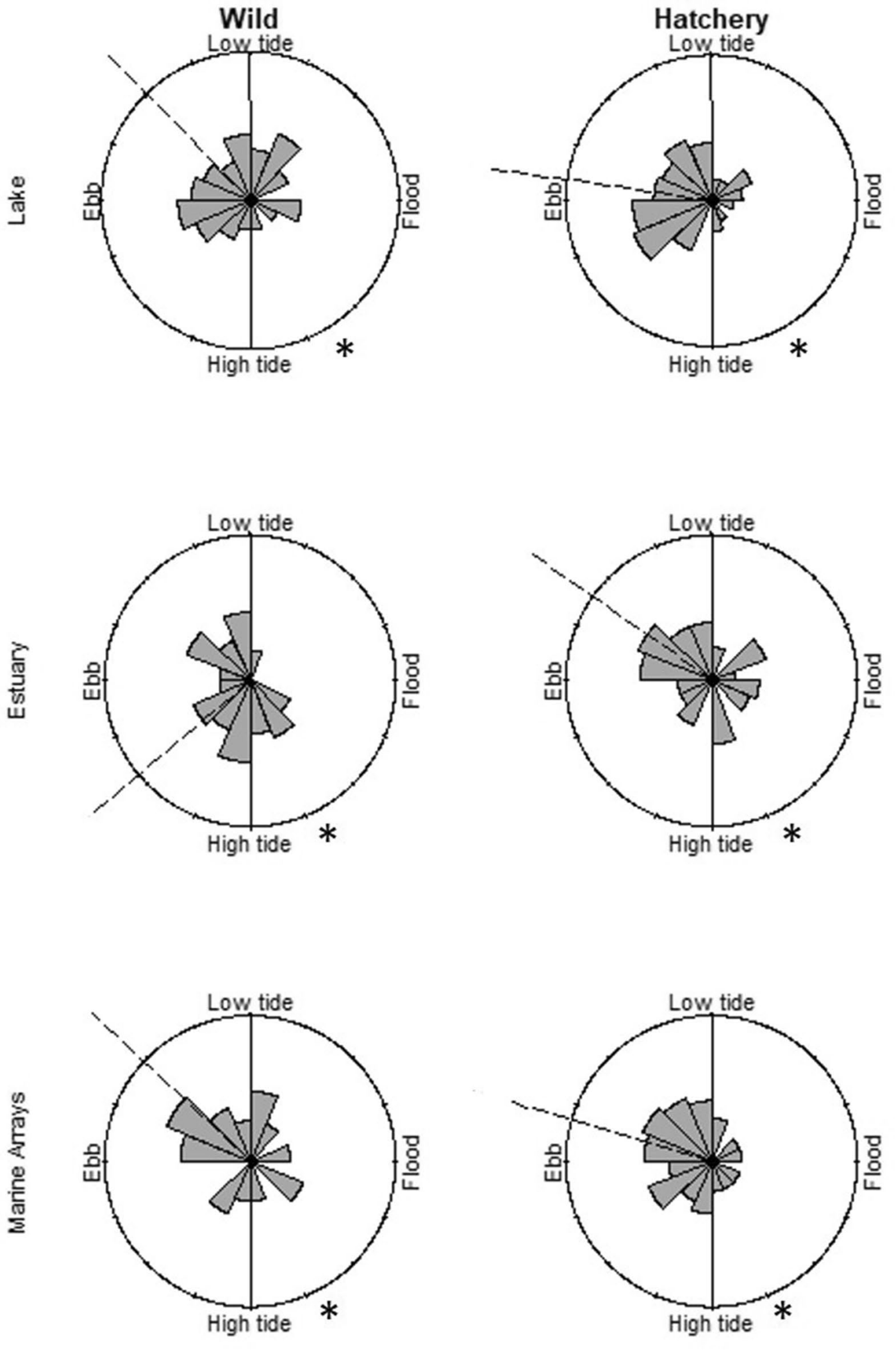

Fig. 4 Circular plots displaying the time (hours since low tide) within the tidal cycle that hatchery and wild Atlantic salmon (*Salmo salar*) smolts left the lake (top panel), left the estuary (middle panel) and arrived at the marine arrays (bottom panel) as indicated by the detections on each receiver. The solid line represents low and high tides (0°/360° and 180°). The long-dash line represents mean movement time within the tidal cycle. The * indicates where movements were significantly related to tidal cycle

Table 5 Mean swimming depth of Atlantic salmon (*Salmo salar*) smolts tagged with V7P tags in 2018 within each partitioned area

Location	Mean swimming depth (m)		
	Overall	Wild ($n=1$)	Hatchery ($n=3$)
Lake	0.9	0.8	0.8
Estuary	1.6	2.0	1.5
Inner bay–Marine	0.4	0.2	0.4
Outer bay–Marine	2.3	1.6	2.4

Inner bay—Marine represents data from the receivers located between the estuary and the marine arrays among the small islands in the inner bay. Outer bay—Marine includes data from the marine arrays

contribute to mortality by reducing a smolt's ability to detect and evade predators or initiating a decline of immune functions and disease resistance [4, 20, 33, 96]. In this study, smolts that were not detected beyond the release location were treated as potential tagging mortalities, as this is the period when tagging-related mortalities were most likely to occur. Movement beyond the release location was taken as an indication that a smolt had recovered well following the procedure and it was assumed that survival thereafter was not majorly influenced by the tagging effects.

Some hatchery smolts ($n=16$) were recorded moving back and forth between the brackish lake, estuary and inner bay before moving out of range of the receivers or being detected at one location for an extended period of time. None of these smolts were detected at the marine arrays. The mean swimming speed for two of these fish increased significantly suggesting that the tags were located in the stomach of a large predator. At the marine array at Clare Island, several tags ($n=7$) from hatchery smolts were detected at the marine arrays between one and three days after migrating through, which may also be indicative of a predation event. Similar movements of tagged smolts were reported in the Burrishoole by Moore et al. [68] and were interpreted as predation events. Following the release of smolts, the majority of losses are likely to be due to mammal, fish and avian predation [13, 25, 26, 32, 47, 90, 92]. Harbour seals (*Phoca vitulina*), which predate on salmonids [12, 82], occur on several of the small islands within the inner bay which the smolts pass on their migration route [59, 72]. The seals are known to enter the brackish lake during the wild smolt run, particularly when large numbers of hatchery smolts are released for the experimental ranching programme. Other potential predators include otter (*Lutra lutra*), mergansers (*Mergus merganser*), cormorant (*Phalacrocorax carbo*) and grey heron (*Ardea cinerea*) (Ger Rogan, *pers. comm.*). Northern Clare Island and Achillbeg Island (located at the main exit route) are host to a number of predatory sea birds including gulls (*Larus* spp.), awks (*Alcidae*) and gannets (*Morus bassana*). Predatory fish including large sea trout (*Salmo trutta*) and pollock (*Pollachius pollachius*), are also present within the bay along with some species of cetaceans. Therefore, migrating smolts are exposed to a wide range of predators during the early phase of the migration and predation is a plausible explanation for the back and forth movements that were observed.

Alternatively, the smolts may have reversed their direction during the migration. Migration reversal behaviour and migration near freshwater inputs has been previously documented for smolts [32, 38, 56, 61, 66] and linked to tidal phases and possible acclimatisation to avoid osmoregulatory issues [22, 32, 38, 56]. Additionally, smolts use flow and discharge in riverine systems as migratory cues during downstream migration [41, 62]. However, the low flow levels and the large tidal influence during this study were unlikely to have influenced directional cues and caused reversal of smolts. Return to fresh water has also been reported to be linked to presence of the parasitic salmon louse (*Lepeophtheirus salmonis*) which exist within the distribution range of Atlantic salmon [24]. Salmon lice have low tolerance to freshwater and smolts may return to reduce infestation and regain any osmoregulatory function effected by the presence of the louse [66, 89, 91]. In this study, the reversal events

Table 6 Predicted probabilities of Atlantic salmon (*Salmo salar*) smolt survival to the marine arrays (S_{MA}) from the best fit GLM modelling survival in relation to movements

Model: $S_{MA} \sim Lake_{EF} + Estuary_{DN}$

$Lake_{EF}$	$Estuary_{DN}$	Fit	SE	Residual scale	95% CI	Predicted probability
Ebb	Day	1.99	0.44	1	0.76–0.95	0.88
Ebb	Night	0.00	0.39	1	0.32–0.68	0.50
Flood	Day	0.00	0.49	1	0.28–0.73	0.50
Flood	Night	−1.99	0.71	1	0.03–0.35	0.12

EF refers to ebb/flood and DN refers to day/night only occurred in hatchery smolts, possibly because they are more vulnerable to osmoregulatory issues or predation [23, 95] or because their larger size makes them more attractive to larger predators [94].

Both wild and hatchery smolts migrated into the estuary and coastal areas primarily on ebb tides. This is consistent with evidence from other populations [21, 38, 53, 61, 65]. In this study, tidally synchronised movement appeared to provide an advantage as migration into the marine during an ebb tide was associated with higher survival probabilities. Mean migration time was approximately 10 h after low water (approximately four hours into an ebbing tide). The results showed that migrating within the main channels, close to the surface (mean 0.4 m within inner bay) and during a time where current speed is high increased the probability of survival; this strategy may allow smolts to reach the open ocean faster with a lower energetic cost [69] while also reducing predation risk [21]. Additionally, smolts that left the estuary during hours of daylight had an increased probability of survival to the marine arrays. While there was no statistically significant association between wild smolt migration and the diel cycle, hatchery smolts were more likely to move into the estuary and arrive at the marine array during hours of daylight. Smolts that migrate during daylight may be able to take advantage of visual cues for navigation or predator avoidance.

Our results showed that Atlantic salmon smolts in the Burrishoole remain in the brackish lake for approximately 2–3 days before moving quickly through the short estuary and marine areas. The majority of smolts followed a route to the North of Clare Island but showed no preference for any part of that channel. A high-resolution model of Clew Bay developed by Nagy et al. [70] describes the main currents around Clare Island, confirming that the strongest currents flow out of Clew Bay through the channel north of Clare Island. It appears that the migrating smolts follow these currents and take the most direct route out of the bay towards feeding grounds to the north. There is little variation in velocity across the area where the marine arrays were located which may explain the movement pattern exhibited by smolts at the northern array. It has been suggested that salmon may be drawn to fish farms encountered on their seaward migration, where predators can also accumulate [53, 91]. However, we found that smolts showed no preference for the route closest to the fish farm receiver and there was no evidence that the presence of the fish farm significantly impacted movements to Clare Island.

In conclusion, this study identified the early marine migration through Clew Bay as an important survival bottleneck for Burrishoole salmon smolts. Results suggest that smolts take advantage of tides and daylight to increase chances of survival. Perhaps the largest threat to smolts is the high numbers of natural predators within coastal environments and these spatially partitioned estimates of mortality rates can inform the design of appropriate management measures such as predator deterrence. Further tagging studies are recommended to identify survival bottlenecks later in the migration and to examine how behaviour varies between catchments due to genetic differences and local adaptations of salmon stocks to environmental variables. These efforts can inform catchment-specific management and conservation efforts to increase the resilience of salmon stocks.

Acknowledgements
This Cullen Fellowship (Grant-aid Agreement No. CF/15/07) is carried out with the support of the Marine Institute and funded under the Marine Research Programme 2014 – 2020 by the Irish Government. Special thanks to our colleagues A. Drumm and J. Cooney for their technical assistance during field work and management of receiver deployment. We are grateful to G. Rogan, P. Hughes, M. Murphy and C. Waters for facilitating fish acquisition and transportation. We thank T. Murphy, F. Egan, E. Tray, H. Maxwell and P. Keena for assistance during the surgical procedure. We also thank H. O'Leary and A. O'Leary of Bruernish ferry for assistance in equipment deployment and recovery. Finally, we would like to acknowledge the staff of the Marine Institute, Newport Facility who contributed to the success of this project.

Author contributions
This project was conceived by DB, DC and NÓM and all authors developed methods. AD, DC and NB preformed field work. AD, DB and DC analysed the data and drafted the manuscript. All authors contributed to drafts and revised and approved the final manuscript.

Funding
This Cullen Fellowship (Grant-aid Agreement No. CF/15/07) is carried out with the support of the Marine Institute and funded under the Marine Research Programme 2014 – 2020 by the Irish Government.

Availability of data and materials
The data collected and analysed in the current study are available on reasonable request from the corresponding author.

Declarations

Ethics approval and consent to participate
All procedures complied with directive 2010/63/EU on the protection of animals used for scientific purposes and were carried out under the Health Products Regulatory Authority (HPRA) licence number AE19121-P002 and approved by the Marine Institute animal welfare committee. Tagging procedures were carried out by persons with HPRA Individual Authorisations and appropriate training (surgical tagging and anaesthesia).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 31 July 2023 Accepted: 26 October 2023

References

1. Agostinelli C, Lund U. *R package 'circular': Circular Statistics (version 0.4–93).* 2017; https://CRAN.R-project.org/package=circular.

2. Ammann AJ, Michel CJ, MacFarlane RB. The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. Environ Biol Fishes. 2013;96(2–3):135–43.
3. Barlaup BT, Rund H, Normann ES, Stranzl S, Mahlum S, Vollset KW. Out of sync: monitoring the time of sea entry of wild and hatchery salmon Salmo salar smolt using floating passive-integrated transponder antennae. J Fish Biol. 2018;93(3):455–64.
4. Barton, B.A., 2002. Stress in fishes: A diversity of responses with particular reference to changes in circulating corticosteroids. *Integrative and Comparative Biology*, 42 (3), Jun, pp. 517–525.
5. Beamish RJ, Mahnken C. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr. 2001;49(1–4):423–37.
6. Birnie-Gauvin K, Candee MM, Baktoft H, Larsen MH, Koed A, Aarestrup K. River connectivity reestablished: effects and implications of six weir removals on brown trout smolt migration. River Res Appl. 2018;34(6):548–54.
7. Brown RS, Cooke SJ, Anderson WG, Mckinley RS. Evidence to challenge the "2% rule" for biotelemetry. North Am J Fish Manag. 1999;19(3):867–71.
8. Browne J. First results from a new method of tagging salmon-the coded wire tag. Fishery Leaflet, Department of Fisheries and Forestry (Trade and Information Section). 1981; https://oar.marine.ie/handle/10793/346.
9. Brunsdon EB, Daniels J, Hanke A, Carr J. Tag retention and survival of Atlantic salmon (Salmo salar) smolts surgically implanted with dummy acoustic transmitters during the transition from fresh to salt water. ICES J Mar Sci. 2019;76(7):2471–80.
10. Butler JR, Middlemas SJ, Graham IM, Thompson PM, Armstrong JD. Modelling the impacts of removing seal predation from Atlantic salmon, Salmo salar, rivers in Scotland: a tool for targeting conflict resolution. Fish Manage Ecol. 2006;13(5):285–91.
11. Carey JB, McCormick SD. Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. Aquaculture. 1998;168(1):237–53.
12. Carter T, Pierce GJ, Hislop J, Houseman J, Boyle PR. Predation by seals on salmonids in two Scottish estuaries. Fish Manage Ecol. 2001;8(3):207–25.
13. Chavarie, L., Honkanen, H.M., Newton, M., Lilly, J.M., Greetham, H.R. and Adams, C.E., 2021. The benefits of merging two tracking approaches: passive acoustic telemetry combined with active acoustic tracking by transects provide new insights into riverine migration by salmonid smolts. *Ecosphere, 13, e4045.* https://doi.org/10.1002/ecs2.4045.
14. Chittenden C, Butterworth K, Cubitt K, Jacobs M, Ladouceur A, Welch D, Mckinley R. Maximum tag to body size ratios for an endangered coho salmon (O-kisutch) stock based on physiology and performance. Environ Biol Fishes. 2009;84(1):129–40.
15. Collins AL, Hinch SG, Welch DW, Cooke SJ, Clark TD. Intracoelomic acoustic tagging of juvenile sockeye salmon: swimming performance, survival, and postsurgical wound healing in freshwater and during a transition to seawater. Trans Am Fish Soc. 2013;142(2):515–23.
16. Cotter D, Vaughan L, Bond N, Dillane M, Duncan R, Poole R, Rogan G, Maoiléidigh Ó, N. Long-term changes and effects of significant fishery closures on marine survival and biological characteristics of wild and hatchery-reared Atlantic salmon Salmo salar. J Fish Biol. 2022;101(1):128–43.
17. Crozier, W.W. & Kennedy, G.J.A., 1999. Relationships between marine growth and marine survival of one sea winter atlantic salmon, salmo salar l., from the river bush, northern ireland. *Fisheries Management and Ecology,* 6(2)**:** 89–96.
18. Dadswell M, Spares A, Reader J, Stokesbury M. The north Atlantic subpolar gyre and the marine migration of Atlantic salmon Salmo salar: the 'merry-go-round' hypothesis. J Fish Biol. 2010;77(3):435–67.
19. Daniels J, Brunsdon EB, Chaput G, Dixon HJ, Labadie H, Carr JW. Quantifying the effects of post-surgery recovery time on the migration dynamics and survival rates in the wild of acoustically tagged Atlantic Salmon Salmo salar smolts. Animal Biotelemetry. 2021;9:1–14.
20. Daniels J, Sutton S, Webber D, Carr J. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (Salmo salar) as suggested by a novel acoustic tag. Anim Biotelemetry. 2019;7:1–11.
21. Davidsen JG, Rikardsen AH, Halttunen E, Thorstad EB, Okland F, Letcher BH, Skardhamar J, Naesje TF. Migratory behaviour and survival rates of wild northern Atlantic salmon Salmo salar post-smolts: effects of environmental factors. J Fish Biol. 2009;75(7):1700–18.
22. Dempson JB, Robertson MJ, Pennell CJ, Furey G, Bloom M, Shears M, Ollerhead LMN, Clarke KD, Hinks R, Robertson GJ. Residency time, migration route and survival of Atlantic salmon Salmo salar smolts in a Canadian fjord. J Fish Biol. 2011;78(7):1976–92.
23. Einum S, Fleming I. Implications of stocking: ecological interactions between wild and released salmonids. Nord J Freshw Res. 2001;75:56–70.
24. Finstad B, Bjørn PA, Todd CD, Whoriskey F, Gargan PG, Forde G, Revie CW. The effect of sea lice on Atlantic salmon and other salmonid species. Atl salmon ecol. 2011. https://doi.org/10.1002/9781444327755.ch10.
25. Flávio H, Caballero P, Jepsen N, Aarestrup K. Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho. Ecol Freshw Fish. 2021;30(1):61–72.
26. Flávio H, Kennedy R, Ensing D, Jepsen N, Aarestrup K. Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. Fish Manag Ecol. 2019. https://doi.org/10.1111/fme.12405.
27. Fox J, Weisberg S. An R companion to applied regression. Second Edition. Sage publications. 2011.
28. Freyhof J. Salmo salar. The IUCN Red List of Threatened Species 2014; e.T19855A2532398. Accessed on 11 November 2022.
29. Friedland KD, Hansen LP, Dunkley DA, MacLean JC. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (Salmo salar l.) in the north sea area. ICES J Mar Sci. 2000;57(2):419–29.
30. Fritts AL, Scott JL, Pearsons TN. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (Oncorhynchus tshawytscha) to predation. Can J Fish Aquat Sci. 2007;64(5):813–8.
31. Gilbey J, Utne KR, Wennevik V, Beck AC, Kausrud K, Hindar K, Garcia de Leaniz C, Cherbonnel C, Coughlan J, Cross TF, Dillane E. The early marine distribution of Atlantic salmon in the North-east Atlantic: a genetically informed stock-specific synthesis. Fish Fish. 2021;22(6):1274–306.
32. Halfyard EA, Gibson AJF, Stokesbury MJW, Ruzzante DE, Whoriskey FG. Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada. Can J Fish Aquat Sci. 2013;70(3):452–60.
33. Handeland SO, Järvi T, Fernö A, Stefansson SO. Osmotic stress, antipredatory behaviour, and mortality of Atlantic salmon (Salmo salar) smolts. Can J Fish Aquat Sci. 1996;53(12):2673–80.
34. Hansen J, Knight P, Mawle G, Ó Maoiléidigh N, Hutchinson P, Forero Segovia SL. Management of single and mixed stock fisheries, with particular focus on fisheries on stocks below their conservation limits. 2014;CNL(14)67. https://nasco.int/wp-content/uploads/2020/02/CNL_14_67.pdf.
35. Hanssen EM, Vollset KW, Salvanes AGV, Barlaup B, Whoriskey K, Isaksen TE, Normann ES, Hulbak M, Lennox RJ. Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (Salmo salar) smolts migrating through lakes. Ecol Freshw Fish. 2022;31(2):424–37.
36. Haraldstad T, Kroglund F, Kristensen T, Jonsson B, Haugen TO. Diel migration pattern of Atlantic salmon (Salmo salar) and sea trout (Salmo trutta) smolts: an assessment of environmental cues. Ecol Freshw Fish. 2017;26(4):541–51.
37. Harbicht AB, Nilsson PA, Österling M, Calles O. Environmental and anthropogenic correlates of migratory speeds among Atlantic salmon smolts. River Res Appl. 2021;37(3):358–72.
38. Hawkes JP, Sheehan TF, Stich DS. Assessment of early migration dynamics of river-specific hatchery Atlantic salmon smolts. Trans Am Fish Soc. 2017;146(6):1279–90.
39. Holbrook CM, Kinnison MT, Zydlewski J. Survival of migrating atlantic salmon smolts through the penobscot river, maine: a prerestoration assessment. Trans Am Fish Soc. 2011;140(5):1255–68.
40. Holm M, Holst JC, Hansen L. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* l.) in the Norwegian sea and adjacent areas. ICES J Mar Sci. 2000;57(4):955–64.
41. Hvidsten NA, Jensen AJ, Vivás H, Bakke Q. Downstream migration of Atlantic Salmon Smolts in relation to water flow, water temperature, moon phase and social. Nord J Freshw Res. 1995;70:38–48.
42. Ibbotson A, Beaumont W, Pinder A, Welton S, Ladle M. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. Ecol Freshw Fish. 2006;15(4):544–51.

43. ICES, 2018. *Report of the Working Group on North Atlantic Salmon (WGNAS) , 4–13 April 2018, Woods Hole, MA, USA. ICES CM 2018/ACOM:21. 386 pp.*
44. ICES, 2019. *Working group on north atlantic salmon (wgnas)*, ICES Scientific Reports.
45. ICES. 2021. Working Group on North Atlantic Salmon (WGNAS). ICES Scientific Reports. 3:29. 407 pp. https://doi.org/10.17895/ices.pub.7923
46. Jensen AJ, Fiske P, Hansen LP, Johnsen BO, Mork KA, Naesje TF. Synchrony in marine growth among atlantic salmon (*Salmo salar*) populations. Can J Fish Aquat Sci. 2011;68(3):444–57.
47. Jepsen N, Holthe E, Okland F. Observations of predation on salmon and trout smolts in a river mouth. Fish Manag Ecol. 2006;13(5):341–3.
48. Jonsson B, Jonsson N, Hansen LP. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. Aquaculture. 1991;98(1–3):69–78.
49. Jonsson N, Jonsson B, Hansen LP. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. J Anim Ecol. 1998;67(5):751–62.
50. Jonsson N, Jonsson B, Hansen LP. The marine survival and growth of wild and hatchery-reared Atlantic salmon. J Appl Ecol. 2003;40(5):900–11.
51. Karppinen P, Jounela P, Huusko R, Erkinaro J. Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecol Freshw Fish. 2014;23(3):438–52.
52. Kennedy RJ, Rosell R, Millane M, Doherty D, Allen M. Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. J Fish Biol. 2018;93(1):134–7.
53. Lacroix GL, Knox D, Mccurdy P. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Trans Am Fish Soc. 2004;133(1):211–20.
54. Lacroix GL, Mccurdy P, Knox D. Migration of Atlantic salmon post-smolts in relation to habitat use in a coastal system. Trans Am Fish Soc. 2004;133(6):1455–71.
55. Larocque SM, Johnson TB, Fisk AT. Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. Freshw Biol. 2020;65(5):835–48.
56. Lilly J, Honkanen HM, Bailey DM, Bean CW, Forrester R, Rodger JR, Adams CE. Investigating the behaviour of Atlantic salmon (*Salmo salar* L.) post-smolts during their early marine migration through the Clyde Marine Region. J Fish Biol. 2022. https://doi.org/10.1111/jfb.15200.
57. Lilly J, Honkanen HM, McCallum JM, Newton M, Bailey DM, Adams CE. Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water. Environ Biol Fish. 2021. https://doi.org/10.1007/s10641-021-01172-x.
58. Lothian AJ, Newton M, Barry J, Walters M, Miller RC, Adams CE. Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. Ecol Freshw Fish. 2017. https://doi.org/10.1111/eff.12369.
59. Lyons, D.O. 2004. Summary of National Parks & Wildlife Service surveys for common (harbour) seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) 1978 to 2003. *Irish Wildlife Manuals,* No. 13. National Parks & Wildlife Service, Department of Environment, Heritage and Local GovernmentDublin, Ireland.
60. Marine Institute. Newport Research Facility, Annual Report No. 63, 2018. Marine Institute. 2019; http://hdl.handle.net/10793/1495. Accessed 26 May 2023.
61. Martin F, Hedger RD, Dodson JJ, Fernandes L, Hatin D, Caron F, Whoriskey FG. Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. Ecol Freshw Fish. 2009;18(3):406–17.
62. McCormick SD, Hansen LP, Quinn TP, Saunders RL. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci. 1998;55(S1):77–92.
63. Mcginnity P, De Eyto E, Cross TF, Coughlan J, Whelan K, Ferguson A. Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. Aquaculture. 2007;273(2–3):257–68.
64. Mcginnity P, Prodöhl P, Ferguson A, Hynes R, Maoiléidigh NÓ, Baker N, Cotter D, O'hea B, Cooke D. & Rogan G. Fitness reduction and potential extinction of wild populations of Atlantic salmon, Salmo salar, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London. Series B: Biological Sciences. 2003;270(1532)**:** 2443–2450.
65. McIlvenny J, Youngson A, Williamson BJ, Gauld NR, Goddijn-Murphy L, Del Villar-Guerra D. Combining acoustic tracking and hydrodynamic modelling to study migratory behaviour of Atlantic salmon (*Salmo salar*) smolts on entry into high-energy coastal waters. ICES J Mar Sci. 2021;78(7):2409–19.
66. Mitamura H, Thorstad EB, Uglen I, Økland F. In situ measurement of salinity during seaward migration of Atlantic salmon post-smolts using acoustic transmitters with data-storage capabilities and conventional acoustic transmitters. Animal Biotelemetry. 2017;5(1):5.
67. Molina-Moctezuma A, Peterson E, Zydlewski JD. Movement, survival, and delays of Atlantic salmon smolts in the Piscataquis River, Maine, USA. Trans Am Fish Soc. 2021;150(3):345–60.
68. Moore A, Cotter D, Quayle V, Rogan G, Poole R, Lower N, Privitera L. The impact of a pesticide on the physiology and behaviour of hatchery-reared Atlantic salmon, Salmo salar, smolts during the transition from fresh water to the marine environment. Fish Manag Ecol. 2008;15(5–6):385–92.
69. Moore A, Ives M, Scott M, Bamber S. The migratory behaviour of wild sea trout (*Salmo trutta* L.) smolts in the estuary of the River Conwy North Wales. Aquaculture. 1998;168(1–4):57–68.
70. Nagy H, Mamoutos I, Nolan G, Wilkes R, Dabrowski T. High-Resolution Model of Clew Bay—Model Set-Up and Validation Results. J Marine Sci Eng. 2023;11(2):362.
71. NASCO. Report of the thirty-fifth annual meeting of the council. 12 -15 June 2018, Portland, Maine, USA. 2018;CNL(18)45 Available at https://nasco.int/annual-meeting/thirty-fifth-annual-meeting-2018/.
72. NPWS. Conservation Objectives: Clew Bay Complex SAC 001482. Version 1.0. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht. 2011; Available at. https://www.npws.ie/protected-sites/sac/001482.
73. Ó'Maoiléidigh N, Browne J, McDermott T, Cullen A, Bond N, McEvoy B, O'Farrell M, O'Connor W. Exploitation and Survival of River Shannon Reared Salmon. Irish Fisheries Leaflet, Department of the Marine 1994; Available at. http://hdl.handle.net/10793/537.
74. Pardo SA, Bolstad GH, Dempson JB, April J, Jones RA, Raab D, Hutchings JA. Trends in marine survival of Atlantic salmon populations in eastern Canada. ICES J Mar Sci. 2021;78(7):2460–73.
75. Peyronnet A, Friedland KD, Maoileidigh NO. Different ocean and climate factors control the marine survival of wild and hatchery atlantic salmon salmo salar in the north-east atlantic ocean. J Fish Biol. 2008;73(4):945–62.
76. Peyronnet A, Friedland KD, Maoileidigh NO, Manning M, Poole WR. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar* L. J Fish Biol. 2007;71(3):684–700.
77. Potter ECE, Ó'Maoiléidigh N. Review of Mixed Stock Fisheries for Atlantic Salmon in European Community Waters, Excluding the Baltic Sea. Preparatory Paper for the European Commission. 2006; Available at. https://epub.sub.uni-hamburg.de/epub/volltexte/2009/1443/.
78. R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ .
79. Reddin DG, Hansen LP, Bakkestuen V, Russell I, White J, Potter E, Dempson JB, Sheehan TF, Maoiléidigh Ó, N. & Smith, G.W. Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. ICES J Mar Sci. 2012;69(9):1589–97.
80. Saloniemi I, Jokikokko E, Kallio-Nyberg I, Jutila E, Pasanen P. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. Ices J of Mar Sci. 2004;61(5):782–7.
81. Salvanes AGV. Are antipredator behaviours of hatchery *Salmo salar* juveniles similar to wild juveniles? J Fish Biol. 2017;90(5):1785–96.
82. Sharples RJ, Arrizabalaga B, Hammond PS. Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. Mar Ecol Prog Ser. 2009;390:265–76.
83. Shephard S, Gargan P. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environ Interact. 2017;9:181–92.
84. Skaala Ø, Besnier F, Borgstrøm R, Barlaup B, Sørvik AG, Normann E, Østebø BI, Hansen MM, Glover KA. An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. Evol Appl. 2019;12(5):1001–16.

85. Solberg MF, Robertsen G, Sundt-Hansen LE, Hindar K, Glover KA. Domestication leads to increased predation susceptibility. Sci Rep. 2020;10(1):1929.
86. Spares AD, Reader JM, Stokesbury MJ, McDermott T, Zikovsky L, Avery TS, Dadswell MJ. Inferring marine distribution of Canadian and Irish Atlantic salmon (*Salmo salar* l.) in the north Atlantic from tissue concentrations of bio-accumulated caesium 137. ICES Journal of Marine Science. 2007;64(2):394–404.
87. Thorstad EB, Bliss D, Breau C, Damon-Randall K, Sundt-Hansen LE, Hatfield EM, Horsburgh G, Hansen H, Maoiléidigh NÓ, Sheehan T, Sutton SG. Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. Aquat Conserv Mar Freshwat Ecosyst. 2021;31(9):2654–65.
88. Thorstad EB, Havn TB, Sæther SA, Heermann L, Teichert MAK, Diserud OH, Tambets M, Borcherding J, Økland F. Survival and behaviour of Atlantic salmon smolts passing a run-of-river hydropower facility with a movable bulb turbine. Fish Manage Ecol. 2017;24(3):199–207.
89. Thorstad EB, Todd CD, Uglem I, Bjørn PA, Gargan PG, Vollset KW, Halttunen E, Kålås S, Berg M, Finstad B. Effects of salmon lice Lepeophtheirus salmonis on wild sea trout Salmo trutta a literature review. Aquac Environ Interact. 2015;7(2):91–113.
90. Thorstad EB, Uglem I, Arechavala-Lopez P, Okland F, Finstad B. Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. Boreal Environment Research. 2011;16(2):115–20.
91. Thorstad EB, Uglem I, Finstad B, Chittenden CM, Nilsen R, Økland F, Bjørn PA. Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. Fish Manage Ecol. 2012;19(5):400–9.
92. Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. J Fish Biol. 2012;81(2):500–42.
93. Todd CD, Hughes SL, Marshall CT, Maclean JC, Lonergan ME, Biuw EM. Detrimental effects of recent ocean surface warming on growth condition of atlantic salmon. Global Change Biol. 2008;14(5):958–70.
94. Vehanen T, Huusko A, Bergman E, Enefalk Å, Louhi P, Sutela T. American mink (Neovison vison) preying on hatchery and wild brown trout (*Salmo trutta*) juveniles in semi-natural streams. Freshw Biol. 2022;67(3):433–44.
95. Weber ED, Fausch KD. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Can J Fish Aquat Sci. 2003;60(8):1018–36.
96. Wendelaar Bonga SE. The stress response in fish. Physiol Rev. 1997;77(3):591–625.
97. Zeileis A, Hothorn T. Achim Zeileis, Torsten Hothorn (2002). Diagnostic Checking in Regression Relationships. R News. 2002;2(3):7–10.

Publisher's Note