Survival of Atlantic salmon and sea trout smolts in transitional waters

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ABSTRACT: Monitoring the first seaward migration of juvenile salmonids, known as smolts, is challenging because there is limited tracking technology suited to their small size. Nevertheless, for their management and conservation purpose, it is critical to understand this phase of their life cycle when they adapt to increased salinity, novel predators and new prey. Smolts of 2 species, Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, were acoustically monitored at 4 study sites, together with biotic and abiotic parameters, to estimate and explain their survival during their estuarine migration to sea. The 2 species exhibited different levels of survival during this seaward migration, with a higher survival for trout smolts. For both species, survival was similar among 3 of the 4 sites. Migration speed and migratory distance influenced smolt estuarine survival, but body length, body condition, sex, age, and environmental parameters (temperature, salinity, dissolved oxygen) did not. Migration speed, potentially reflecting smolts′ capacity to avoid predators or escape dangerous areas, had a positive effect on their survival. Increased distance negatively influenced estuarine survival, which could lead to lower survival rate in the River Frome Estuary where orientation is more difficult for smolts due to widely separated environmental cues. Overall, smolt survival through estuaries was estimated between 51 and 97 % among 4 populations, suggesting that estuaries are variably challenging environments for migrating smolts, accounting for non-negligible early marine survival. Understanding which estuaries have low survival and why is imperative to prioritise management actions.

KEY WORDS: Acoustic telemetry · Cormack–Jolly–Seber model · CJS model · Migration speed · Early marine stage

1. INTRODUCTION

The management of anadromous taxa that complete part of their life cycle in fresh water, where they reproduce, and marine waters, where they take advantage of more favourable feeding habitats, is complex because they occupy a wide range of habitats during their lifetime (Erkinaro et al. 2019). At the

end of their freshwater phase, young anadromous salmonids undergo physiological changes that enable them to tolerate salt water and become 'smolts' that are ready for their first migration to sea and leave their natal river to spend several months to several years at sea before returning to reproduce (Hansen & Quinn 1998, Quinn 2018). The life cycle of partially anadromous taxa is even more complex, as some individuals remain freshwater resident, while others migrate to sea in order to maximise their growth (Nevoux et al. 2019). While anadromy promotes growth and fecundity, it also imposes challenges that can affect their survival (Klemetsen et al. 2003, Birnie-Gauvin et al. 2019, Nevoux et al. 2019). Understanding these trade-offs and what affects them is, however, challenging because of the complex life cycle of salmonids and the change of habitats throughout their life.

Salmonid populations have declined drastically in the last 4 decades with declines observed throughout large parts of their distribution (Mills et al. 2013, ICES 2020a,b, Wilson et al. 2022). Multiple freshwater factors, such as river fragmentation (Parrish et al. 1998) and habitat loss or alteration (Marsh et al. 2020, 2022, Thorstad et al. 2021) have been associated with population declines. The recent decrease in marine return rates of salmon (ICES 2020a) suggests that salmonid populations could be more impacted during the marine phase than previously recognised (Otero et al. 2011, Kilduff et al. 2015, Chaput et al. 2019). Physical, chemical and biological variations in the marine ecosystem have been correlated with increased marine mortality of salmonids (Kilduff et al. 2015, Olmos et al. 2020). How these factors contribute to marine mortality is still unclear (Thorstad et al. 2012), but smolt size on leaving the river (Davidsen et al. 2009, Russell et al. 2012, Armstrong et al. 2018, Chaput et al. 2019, Gregory et al. 2019, Simmons et al. 2022) and their growth during their early sea migration (Tréhin et al. 2021) have been proposed as important factors for overall marine survival. It is, however, difficult to partition an overall marine survival (from departure from freshwater to return to freshwater), into specific environments such as the lower river, estuary or coastal environments. Thus there is a lack of knowledge regarding the early marine stage in transitional waters (Welch et al. 2009), despite speculation that mortality in this phase could be high due to the high levels of human activity and other pressures concentrated in estuaries and coastal waters (Thorstad et al. 2012). While migrating to sea, juvenile anadromous fish face multiple natural (salinity and temperature gradients, predation) and anthropogenic (fishing activities, migratory barriers, coastal developments) challenges (Ruggles 1980, Noakes et al. 2000, Clarke et al. 2021) that should be better understood to enable effective management and conservation of salmonid populations (Lacroix 2008, Welch et al. 2009, Holbrook et al. 2011).

With recent developments in telemetry technology and the miniaturisation of passive acoustic tags, it is now possible to track individual smolts during their seaward migration. Passive acoustic telemetry enables determination of spatio-temporal patterns of individual fish behaviour and distribution among estuarine and marine habitats, as well as identification of locations and critical periods for their migration success and survival (e.g. Hubley et al. 2008, Thorstad et al. 2012, Hussey et al. 2015, Chaput et al. 2019). An increasing number of studies have used acoustic telemetry to estimate and describe factors that affect smolt survival during their seaward migration. Findings from these studies have highlighted distance from point of tagging (Welch et al. 2009, Larocque et al. 2020) and fish length at tagging (Chaput et al. 2019) as variables influencing the survival of smolts during their seaward migration. However, in their review examining behaviour and survival of anadromous salmonids, Drenner et al. (2012) emphasised the need for more studies including more biotic, abiotic and physiological factors to explain smolt survival.

Most studies on smolt seaward migration have focused on salmon, fewer have focused on trout, and still fewer have considered both species — even though they are closely related, are often sympatric, and thus could be sensitive to similar environmental changes. This study aimed to estimate and describe smolt survival of 2 species, Atlantic salmon *Salmo salar* (hereafter 'salmon') and brown trout *Salmo trutta* (hereafter 'sea trout') in a selection of rivers around the English Channel. Both species undergo their first seaward migration during spring, with sea trout migrating slightly earlier than salmon and potentially coming back after 3 mo at sea (Nevoux et al. 2019) while salmon, which migrate further, return after one or more winters at sea (Klemetsen et al. 2003). Smolt survival in transitional waters from leaving fresh waters to arrival in the marine environment, was assessed as a function of several measured explanatory variables including fish characteristics (e.g. body size and condition) and environmental measurements (e.g. temperature and oxygen). Our acoustic telemetry study was designed to be a broader investigation of salmonids smolt survival in

transitional waters than most telemetry studies, by implementing a multi-species and multi-site sampling strategy of a large number of wild individuals. Different state-space models were tested and compared to explore the spatio-temporal variation in smolt survival during their seaward migration. Then, using the best structural model, the specific objectives were to (1) compare the apparent survival between species, (2) compare the apparent survival between sites, and (3) explore the effect of a broad range of biotic and abiotic variables monitored during the study to better understand the factors that influence their survival during this phase of their lifecycle.

2. MATERIALS AND METHODS

2.1. Study sites, smolt collection and tagging

Salmon and trout smolts were tracked during their seaward migration in 4 estuaries discharging into the English Channel and the northern part of the Bay of Biscay, 2 in southern England (rivers Frome and Tamar) and 2 in northern France (rivers Bresle and Scorff; Fig. 1). There are several notable differences among the study sites (Table 1). First, the rivers Frome and Bresle are aquifer-fed chalk streams, whereas the Tamar and Scorff are rain-fed spate rivers. Second, the rivers Frome, Tamar and Scorff all have long natural estuaries, whereas the Bresle Estuary represents a highly regulated harbour, designed to control the movement of water in and out of the river, generating a considerable salinity gradient of 0 to 35 (measured on the practical salinity scale; IAPSO 1985) across a short distance (a few meters). Third, the rivers Frome, Bresle and Scorff consist largely of a main channel with few tributaries; conversely, the River Tamar has many tributaries, particularly in its upper reaches, also exhibiting an annual mean discharge of 23 m^3 s^{-1}, which is almost 4 times higher than the mean discharge of the 3 other rivers. Fourth, the Frome Estuary forms a wide and complex shape while the others are comparatively narrow and unidirectional estuaries. Finally, both salmon and trout inhabit the rivers Frome, Tamar and Bresle, whereas only salmon are found in significant numbers in the River Scorff.

The collection of smolts took place in spring 2018 and again in 2019, with 474 salmon and 360 trout smolts captured in rotary screw traps or wolf traps (Wolf 1951) between 1 and 22 km upstream of the upper saline limit of each river's estuarine area

(Fig. 1). All smolts selected for tagging were >13 cm fork length (FL) to keep the tag burden under 2% body weight as a precaution (Jepsen et al. 2005, Smircich & Kelly 2014). Trout smolts were implanted with V5 2H acoustic transmitters (180 kHz, 5 mm diameter, 0.77 g in air, Innovasea; hereafter 'tags') and salmon smolts with V5 1H tags (180 kHz, 5 mm diameter, 0.65 g in air, Innovasea). Both acoustic tag types were tuned to emit a unique ultrasonic signal coding for an identification number (or ID) on a random interval of 20–40 s, with an estimated battery life of 90 d for V5 1H and 108 d for V5 2H to enable detections of early returning trout individuals.

Smolts were held on site, in oxygenated river water, before the surgery procedure. Smolts were anesthetised with 2-phenoxy-ethanol (England) or benzocaine (France) following the ethical committee approval of the respective country: in England, UK Home Office A(SP)A licence PPL 30/3277; and in France, the Animal Care Committee under the official certification of INRA A3523843. Smolts were then measured (FL ± 0.1 cm), weighed (±1 g) and a scale sample was collected for identification of age and sex before transferring the fish into a surgery tank that maintained the gills submerged in a reduced anaesthetic concentration. Lidocaïne was injected intramuscularly prior to the incision to reduce the potential pain of the procedure. Tags were disinfected with AntiSept (Dechra) and implanted through a 1 cm incision which was subsequently sutured with resorbing monofilament (4-0 ethicon® monocryl™ using a 19 mm 3/8c needle), and the fish allowed to recover in oxygenated river water for a period of at least 30 min. Smolts were released at the site of capture after full recovery from the procedure. Generally, trout smolts were captured, tagged and released earlier in the year than salmon smolts, although dates varied by site and year, from 20 March to 8 May.

2.2. Assessment of direct impact of tagging on health condition and survival

An experiment was conducted in March 2018 on 4 groups of 10 salmon smolts in order to assess the effect of tagging on their condition and survival. To reduce the number of wild fish manipulated, this experiment focused on salmon smolts only. In the 4 study sites, trout smolts are larger and therefore considered less sensitive to the tagging procedure than salmon smolts. Fish in Group 1 were not subjected to any surgical procedure but were held as a control
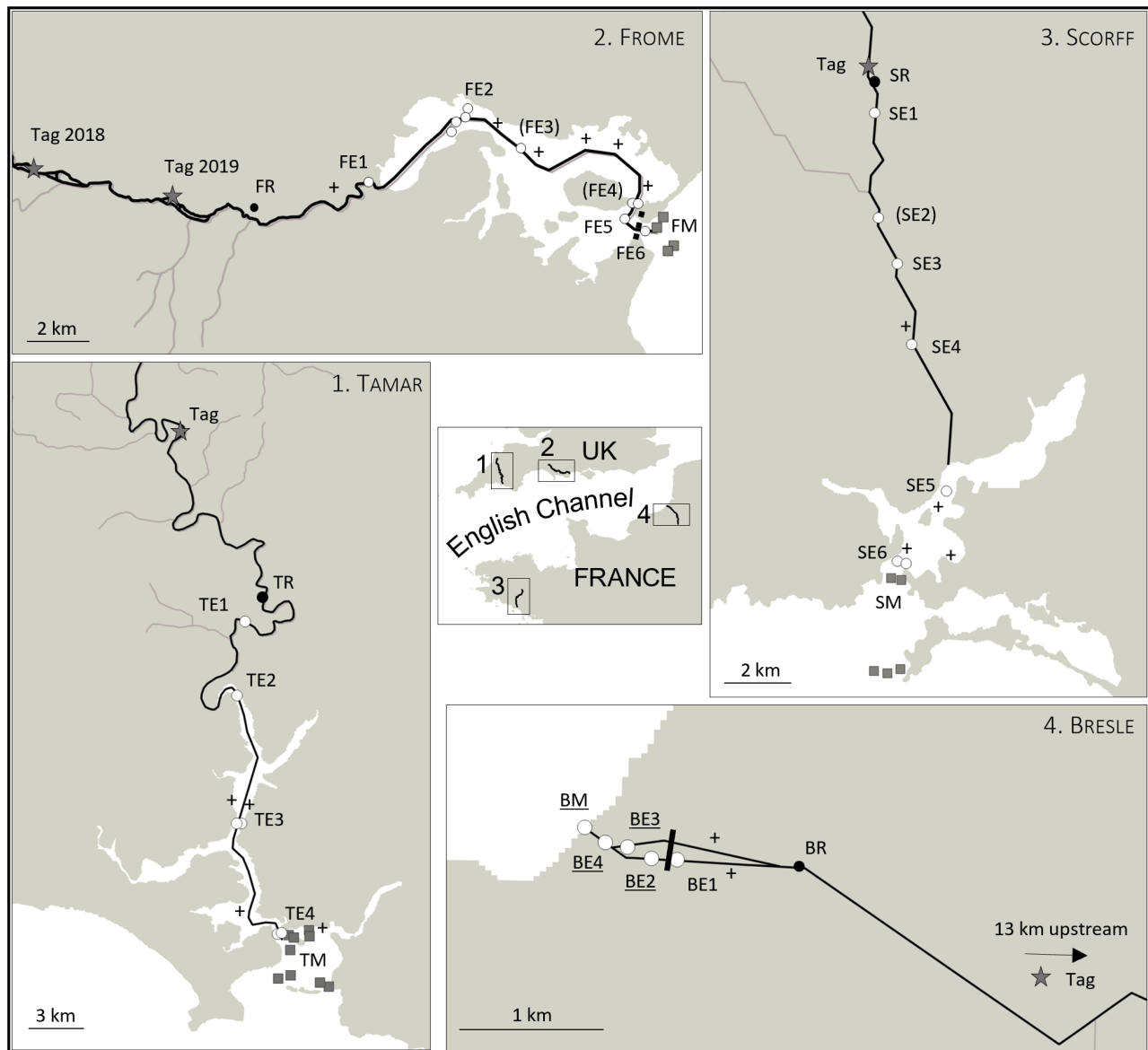
Fig. 1. Map of the rivers Frome (F), Tamar (T), Scorff (S) and Bresle (B), with study site locations where tagging occurred (star), and where passive acoustic receivers were deployed in riverine (R, black circle), estuarine (E, open circle) and marine (M, grey square) waters on the migratory path of salmon and trout smolts in 2018 and 2019. Receivers enclosed in parentheses were deployed in 2019 only and underlined receivers (Bresle Estuary) were out of water at spring low tides. Locations of principal human created structures: harbours (+), sluice gates (—) and chain ferry (▪▪▪) appear on the map. See Table 1 for river descriptions

group. Fish in the 3 other groups underwent the tagging surgery procedure as follows: Group 2, no tag insertion and the incision sutured with monofilament; Group 3, no tag insertion and the incision sutured with ethicon® coated vicryl rapid filament; and Group 4, V5 tag insertion with the incision sutured and disinfected as described in Section 2.1. Contrary to monofilament, vicryl rapid is a braided multifilament, potentially facilitating the adhesion (and entry) of bacteria while still reabsorbing faster than monofilament. All 40 fish were kept for 2 wk in a circular tank of 1.20 m diameter continuously supplied with river water. The tank was inspected every day, to monitor for expelled tags and smolt mortalities. On Day 14, Group 4 were checked for tag retention and all individuals were measured, weighed, and assessed for their health condition (alive/dead, healing status of the scar, infections). Results from this experiment guided the choice of suture to minimise inflammatory reaction and helped to ensure

Table 1. Description of the 4 study sites in England (Frome, Tamar) and France (Bresle, Scorff) with information on tagging locations (see Fig. 1)

Site	——————— River ———————			————— Estuary —————					Tagging location distance (km)	
	Type	Length (km)	Annual mean discharge (m^3 s^{-1})	Length (km)	Entry width (m)	Exit width (m)	Entry depth (m)	Exit depth (m)	To estuary entry	To estuary exit
Frome	Aquifer-fed	70	6	14	31	315	1	9	22 (2018), 14 (2019)	36 (2018), 28 (2019)
Tamar	Rain-fed	75	23	23	68	318	2	28	21	44
Scorff	Rain-fed	62	5	16	39	600	1	21	1	17
Bresle	Aquifer-fed	72	7	2	60	60	4	4	15	17

that the tagging procedure (i.e. method from Group 4) would not induce unnecessary mortality in tagged smolts.

2.3. Acoustic receiver deployment

Prior to smolt migration, 15 to 20 VR2W acoustic receivers (180 kHz, Innovasea; hereafter 'receivers'), able to detect, decode and record the signal transmitted by V5 tags, were deployed in each study system along the smolts migration path from the tagging site to the exit of each estuary. The maximum possible detection range of the receivers was 200 m (400 m diameter), so 2 or more receivers were deployed where the channel widths exceeded 350 m to maximise detection coverage (Fig. 1). In the widest areas of the Frome Estuary, it was impossible to achieve complete coverage, even under maximum possible detection range. In these locations, a unique receiver was deployed on the main probable migration route. Detection efficiencies and maximum detection distance of all receivers were assessed with repeated stationary boat-range tests, performed at distance intervals of 25 m from 0 to 200 m from the receiver (i.e. 9 times) in each of the 4 cardinal directions. For each assessment, a V9 test tag (Innovasea, 180 kHz) transmitting every 10 s was held underwater for 2 min at approximately 1 m below the surface. Range tests were performed with the engine and sounder off to avoid acoustic interference.

Detections from areas covered by multiple receivers were pooled and treated as a single acoustic gate. Each estuary had 5 to 7 acoustic gates, the first gate (E1) being located at the saline limit (entry) of the estuary, and the penultimate at the exit of the estuary (E4 or E6). The last acoustic gate was located in the marine environment (M; Fig. 1).

Most receivers remained deployed on site for the entire study period, with regular maintenance under-

taken to remove biofouling, repair damage, and implement battery changes and data downloads. In 2019, 2 additional receivers were deployed in the Frome Estuary, as well as one more receiver in the Scorff Estuary. The Bresle Estuary is dry at very low tide, so the 4 receivers deployed in this estuary were emersed for part of the daily tidal cycle during spring low tides.

2.4. Abiotic and biotic variables measurement and calculation

In 2019, loggers recording temperature (U22, Hobo), salinity (U24, Hobo) and dissolved oxygen (DO) (U26, Hobo) every 15 min were deployed at the entrance of each estuary at around 2 m depth, to measure changes in environmental variables that could influence smolts' survival during their seaward migration. Smolt detections were matched spatially and temporally to the nearest temperature, salinity, and DO recordings.

Discharge data were extracted from online databases for the rivers Bresle and Scorff (www.hydro. eaufrance.fr/, in French) and provided by the UK Environment Agency database in 2020 for the rivers Tamar and Frome. The mean discharge between the date of tagging and date of entrance to the estuary was calculated for each individual and used to explore the relationship between river discharge and smolt survival through the estuary.

'Distance' (m) was measured as the shortest-line between 2 successive receivers following the course of the river and 'cumulative distance' (m) was the cumulative sum of all inter-receiver distances, from the first receiver in the estuary (E1) to the marine gate (M).

Biotic variables collected for individual fish included FL (mm), total wet weight (g), body condition index (BCI) and age (yr) at the time of tagging, as

well as sex. BCI was calculated as the residuals of the regression of weight vs. FL (Jakob et al. 1996, Armstrong et al. 2018). Age was determined by making scale-annulus counts under a Discovery V8 (Zeiss) stereomicroscope at 63× magnification (Caillart & Morize 1989). Sex was determined genetically by extraction of genomic DNA from scale samples (as per Truett et al. 2000), and duplex polymerase chain reaction (PCR) using primers that amplify a male-specific gene (Yano et al. 2013, King & Stevens 2020). The PCR products were visualised on ethidium bromide stained 1.5% agarose gels. A negative control (water-only template) and 2 positive controls (DNA from 1 known male and 1 known female fish) were included in each batch of amplifications. Also recorded was the day of year of entry to the estuary (DoY) of each smolt, which was expected to capture any progressive but unmeasured environmental changes that might explain differences between smolts migrating on different days.

Migration speed (m s^{-1}) was calculated by dividing the distance between 2 receivers by the duration (s) between the last detection time at an upstream receiver and the first detection time at the next receiver downstream. The migration speed of a smolt through the estuary was then calculated by averaging these transit migration speed values. When fish were not detected again after estuary entrance (n = 40), migration speed was calculated using data collected just upstream of the estuary entrance at a receiver deployed in freshwater and the one located at the estuary entrance (Fig. 1).

2.5. Data analysis

A database containing dates, time and locations of tagged fish detections was compiled. Detections were considered as false and excluded prior to analyses if the tag number was detected only once during the study or if the tag was heard on other receiver(s) around the time period of the suspect detection. Also, any periods during which the receivers could not detect tags were set to NA (e.g. daily low spring tide on the Bresle).

A Bayesian state-space implementation of a Cormack–Jolly–Seber (CJS) model was used to disentangle the apparent survival (ϕ) of smolts during their seaward migration from the imperfect detection efficiency (p) of the acoustic receivers. The estimated survival is the joint probability of a tagged individual surviving to a receiver gate and of the tag being detected at that gate. The unobserved survival pro-

cess model (Eq. 1) assumes that if a tagged individual (i) is alive on the previous sample occasion ($j-1$), its survival state on sample occasion j is a realisation from a Bernoulli process with the parameter ϕ_j. The state process (survival) is represented by the binary variable $z(i, j)$, which takes the value 1 if the individual is alive on sample occasion j or 0 otherwise. It is given by:

$$z(i,j)\,|\,z(i,j-1), \phi_i \sim \text{Bernoulli}(z[i,j-1]\,\phi_i)$$
$$\text{logit}(\phi_i) = \alpha + \beta X_i + \varepsilon_i \tag{1}$$

where ϕ_i is the survival of individual i from state $z(j-1)$ to state $z(j)$ given the individual covariates in matrix X. The constant α and the vector of coefficients β represent the effects of individual covariates on individual survival. A term representing individual random errors, ε, was included to better describe the part of the variation of survival that is not fully explained by covariates.

The probability of being alive at the first sample occasion (tagging) was set equal to 1. The number of subsequent sample occasions varies on each site according to the number of acoustic gates deployed: 5 on the Tamar and Bresle estuaries and 7 on the Frome and Scorff estuaries. If the state of the individual is estimated as dead (or it has stopped migrating) at $j-1$, then $z(i, j) = 0$ with probability 1.

Results of intensive boat-based range tests undertaken around each receiver gate during the study suggested variability of detection efficiency between and among receivers. The probability of detection was therefore set to vary between each gate and year of the study. The observation process $y(i, j)$, modelled as an independent Bernoulli random draw, is conditioned on the state process $z(i, j)$ and the probability of detection (p):

$$y(i,j)\,|\,z(i,j), p_j \sim \text{Bernoulli}(z[i,j]\,p_j)$$
$$\text{logit}(p[t,j]) \sim \text{dunif}(0,1) \tag{2}$$

where $p[t,j]$ is the probability of detection of the receiver gate j at year t. The observation process $y(i, j)$ is equal to 0 with the probability 1 if the individual survival $z(i, j)$ is equal to 0. Logit-transforming parameters p and ϕ ensured that they were bound between 0 and 1.

The model estimates the survival ϕ_{ij} between 2 observations or receivers. To summarise to the scale of the estuary, total apparent survival of an individual smolt during its seaward migration ψ_i was estimated as the product of these survival estimates through each of the intergate distances. For example, in a system

with 5 receiver gates, total apparent survival of an individual smolt would be calculated as follows:

$$\psi = \prod_{j=1}^{4} \phi_{ij} \qquad (3)$$

Individual total apparent survivals were then averaged to get the total apparent survival of a group of individuals (e.g. salmon, or smolts from a specific site) ψ. Total apparent survival referred to the survival of an individual or group of individual from the beginning until the end of the estuary. These survival estimates were different to the localised survival estimates between 2 acoustic gates and enabled inferences at the scale of the estuaries.

To standardise the measure of survival between sites, we computed the survival rate per km (ψ_{km}, % km^{-1}), which accounts for differences in the distance that smolts travelled. Survival rate per km was calculated from total apparent survival values ψ and the length of the estuary (d, km):

$$\psi_{km} = \exp\left(\frac{\ln(\psi)}{d}\right) \qquad (4)$$

Different variations of the described state-space model were tested to identify which model best represented smolt survival through these estuaries during their seaward migration. A set of plausible models was selected following a 2-step approach. The first step involved the selection of a saturated model with the most parsimonious spatio-temporal structure in smolt survival (Models 1a & 1b; see Table 4). This saturated model included all explanatory variables representing *a priori* testable hypotheses of their impacts on smolt survival (Table 2). Four spatio-temporal structures of smolts survival were tested (see Table 4): no spatio-temporal variation ($\phi\ p_{t,j}$), temporal variation only ($\phi_t\ p_{t,j}$), spatial variation only ($\phi_t\ p_{t,j}$) and both spatial and temporal variation ($\phi_{tj}\ p_{t,j}$). The second step was a simplification of Models 1a & 1b by iteratively removing explanatory variables with weak effects, i.e. those with credible intervals intercepting 0 (no effect), until Watanabe–Akaike information criterion was minimised (Models 2a & 2b; see Table 4).

The explanatory variables temperature, salinity, and DO were only recorded during the spring of 2019. Therefore, hypothesised effects of individual covariates on survival were also examined in 2 phases. First, survival was estimated by including all individuals but excluding temperature, salinity, and DO from the explanatory variables (Models 1a & 2a; see Table 4). Second, all explanatory variables were considered with only the fish tagged in 2019 (Models 1b & 2b; see Table 4).

FL, BCI, DoY and migration speed varied among species and sites. Therefore, these variables were included as an interaction with site and species. In the same way, discharge, distance, and cumulative distance between receivers differed among sites and were included in the model as an interaction with site.

All continuous explanatory variables were *z*-standardised by subtracting their mean and dividing by their standard deviation (SD), and explored for correlations: only continuous variables that were considered not correlated (Pearson's $r < |0.7|$; Dormann et al. 2013) were included in models together. Hence, weight (which was correlated with FL) was excluded from the tested explanatory variables.

Model parameters were estimated using Markov chain Monte Carlo (MCMC). A total of 50 000 MCMC iterations on each of 3 chains was used. For each chain, the first 30 000 iterations were discarded, and the remaining 20 000 were thinned by 10 to produce 2000 MCMC estimated values to summarise the posterior distributions. Convergence was assessed by examining the Gelman-Rubin r-hat value (<1.1), the effective sample size n.eff value (>100), and the visual inspection of the posteriors (unimodal) and MCMC chain-plots (mixing).

3. RESULTS

Fourteen days after the surgical procedure, all 40 experimental fish assessed for the direct effects of tagging on health, condition and survival were alive, suggesting that the tagging process did not induce any direct mortality. Five individuals (16.7%, one from Group 2, 3 from Group 3 and one from Group 4) presented minor inflammation around the scar, but without infection; this suggests for all individuals good healing of the wound. No tag loss from Group 4 was observed over this time, implying that the rate of tag loss may be considered low, at least for the duration of transit through the estuary (mean ± SD observed duration was 5.9 ± 5.4 d).

Of the 834 tagged smolts, 730 (87.5%) were detected at the entrance of the estuary. The 12.5% of individuals that did not reach the entrance were excluded from the analysis as well as 8 individuals whose *age* or *sex* could not be determined. Thirty-five Tamar trout were 3 yr old; as this age-category was missing in all other sites, they were also omitted from the analyses. A total of 687 smolts were included in the analyses (Table 3). Only 288 of the 687 smolts were considered when analysing

Table 2. Explanatory variables hypothesised to explain variation in the survival of Atlantic salmon and sea trout smolts migrating through estuaries (see Fig. 1)

Variables	Type	Method	Hypothesis regarding survival	Hypothesis source
Site	Categorical (N = 4)	NA	Frome ≠ Bresle ≠ Scorff ≠ Tamar	Chaput et al. (2019)
Species	Categorical (N = 2)	NA	salmon < trout	Present study
Year	Categorical (N = 2)	NA	2018 ≠ 2019	Chaput et al. (2019), Welch et al. (2009)
River type	Categorical (N = 2)	NA	Aquifer-fed < Rain-fed	Present study
Age (yr)	Categorical (N = 2)	Scale reading	Younger < older	Meuthen et al. (2018)
Sex	Categorical (N = 2)	Genetic analysis	Females < males	Blair Hotby & Healey (1990), Tamate & Maekawa (2004)
Fork length (FL) (mm)	Continuous	Measurement	Shorter < longer	Chaput et al. (2019), Gregory et al. (2019)
Body condition index	Continuous	Residual of weight:FL ratio	Higher < lower	Heim et al. (2016)
Migration speed (m s^{-1})	Continuous	River distance between receivers 1 and 2 / Time spent in between receivers 1 and 2	Slower < faster	Vollset et al. (2016)
Day of Year of migration (DoY)	Continuous	Day of year at estuary entrance	Earlier < later	Russell et al. (2012), Furey et al. (2015)
Temperature at estuary entrance (°C)	Continuous	Measurement with data logger	Warm < cold	Marsh et al. (2021)
Dissolved oxygen (% sat) at estuary entrance	Continuous	Measurement with data logger	Low < high	Maes et al. (2007), Friedland et al. (2017)
Salinity at estuary entrance	Continuous	Measurement with data logger	High < low	Friedland et al. (2017)
Discharge (m^3 s^{-1})	Continuous	Download online	Low < high	Bret et al. (2017)
Distance (m)	Continuous	River distance between 2 adjacent receivers	Further < nearer	Larocque et al. (2020), Welch et al. (2009)
Cumulative distance (m)	Continuous	River distance between the first and the last acoustic gate	Further < nearer	Larocque et al. (2020), Welch et al. (2009)

only the 2019 data because of missing DO values.

Detection efficiencies of receiver gates were estimated by the models to be between 61 and 99 % (Table S1 in the Supplement at www.int-res.com/articles/suppl/m709p091_supp.pdf). When comparing the 4 survival models, using all data (both 2018 and 2019) to decide on the most suitable spatio-temporal structure of survival for subsequent models, the strongest support was found for a model that allowed for spatial variation only ($\phi_{tj}\, \rho_{t,j}$, Model 1a; Table 4). Using the structure of Model 1a, variables with weak effects were iteratively removed to obtain the most parsimonious model (Model 2a). Of all the models tested, the most parsimonious model included site, year, river type, species, distance and migration speed (Table 4).

Using only the 2019 data, the structural model allowing for spatio-temporal variation in survival between receivers had the strongest support (Model 1b, Table 4). The effects of all explanatory variables included in Model 1b were weak and so variables removed from Model 1a (2018 and 2019 data together) were removed iteratively first, before iteratively removing those explanatory variables retained in Model 2a. The most parsimonious model (Model 2b) included effects of site, river type, species, migration speed and distance. Adding any combinations of the variables oxygen, salinity and temperature to Model 2b did not change the outputs (Table 4).

Model 2a and Model 2b converged with the Gelman-Rubin r-hat value < 1.1 and the effective sample size n.eff > 200 for all parameters estimates (Fig. S1 in the Supplement). Spatial variation of smolt estuarine survival was confirmed in Models 2a & 2b. Indeed, for both species, survival decreased as smolts progressed through the estuary, with only a slight difference in rates between 2018 and 2019 (Fig. 2).

Considering both species and all sites, smolts exhibited 83 ± 15 % total survival (ψ) during their estuarine migration to

Table 3. Atlantic salmon and sea trout smolts acoustically tagged to estimate their estuarine survival during outmigration for rivers in England (Frome, Tamar) and France (Bresle, Scorff). N: number of individuals included in the analysis per species, site, and year; FL: initial fork length; BCI: initial body condition index; %1yr, %2yr, %M: percentage of 1 yr old, 2 yr old and male among tagged individuals; DoY: day of the year at estuary entrance; Speed: migration speed; DO: dissolved oxygen (%sat: percent saturation). Discharge is the mean between the date of tagging and date of entrance to the estuary; temperature was recorded at the estuary entrance. Error terms are SD; NA: not available

Species	Site	Year	N	FL (mm)	BCI	%1yr	%2yr	%M	DoY	Speed (m s⁻¹)	Discharge (m³ s⁻¹)	DO (%sat)	Salinity	Temperature (°C)
Salmon	Frome	2018	24	142.0 ± 6.7	0.21 ± 0.0	100	0	57	119 ± 7	0.33 ± 0.18	10.4 ± 1.4	NA	NA	NA
		2019	78	142.8 ± 10.3	0.22 ± 0.0	93	7	53	119 ± 10	0.42 ± 0.21	6.1 ± 1.4	103.4 ± 6.0	1.2 ± 1.3	12.7 ± 1.0
	Tamar	2018	50	151.5 ± 8.5	0.22 ± 0.0	41	59	39	110 ± 6	0.56 ± 0.15	19.5 ± 4.3	NA	NA	NA
		2019	51	146.5 ± 9.4	0.23 ± 0.0	12	88	52	123 ± 5	0.49 ± 0.18	9.7 ± 5.6	93.3 ± 6.8	0.6 ± 1.4	12.5 ± 0.3
	Bresle	2018	37	149.5 ± 7.5	0.24 ± 0.0	98	2	38	106 ± 5	0.25 ± 0.18	10.0 ± 0.2	NA	NA	NA
		2019	57	152.8 ± 11.5	0.26 ± 0.0	97	3	26	112 ± 5	0.55 ± 0.62	7.4 ± 1.1	104.4 ± 7.1	4.0 ± 0.9	13.8 ± 0.5
	Scorff	2018	59	143.8 ± 8.7	0.22 ± 0.0	58	42	42	114 ± 1	0.44 ± 0.11	5.7 ± 1.7	NA	NA	NA
		2019	58	147.0 ± 11.3	0.22 ± 0.0	48	52	53	113 ± 3	0.49 ± 0.14	5.0 ± 1.8	89.2 ± 3.9	23.8 ± 2.4	14.6 ± 0.6
	Total		414											
Trout	Frome	2018	45	193.7 ± 22.6	0.39 ± 0.1	50	50	53	95 ± 7	0.26 ± 0.17	16.1 ± 1.4	NA	NA	NA
		2019	51	185.4 ± 28.6	0.68 ± 0.1	59	41	51	114 ± 11	0.26 ± 0.15	9.0 ± 2.9	93.8 ± 6.7	1.8 ± 1.9	12.7 ± 1.5
	Tamar	2018	27	195.1 ± 19.0	0.39 ± 0.1	7	93	25	102 ± 10	0.48 ± 0.15	34.4 ± 14.4	NA	NA	NA
		2019	45	203.8 ± 20.1	0.41 ± 0.1	0	100	47	95 ± 5	0.46 ± 0.15	20.3 ± 11.0	96.4 ± 1.9	0.1 ± 0.0	8.7 ± 0.5
	Bresle	2018	48	202.9 ± 31.1	0.48 ± 0.1	33	67	33	100 ± 6	0.33 ± 0.35	9.9 ± 0.7	NA	NA	NA
		2019	57	218.0 ± 32.7	0.48 ± 0.1	32	68	43	95 ± 8	0.53 ± 0.56	8.3 ± 1.2	100.4 ± 7.2	1.8 ± 1.9	11.6 ± 0.6
	Total		273											

the sea (Table 5). Of all the variables tested in Models 1a & 2a, species, migration speed, distance and cumulative distance significantly influenced smolt survival (coefficient and credible interval do not overlap 0; Fig. 3). At all sites and in both years, salmon smolts exhibited lower total survival than trout smolts with a mean total survival of 79 ± 17 % and 88 ± 12 %, respectively (positive coefficient for trout in Fig. 3A and Table 5). Also, fish that exhibited a higher migration speed during their estuarine migration showed a better survival than slower individuals (Fig. 4A). For both species, survival between acoustic receiver gates decreased with distance as well as with cumulative distance covered during their migration (Fig. 4B). Neither species displayed a large difference in survival between years.

Even though the explanatory variables site, year and river type only weakly influenced survival (φ) their inclusion in the modelling improved model performance (Table 4). Considering total survival, for both species, there was some between-site variation with the lowest estimated estuarine survival for both salmon and trout smolt on the Frome Estuary (60 ± 6 %) followed by Scorff (85 ± 2 %), Bresle (92 ± 2 %) and Tamar (93 ± 2 %; Table 5) estuaries. Smolts estuarine total survival showed temporal stability during the 2 years of survey with 86 ± 13 % in 2018 and 80 ± 18 % in 2019 (Fig. 3A, Table 5). Smolts from aquifer-fed rivers had a lower survival than those from rain-fed rivers (Fig. 5) and salmon smolts had a lower survival than trout smolts (Table 5, Fig. 5). There was no discernible effect of smolt FL, BCI, age, or sex on their estuarine survival (Fig. 3A). In 2019 (Models 1b & 2b), when data was available for salinity, DO and temperature at the estuary entrance, none of these explanatory variables appeared to affect estuarine survival (Fig. 3B, Table 4).

4. DISCUSSION

This study demonstrated how fish passage in transitional waters can be challenging for salmonid smolts. In particular, salmon exhibited a lower survival during their seaward migration than trout smolts, and faster smolts survived better than slower ones. Migratory distance (both since tagging and between 2 receiver gates) negatively influenced smolt survival. Smolt total survival was similar for 3 of the 4 sites, but lower in the Frome Estuary. Similarly, aquifer-fed rivers showed a lower smolt total survival than rain-fed rivers. Overall, smolt survival through these 4 estuaries was estimated to be between 51 %

Table 4. Comparison of models using Watanabe−Akaike information criterion (WAIC) to find the most parsimonious spatio-temporal structure (Model 1a; see Section 2.5) and most important covariates (Model 2a & 2b) to estimate Atlantic salmon and brown trout smolt survival during their first seaward migration in both 2018 and 2019 (all) and 2019 only. The most parsimonious models taken forward for inference are shown in **bold** (Model 2a & 2b)

Model	Year	Model structure	Variables	WAIC
Model 1a	All	$\phi\, p_{tj}$	All	1796.58
	All	$\phi_t\, p_{tj}$	All	1798.61
	All	$\phi_j\, p_{tj}$	All	1747.33
	All	$\phi_{tj}\, p_{tj}$	All	1748.78
	All	$\phi_j\, p_{tj}$	Site, year, species, speed, distance, day of year	1737.14
	All	$\phi_j\, p_{tj}$	Species, speed, distance	1733.02
	All	$\phi_j\, p_{tj}$	Site, species, speed, distance	1726.54
	All	$\phi_j\, p_{tj}$	Site, year, species, speed, distance	1724.16
	All	$\phi_j\, p_{tj}$	Site, year, species, speed, distance, river type	1722.24
Model 2a	**All**	$\phi_j\, p_{tj}$	**Site, year, species, speed, distance, river type without interactions**	**1714.53**
Model 1b	2019	$\phi\, p_{tj}$	All + DO, salinity, temperature	780.04
	2019	$\phi_j\, p_{tj}$	All + DO, salinity, temperature	775.82
	2019	$\phi_j\, p_{tj}$	All + DO, salinity, temperature without interaction	769.43
Model 2b	**2019**	$\phi_j\, p_{tj}$	**Site, species, speed, distance, river type without interactions**	**754.31**
	2019	$\phi_j\, p_{tj}$	Site, species, speed, distance without interaction	756.74

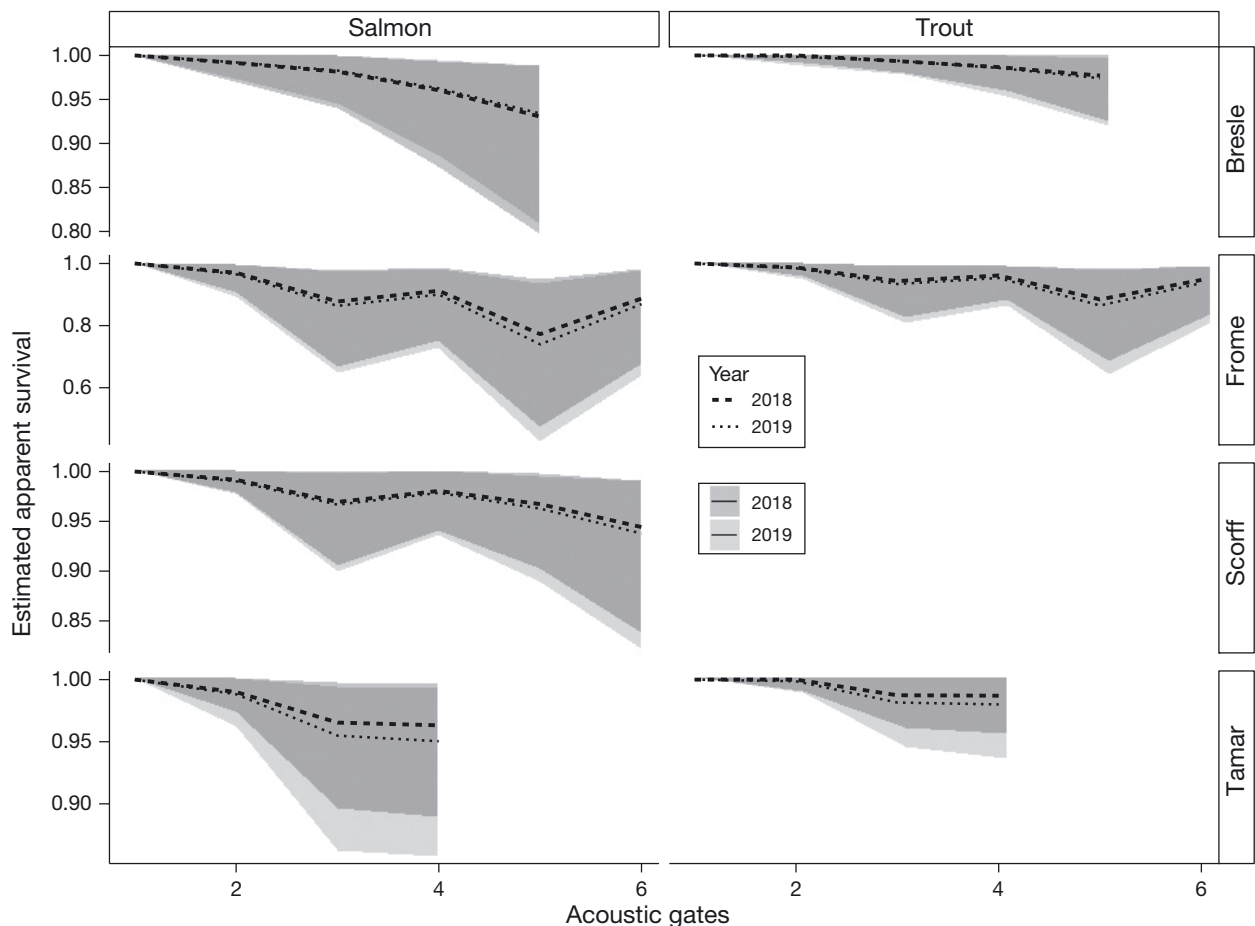Fig. 2. Estimated apparent survival (lines) ± 95% credible interval (grey areas) of salmon and trout smolts between acoustic receiver gates through the estuarine part of the smolt outmigration to sea (Model 2a) for rivers in England (Frome, Tamar) and France (Bresle, Scorff). Six gates were deployed in the rivers Frome and Scorff, 5 on the River Bresle and 4 on the River Tamar

Table 5. Mean ± SD total apparent survival (%, Model 2a) and survival rate per km of Atlantic salmon and sea trout smolts during their seaward migration along the rivers Tamar (23 km), Frome (14 km), Scorff (16 km) and Bresle (2 km) to their respective estuaries in 2018 and 2019

River Species	2018	2019	Mean	Mean % km^{-1}
Tamar				
Salmon	92.0 ± 2.1	89.7 ± 2.8	90.8 ± 2.5	99.5 ± 0.2
Trout	97.4 ± 0.8	96.0 ± 1.1	96.7 ± 0.9	99.9 ± 0.1
Both species	93.9 ± 1.7	92.6 ± 2.0	93 ± 2.0	99.7 ± 0.2
Frome				
Salmon	53.2 ± 6.5	48.2 ± 7.0	50.7 ± 7.7	95.3 ± 1.0
Trout	74.9 ± 3.7	71.0 ± 4.1	72.9 ± 3.9	97.8 ± 0.4
Both species	66.8 ± 4.6	56.5 ± 5.9	60 ± 6.0	96.4 ± 0.7
Bresle				
Salmon	86.9 ± 2.6	87.6 ± 2.7	87.2 ± 2.7	93.3 ± 1.5
Trout	95.7 ± 1.4	95.2 ± 1.7	95.5 ± 1.6	98.0 ± 1.0
Both species	92.2 ± 2.0	91.3 ± 2.3	91.8 ± 2.1	95.9 ± 0.8
Scorff				
Salmon	86.1 ± 2.3	84.6 ± 2.5	85.3 ± 2.4	99.0 ± 0.3
Trout	–	–	–	–
Both species	86.1 ± 2.3	84.6 ± 2.5	85.3 ± 2.4	99.0 ± 0.3
All sites				
Salmon	83.7 ± 13.6	75.1 ± 19.3	79.4 ± 16.6	96.8 ± 3.0
Trout	88.4 ± 11.1	87.6 ± 12.3	88.0 ± 11.7	98.6 ± 1.0
Both species	85.6 ± 12.8	79.9 ± 18.0	82.7 ± 15.4	97.7 ± 2.0

and 97%, suggesting that estuaries are challenging habitats for migrating salmonid smolts, accounting for non-negligible reductions in early marine survival.

other estuaries was not expected as each had specific and somewhat contrasting characteristics (see Section 2.1), and smolt survival can vary widely from one site to another. For example, Thorstad et al. (2012) reviewed aspects of salmon migration and reported 36 to 100% survival in estuarine habitats. Smaller variation was reported for trout survival during their estuarine migration, with total survival ranging from 76 to 87% (Dieperink et al. 2002, Koed et al. 2006, Lauridsen et al. 2017) although the number of studies are limited and the sample sizes in these studies were modest. Comparison of these results with reported survival from other studies is challenging (Chaput et al. 2019) due to variations in study design and methodology, as well as physical and chemical characteristics relating to geography and site-specific habitat dynamics. In particular, the boundaries between different transitional habitats are not always clearly delineated. In this study, estuary boundaries were defined based on the salinity gradient (from 0 to 35) but the limit of tidal influence can also be used, which could extend the 'estuarine' section of a waterway several kilometers further upstream. A standardisation of

4.1. Spatio-temporal variations in smolt estuarine survival

Incorporating temporal variation in the models did not improve their performance, suggesting that smolt estuarine survival did not vary substantially between the 2 years of study. As more between-years variability was expected (Welch et al. 2009, Chaput et al. 2019), repeating this survey regularly would confirm whether smolt survival is constant through time.

Although *site* only had a weak effect on smolt survival estimated by Models 2a & 2b (Fig. 3), the Frome Estuary exhibited a lower total survival of both salmon (51 ± 7%) and trout (73 ± 4%) smolts compared with the 3 other estuaries (~88 ± 2% for salmon smolts and 96 ± 1% for trout smolts; Table 5). The similarity in survival between the 3
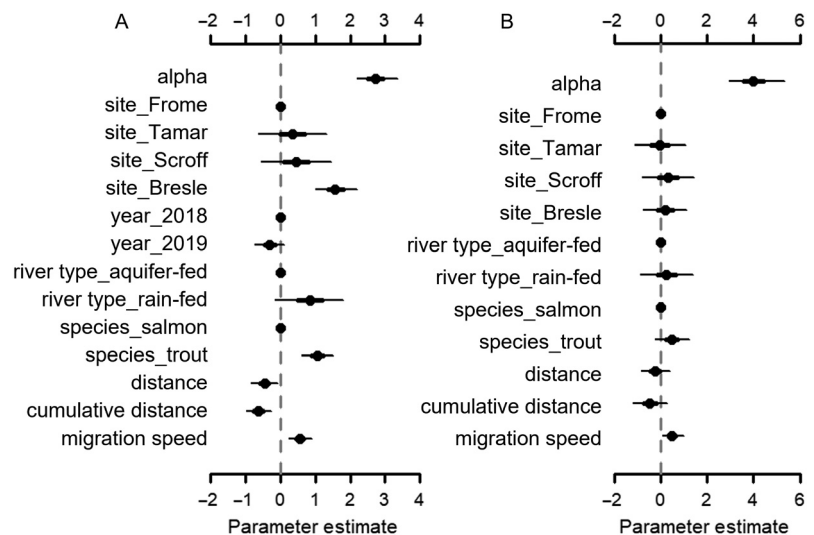

Fig. 3. Mean ± 50−95% credible interval (thicker and thinner bars, respectively) coefficients included in (A) Model 2a and (B) Model 2b to estimate apparent survival of Atlantic salmon and brown trout smolts during their estuarine seaward migration. When the credible interval does not overlap 0, the variable is considered to significantly influence survival of smolts positively when the coefficient estimate is >0, or negatively when the coefficient estimate is <0

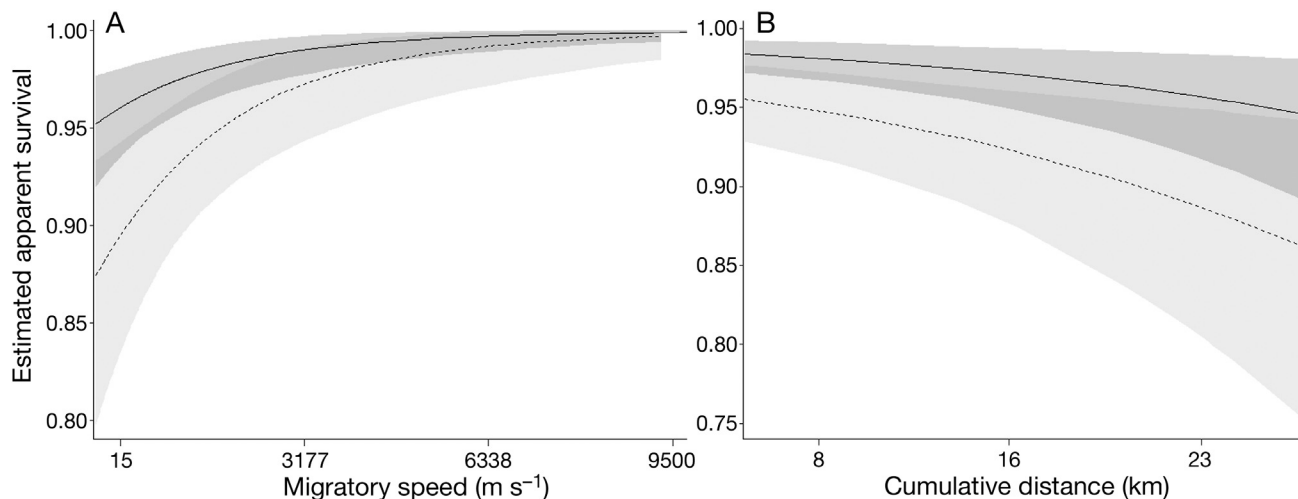Fig. 4. Marginal mean estimated (± 95% credible interval) apparent survival (from Model 2a) of Atlantic salmon (dashed line) and sea trout (solid line) smolts as a function of (A) standardised migration speed and (B) standardised cumulative distance during estuarine seaward migration

these boundaries would improve the comparison and transferability of estuarine survival results, the best being to monitor survival from freshwater to the marine environment with tracking equipment (e.g. acoustic receivers) deployed at both the tidal and salinity limits.

All results supported within-site spatial variation in smolt estuarine survival: from the most parsimonious model that incorporated variation between receiver gates, to survival of both species that decreased toward estuary exits and the negative influence of

Fig. 5. Marginal mean estimated apparent estuarine survival ± 95% credible interval of Atlantic salmon and sea trout smolts from aquifer or rain-fed rivers in England and France

distance (distance and cumulative distance) on smolt survival. These results matched with our expectations as the distance smolts travelled during their migration, has been reported to influence their survival negatively in many studies (e.g. Welch et al. 2009, Plantalech Manel-La et al. 2011, Larocque et al. 2020).

If migratory distance negatively influences smolt survival, we might expect higher survival through shorter estuaries. This was, however, not what we observed here whereby the highest survival was observed in the longest estuary (Tamar). This suggests that survival cannot be explained by migratory distance alone but rather is better explained by combinations and interactions of several variables. For example, despite an apparent high total survival (92 ± 2%), the Bresle and Frome estuaries exhibited the lowest survival rates per km (95.9 ± 0.8 and 96.4 ± 0.7% km^{-1}, respectively). This suggests that mortality along the Bresle is more intense within its 2 km estuary than at the other sites. The difference in survival rate per km between the Frome and Bresle estuaries and the Tamar and Scorff estuaries might be explained by different chemical characteristics of the water; the Bresle and Frome are chalk (aquifer-fed) rivers, whereas the Scorff and Tamar are rain-fed rivers. River type — even though only weakly influential on smolt estuarine survival — does have an effect on total survival, with higher levels in rain-fed than in aquifer-fed rivers (Fig. 4). We have no knowledge of studies comparing rivers of contrasting chemical characteristics and so this result appears to constitute a new, hitherto unreported, finding. This
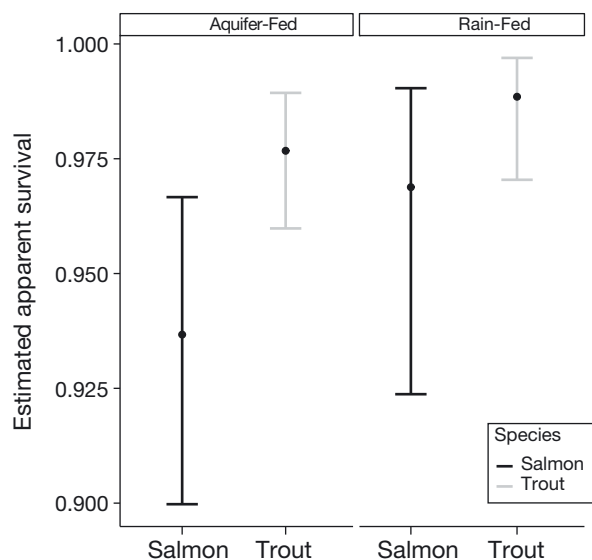
observation might be triggered by the low survival of smolts through the Frome Estuary, and further investigation would help strengthen this new hypothesis.

Another potential source of spatial variation in smolt survival could be the differences in the geomorphology of the estuarine systems. The Tamar and Scorff estuaries represent narrow unidirectional estuaries with no physical barriers. In contrast, the Frome Estuary is wide and complex, offering fish a multitude of migratory routes, all of which they use (Thorstad et al. 2004) without necessarily following the water current. According to this hypothesis, and the prior finding where distance and cumulative distance negatively impact smolt survival in estuaries, smolts arriving in the Frome Estuary may range around it widely, travelling distances that are not captured by the study design, and this way increasing their swimming distance and therefore decreasing proportionally their chance of survival. It would be interesting to monitor the exact migration path of smolts in complex and/or wide estuaries to confirm this hypothesis. The Bresle Estuary is highly managed, with floodgates that close the principal route out to sea for out-migrating fish. Indeed, obstacles and dams located on the migration routes of smolts negatively impact the survival of smolts (Aarestrup & Koed 2003, Holbrook et al. 2011, Stich et al. 2015).

4.2. Species-specific and individual survival

Few studies have included both salmon and trout smolts, even though the 2 species are similar and often inhabit the same rivers. Here, we incorporated both species in the same model to identify what parameters could affect both species, as well as directly comparing their survival. To our knowledge, this is the first time both species have been considered together in the same analysis.

Our study revealed differences in estuarine survival between the 2 species. In all study sites and in both years, trout smolt survival was higher than that of salmon smolts. A similar trend was reported for these 2 species tracked through the River Skjern and its estuary in Denmark (Dieperink et al. 2002; Koed et al. 2006). In these studies, the estuarine total survival of salmon smolt survival (61%) was much lower than that of trout smolts (88%) which was explained mainly by great cormorant *Phalacrocorax carbo sinensis* predation in conjunction with a migratory behaviour strategy that would disadvantage salmon. Both species were also surveyed in the Romsdals Fjord (Norway), where fewer trout smolts were

detected at the exit of the fjord compared to salmon smolts (Finstad et al. 2005, Thorstad et al. 2007). However, for the Romsdals trout population, the fjord system was not a transitioning habitat, but the main feeding habitat used whilst in the marine area and so the number of detections at the exit of the fjord reflected their migration behaviour in the fjord rather than their survival. In the 4 studied systems presented here, trout smolts are also bigger than their salmon counterparts, with trout size ranging over 110–313 mm FL compared to 90–192 mm for salmon (data from the 4 study sites). Assuming our sampling strategy was representative of the size difference between the 2 species (Table 3), FL explained only negligible variation in survival in this study, as did BCI, the latter of which was different between the 2 species and could have explained their different estuarine survival. Migration speed appeared to be positively related to the survival of smolts, with a higher speed associated with a higher survival (Fig. 4A). Faster swimming might enable fish to cross dangerous areas quickly (Thorstad et al. 2012) and to avoid predators (Jepsen et al. 2006, Riley et al. 2011). This does not explain the higher survival of trout smolts because their mean swimming speed was slower than salmon smolts (Table 3). In dangerous situations, however, it might be their capacity to accelerate quickly rather than their mean migratory speed that influences their survival, for which trout smolts could be faster than salmon due to their larger size.

At the individual level, longer vs. shorter salmon and trout smolts survive better during their migration (e.g. salmon: Saloniemi et al. 2004, Davidsen et al. 2009, Russell et al. 2012, Jonsson & Jonsson 2014, Armstrong et al. 2018, Chaput et al. 2019, Gregory et al. 2019; trout: Kallio-Nyberg et al. 2006, Jensen et al. 2022). The influence of size on smolt survival during marine migration has been demonstrated in sites from southern England to Norway, highlighting the strength of this relationship for marine return rates.

Hoewever, the present study did not detect an influence of smolt size on their estuarine survival. Our conclusions regarding effect of size on salmon survival are limited due to our limited sampling of individuals >13 cm FL, representing only the biggest salmon smolts in the populations (e.g. Koed et al. 2006). However, this was not the case for trout smolts where tagging was carried out across the entire size range of the populations. Most studies reporting an influence of smolt size on their survival focused on marine return rates that included the lower-river, estuarine and marine environments, rather than only

the estuarine stage. It is therefore possible that the effect of smolt size is related only to later stages in the migration and would reflect their ability to endure poor feeding conditions at sea rather than during the short estuarine phase. Like body length, BCI did not explain variation in apparent survival in this study, possibly for the same reason as body length.

Contrary to our prediction that older individuals and males were expected to survive better, age and sex did not explain significant variation in smolt estuarine survival. This result differs from other reports, such as cichlid fish for which age and sex influenced some predator avoidance behaviour (Meuthen et al. 2018). Tamate & Maekawa (2004) demonstrated sex-specific mortality rates in salmonids, with females demonstrating riskier feeding behaviour compared with males so as to increase their growth rate and thereby fecundity.

Although we found no effect of BCI, age, or sex on smolt survival during their short estuarine migration phase, these parameters might well impact survival and growth during later stages of the marine phase.

4.3. No influence of environmental variables on smolt estuarine survival

Except for distance, no other environmental variables were found to influence smolt survival in this study, despite their reported effects in other studies (timing of migration: Hansen & Jonsson 1989, Dempson et al. 2011, Russell et al. 2012, Jonsson & Jonsson 2014, Furey et al. 2015; temperature and discharge: Friedland et al. 1998, Jonsson & Jonsson 2009, Bret et al. 2017; salinity and oxygen level: Friedland et al. 2017). A lower sample size (288 individuals) was considered in the model which incorporated temperature, salinity and oxygen. This might not represent a sufficient sample size to detect an influence of one or several explanatory variables included in Model 1b. Also, temperature, salinity, and DO level were recorded at the moment (±8 min) at which individuals were detected at the estuary entrance, providing a representation of the estuary entry condition experienced by each tagged fish. Taking the gradient of these variables between the estuary entrance and exit may have yielded more explicative data than values at departure alone. However, for individuals that never reached the exit, oxygen, temperature and salinity values at the exit were missing and inferring such data from detected individuals could induce a degree of circularity. The receiver gate design of the present study

did not enable the determination of exact location and timing of individual smolt mortality events, limiting the possible interpretation and data extraction of environmental variables to explain their survival during their estuarine migration to sea. Deploying more receivers or using sensor acoustic tags recording these parameters could refine location, timing and reason for the mortality event, and should be considered for future tracking studies.

Arriving in the estuaries, smolts face a new environment where water characteristics (salinity, temperature) change and smolts encounter new predators. No predator survey was undertaken during this study, although predation appears to be a credible hypothesis with which to explain the decrease of survival through estuaries. Predators such as marine birds and piscivorous fishes have previously been described as responsible for smolt mortality in salmon (Daniels et al. 2018, 2019, Kennedy et al. 2018, Lothian et al. 2018) and trout (Dieperink et al. 2001, 2002, Koed et al. 2006). In a study looking at marine return rate of salmon smolts, Simmons et al. (2022) found a negative, though non-significant, relationship with the density of sea bass in coastal areas close to the mouth of the Frome Estuary.

In our study, individuals that were undetected after some point of their migration and that never reached the exit, designated as non-survivors, may have been subject to predation events by avian, fish or mammal predators. Except in the case of an obvious change in smolt behavior (e.g. movement upstream, observation of which would also depend on detection probability), any predation event would have been difficult to identify with certainty. The use of a predation tag would help to reduce this bias.

Furey et al. (2015) identified migration routes chosen by individuals as a factor that influenced the smolt survival of 2 species of salmonid: sockeye salmon *Oncorhynchus nerka* and steelhead *Oncorhynchus mykiss* along the British Columbian coastline. Therefore, in the future the receiver gate design could be adapted to ascertain whether smolts following a specific migratory route were disadvantaged relative to other routes. This hypothesis would be even more important for the River Frome Estuary which displays a 'balloon' shape and hence offers a multitude of possible routes. Finally, Stich et al. (2015) demonstrated that the physiological state of smolts, i.e. a lower Na^+K^+-ATPase enzyme activity that results in reduced salinity tolerance, had an impact on their survival during their migration (Wedemeyer et al. 1980, McCormick et al. 1999). Information on individual physiological state, collected at the

same time of capture or during tracking, could bring new insights into the mechanisms causing variation in smolt survival during their estuarine migration.

4.4. Tagging effects on survival of smolts

Investigations of the survival and behaviour of aquatic animals using a surgically implanted tag raises a number of concerns: (1) the surgical procedure might directly or indirectly impact the behaviour and survival of the animal (Drenner et al. 2012); (2) tag loss, tag failure or tag-expulsion could introduce bias into estimates of survival or behaviour (Moore et al. 1990, Knudsen et al. 2009, Foldvik & Kvingedal 2018); (3) results might not be directly transferable from tagged to untagged individuals (Riley et al. 2018), just as results from reared animals are thought not to transfer well to wild animals (Bridger & Booth 2003, Holbrook et al. 2011, Drenner et al. 2012, Larocque et al. 2020); and (4) the process is inherently time-consuming and expensive, and so sample sizes tend to be small, raising concerns of the transferability of the results to a broader scale. Even though the miniaturisation of batteries and tags should lessen their impact on the tagged animal's survival and behaviour (Rechisky & Welch 2010), tag burden, handling of the animal and their consequences are still a subject of debate (Jepsen et al. 2005, Thorstad et al. 2013, Riley et al. 2018). The determination of a tagging size limit seems to be researcher-specific, leading to a variety of tag sizes (and therefore levels of tag burden) being applied to fish of similar size (Jepsen et al. 2005). Consequently, studies that report an effect of fish length or susceptibility to predation on the animal's survival could be an artefact of tagging procedures, and might not be generalisable, especially if there was no simultaneous study to understand the possible impact of the tagging procedure.

Most of these concerns were addressed in our study. Firstly, we used one of the smallest acoustic tags available, which should have reduced the impact on fish natural behaviour. Despite this, the survival of tagged individuals could be impacted indirectly, no matter how small the tag, through increasing energetic costs of carrying the tag (e.g. tag transport, reduced swimming speed), and subsequent increased probability of predation (Furey et al. 2016). Secondly, the tagging procedure developed in this study was tested experimentally to quantify its direct effect on survival and tag loss, during 14 d after surgery, which was longer than it took for most smolts to reach the exit of the estuaries after tagging. This experiment was conducted under semi-natural conditions, with water pumped from the river that induced the fish to swim against the current. Nevertheless, bias unrelated to tagging could have persisted, notably due to the small sample size of the 4 groups in our tagging-survival experiment, imperfect detection, and the difficulty to quantify other bias that could lead to over or under-estimation of smolt survival during their migration, such as predation events. For all these reasons, results reported here represent apparent smolt survival rather than true smolt survival.

In conclusion, estuaries represent only a small portion of the migration that smolts undertake, but the present study found a total survival of 51 to 91 % for the salmon smolts and 73 to 97 % for trout smolts. On their return, smolts will cross estuaries again which could also potentially account for additional loss. Therefore, estuaries seem to represent challenging habitats in the smolts' progression through their life cycle, possibly inflicting large losses to the stocks of these 2 native salmonid species. Estuarine survival of salmonid smolts is influenced by a combination of biotic and abiotic parameters (e.g. distance, speed, site shape, presence of barriers, presence of predators) rather than one main variable, complicating management efforts. As a result of this complexity more estuaries should be monitored to identify where management efforts should be prioritised at a national level.

LITERATURE CITED

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

Armstrong JD, McKelvey S, Smith GW, Rycroft P, Fryer RJ (2018) Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. J Fish Biol 92:569–578

Birnie-Gauvin K, Thorstad EB, Aarestrup K (2019) Overlooked aspects of the *Salmo salar* and *Salmo trutta* lifecycles. Rev Fish Biol Fish 29:749–766

Bret V, Capra H, Gouraud V, Lamouroux N, Piffady J, Tissot L, Rivot E (2017) Understanding inter-reach variation in

brown trout (*Salmo trutta*) mortality rates using a hierarchical Bayesian state-space model. Can J Fish Aquat Sci 74:1612–1627

Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Rev Fish Sci 11:13–34

Caillart B, Morize E (1989) Etude du rythme de dépôt des microstries sur les otolithes d'un serranidé tropical, *Epinephelus microdon* à l'aide d'un marqueur fluorescent: l'oxytétracycline. Aquat Living Resour 2:255–261

Chaput G, Carr J, Daniels J, Tinker S, Jonsen I, Whoriskey F (2019) Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. ICES J Mar Sci 76:1107–1121

Clarke D, Allen C, Artero C, Wilkie L, Whelan KF, Roberts D (2021) Acoustic tracking in Wales — designing a programme to evaluate marine renewable energy impacts on diadromous fish. NRW Evidence Rep No. 553. National Resources Wales, Bangor

Daniels J, Chaput G, Carr J (2018) Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. Can J Fish Aquat Sci 12:1–12

Daniels J, Sutton S, Webber D, Carr J (2019) Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. Anim Biotelem 7:1–11

Davidsen JG, Rikardsen AH, Halttunen E, Thorstad EB and others (2009) Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. J Fish Biol 75:1700–1718

Dempson JB, Robertson MJ, Pennell CJ, Furey G and others (2011) Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. J Fish Biol 78:1976–1992

Dieperink C, Pedersen S, Pedersen MI (2001) Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. Ecol Freshwat Fish 10:177–183

Dieperink C, Bak BD, Pedersen LF, Pedersen MI, Pedersen S (2002) Predation on Atlantic salmon and sea trout during their first days as postsmolts. J Fish Biol 61:848–852

Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG (2012) A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLOS ONE 7:e31311–e31311

Erkinaro J, Czorlich Y, Orell P, Kuusela J and others (2019) Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. Can J Fish Aquat Sci 76:42–55

Finstad B, Økland F, Thorstad EB, Bjørn PA, McKinley RS (2005) Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. J Fish Biol 66:86–96

Foldvik A, Kvingedal E (2018) Long-term PIT tag retention rates in Atlantic salmon (*Salmo salar*). Anim Biotelem 6:3

Friedland KD, Hansen LP, Dunkley DA (1998) Marine temperatures experienced by postssmolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. Fish Oceanogr 7:22–34

Friedland KD, Dannewitz J, Romakkaniemi A, Palm S, Pulkkinen H, Pakarinen T, Oeberst R (2017) Post-smolt survival of Baltic salmon in context to changing environmental conditions and predators. ICES J Mar Sci 74:1344–1355

Furey NB, Vincent SP, Hinch SG, Welch DW (2015) Variability in migration routes influences early marine survival of juvenile salmon smolts. PLOS ONE 10:e0139269

Furey NB, Hinch SG, Bass AL, Middleton CT, Minke-Martin V, Lotto AG (2016) Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. J Anim Ecol 85:948–959

Gregory SD, Ibbotson AT, Riley WD, Nevoux M and others (2019) Atlantic salmon return rate increases with smolt length. ICES J Mar Sci 76:1702–1712

Hansen LP, Jonsson B (1989) Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. Aquaculture 82:367–373

Hansen LP, Quinn TP (1998) The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can J Fish Aquat Sci 55:104–118

Heim KC, Wipfli MS, Whitman MS, Seitz AC (2016) Body size and condition influence migration timing of juvenile Arctic grayling. Ecol Freshw Fish 25:156–166

Holbrook CM, Kinnison MT, Zydlewski J (2011) Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a prerestoration assessment. Trans Am Fish Soc 140:1255–1268

Holtby LB, Healey MC (1990) Sex-specific life history tactics and risk-taking in coho salmon. Ecology 71:678–690

Hubley PB, Amiro PG, Gibson AJF, Lacroix GL, Redden AM (2008) Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. ICES J Mar Sci 65:1626–1634

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ and others (2015) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642

IAPSO (Working Group on Symbols, Units and Nomenclature in Physical Oceanography) (1985) The International System of Units (SI) in oceanography. Unesco Tech Pap Mar Sci 45 (IAPSO Publ Sci 42), Unesco, Paris. doi:10.25607/OBP-666

ICES (2020a) Nasco Workshop for North Atlantic salmon atsea mortality (Wksalmon, outputs from 2019 meeting). ICES Sci Rep 2:69

ICES (2020b) Working Group with the aim to develop assessment models and establish biological reference points for sea trout (anadromous *Salmo trutta*) populations (WGTRUTTA; outputs from 2019 meeting). ICES Sci Rep 59

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77:61–67

Jensen AJ, Diserud OH, Finstad B, Fiske P, Thorstad EB (2022) Early-season brown trout (*Salmo trutta*) migrants grow and survive better at sea. J Fish Biol 100:1419–1431

Jepsen N, Schreck C, Clements S, Thorstad EB (2005) A brief discussion on the 2% tag/bodymass rule of thumb. In: Spedicato MT, Lembo G, Marmulla G (eds) Aquatic telemetry: advances and applications. FAO/COISPA, Ustica, p 255–259

Jepsen N, Holthe E, Økland F (2006) Observations of predation on salmon and trout smolts in a river mouth. Fish Manag Ecol 13:341–343

Jonsson B, Jonsson N (2009) A review of the likely effects of

climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. J Fish Biol 75: 2381−2447

Jonsson N, Jonsson B (2014) Time and size at seaward migration influence the sea survival of *Salmo salar*. J Fish Biol 84:1457−1473

Kallio-Nyberg I, Jutila E, Jokikokko E, Saloniemi I (2006) Survival of reared Atlantic salmon and sea trout in relation to marine conditions of smolt year in the Baltic Sea. Fish Res 80:295−304

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

Kilduff DP, Di Lorenzo E, Botsford LW, Teo SLH (2015) Changing central Pacific El Niños reduce stability of North American salmon survival rates. Proc Natl Acad Sci USA 112:10962−10966

King RA, Stevens JR (2020) An improved genetic sex test for Atlantic salmon (*Salmo salar* L.). Conserv Genet Resour 12:191−193

Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, 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. Ecol Freshwat Fish 12:1−59

Knudsen CM, Johnston MV, Schroder SL, Bosch WJ, Fast DE, Strom CR (2009) Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. N Am J Fish Manage 29:658−669

Koed A, Baktoft H, Bak BD (2006) Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. River Res Appl 22:69−78

Lacroix GL (2008) Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. Can J Fish Aquat Sci 65:2063−2079

Larocque SM, Johnson TB, Fisk AT (2020) Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. Freshw Biol 65: 835−848

Lauridsen RB, Moore A, Gregory SD, Beaumont WRC, Privitera L, Kavanagh JA (2017) Migration behaviour and loss rate of trout smolts in the transitional zone between freshwater and saltwater. In: Harris G (ed) Sea trout science and management. Troubador Publishing, Market Harborough, p 292−307

Lothian AJ, Newton M, Barry J, Walters M, Miller RC, Adams CE (2018) Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. Ecol Freshwat Fish 27:549−558

Maes J, Stevens M, Breine J (2007) Modelling the migration opportunities of diadromous fish species along a gradient of dissolved oxygen concentration in a European tidal watershed. Estuar Coast Shelf Sci 75:151−162

Marsh JE, Lauridsen RB, Gregory SD, Beaumont WRC, Scott LJ, Kratina P, Jones JI (2020) Above parr: lowland river habitat characteristics associated with higher juvenile Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) densities. Ecol Freshwat Fish 29:542−556

Marsh JE, Lauridsen RB, Riley WD, Simmons OM and others (2021) Warm winters and cool springs negatively influ-

ence recruitment of Atlantic salmon (*Salmo salar* L.) in a southern England chalk stream. J Fish Biol 99: 1125−1129

Marsh JE, Lauridsen RB, Gregory SD, Kratina P, Scott LJ, Cooling D, Jones JI (2022) High summer macrophyte cover increases abundance, growth, and feeding of juvenile Atlantic salmon. Ecol Appl 32:e2492

McCormick SD, Cunjak RA, Dempson B, O'Dea MF, Carey JB (1999) Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the wild. Can J Fish Aquat Sci 56:1649−1658

Meuthen D, Baldauf SA, Bakker TCM, Thünken T (2018) Neglected patterns of variation in phenotypic plasticity: age- and sex-specific antipredator plasticity in a cichlid fish. Am Nat 191:475−490

Mills KE, Pershing AJ, Sheehan TF, Mountain D (2013) Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Glob Change Biol 19:3046−3061

Moore A, Russell IC, Potter ECE (1990) The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. J Fish 37:713−721

Nevoux M, Finstad B, Davidsen JG, Finlay R and others (2019) Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). Fish Fish 20:1051−1082

Noakes DJ, Beamish RJ, Kent ML (2000) On the decline of Pacific salmon and speculative links to salmon farming in British Columbia. Aquaculture 183:363−386

Olmos M, Payne MR, Nevoux M, Prévost E and others (2020) Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. Glob Change Biol 26:1319−1337

Otero J, Jensen AJ, L'Abée-Lund JH, Stenseth NC, Storvik GO, Vøllestad LA (2011) Quantifying the ocean, freshwater and human effects on year-to-year variability of one-sea-winter Atlantic salmon angled in multiple Norwegian rivers. PLOS ONE 6:e24005

Parrish DL, Behnke RJ, Gephard SR, McCormick SD, Reeves GH (1998) Why aren't there more Atlantic salmon (*Salmo salar*)? Can J Fish Aquat Sci 55:281−287

Plantalech Manel-La N, Chittenden CM, Økland F, Thorstad EB and others (2011) Does river of origin influence the early marine migratory performance of *Salmo salar*? J Fish Biol 78:624−634

Quinn TP (2018) The behavior and ecology of Pacific salmon and trout, 2nd edn. University of Washington Press & American Fisheries Society, Seattle, WA

Rechisky EL, Welch DW (2010) Surgical implantation of acoustic tags: influence of tag loss and tag-induced mortality on free-ranging and hatchery-held spring Chinook salmon (*Oncorhynchus tshawytscha*) smolts. In: Wolf KS, O'Neal JS (eds) PNAMP Special Publication: Tagging, telemetry and marking measures for monitoring fish populations — a compendium for new and recent science for use in informing technique and decision modalities. Spec Publ 2010-002, Pacific Northwest Aquatic Monitoring Partnership. https://www.rmpc.org/files/TTM_Compendium_2010.pdf

Riley WD, Ibbotson AT, Beaumont WRC, Pawson MG, Cook AC, Davison PI (2011) Predation of the juvenile stages of diadromous fish by sea bass (*Dicentrarchus labrax*) in the tidal reaches of an English chalk stream. Aquat Conserv 21:307−312

Riley WD, Ibbotson AT, Gregory SD, Russell IC and others (2018) Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts affect probability of return as adults? J Fish Biol 93:477–489

Ruggles CP (1980) A review of the downsream migration of Atlantic salmon. Can Tech Rep Fish Aquat Sci 952:1–39

Russell IC, Aprahamian MW, Barry J, Davidson IC and others (2012) The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. ICES J Mar Sci 69:1563–1573

Saloniemi I, Jokikokko E, Kallio-Nyberg I, Jutila E, Pasanen P (2004) Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES J Mar Sci 61:782–787

Simmons OM, Britton JR, Gillingham PK, Nevoux M, Riley WD, Rivot E, Gregory SD (2022) Predicting how environmental conditions and smolt body length when entering the marine environment impact individual Atlantic salmon *Salmo salar* adult return rates. J Fish Biol 101:378–388

Smircich MG, Kelly JT (2014) Extending the 2% rule : the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. Anim Biotelem 2:16

Stich DS, Zydlewski GB, Kocik JF, Zydlewski JD (2015) Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. Mar Coast Fish 7:68–86

Tamate T, Maekawa K (2004) Female-biased mortality rate and sexual size dimorphism of migratory masu salmon, *Oncorhynchus masou*. Ecol Freshwat Fish 13:96–103

Thorstad EB, Okland F, Finstad B, Sivertsga R, Bjørn PA, Mckinley RS (2004) Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. Environ Biol Fishes 71:305–311

Thorstad EB, Okland F, Finstad B, Sivertsgård R, Plantalech N, Bjørn PA, McKinley RS (2007) Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. Hydrobiologia 582:99–107

Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B (2012) A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. J Fish Biol 81: 500–542

Thorstad EB, Økland F, Westerberg H, Aarestrup K, Metcalfe JD (2013) Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials. Mar Freshw Res 64:324–331

Thorstad EB, Bliss D, Breau C, Damon-Randall K and others (2021) Atlantic salmon in a rapidly changing environment — facing the challenges of reduced marine survival and climate change. Aquat Conserv 31: 2654–2665

Tréhin C, Rivot E, Lamireau L, Meslier L, Besnard AL, Gregory SD, Nevoux M (2021) Growth during the first summer at sea modulates sex-specific maturation schedule in atlantic salmon. Can J Fish Aquat Sci 78: 659–669

Truett GE, Heeger P, Mynatt RL, Truett AA, Walker JA, Warman ML (2000) Preparation of PCR-quality mouse genomic DNA with hot sodium hydroxide and Tris (Hot-SHOT). Biotechniques 29:52–54

Vollset KW, Barlaup BT, Mahlum S, Bjørn PA, Skilbrei OT (2016) Estimating the temporal overlap between post-smolt migration of Atlantic salmon and salmon lice infestation pressure from fish farms. Aquacult Environ Interact 8:511–525

Wedemeyer GA, Saunders RL, Clarke WC (1980) Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar Fish Rev 42: 1–14

Welch DW, Melnychuk MC, Rechisky ER, Porter AD and others (2009) Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Can J Fish Aquat Sci 66: 736–750

Wilson KL, Bailey CJ, Davies TD, Moore JW (2022) Marine and freshwater regime changes impact a community of migratory Pacific salmonids in decline. Glob Change Biol 28:72–85

Wolf P (1951) A trap for the capture of fish and other organisms moving downstream. Trans Am Fish Soc 80:41–45

Yano A, Nicol B, Jouanno E, Quillet E, Fostier A, Guyomard R, Guiguen Y (2013) The sexually dimorphic on the Y-chromosome gene (*sdY*) is a conserved male-specific Y-chromosome sequence in many salmonids. Evol Appl 6: 486–496

Table S1. Detection efficiency (%) of receiver gates deployed on the Frome, Tamar, Scorff and Bresle estuaries for both year of the study (2018 and 2019) as estimated by the Model 2a.

Receiver gate	Frome		Tamar		Scorff		Bresle	
	2018	2019	2018	2019	2018	2019	2018	2019
E1	99	99	98	99	98	99	98	98
E2	96	98	99	98	NA	98	84	80
E3	NA	68	99	99	98	98	73	83
E4	81	84	96	96	98	98	89	97
E5	NA	61			76	69		
E6	83	72			94	95		

(A)
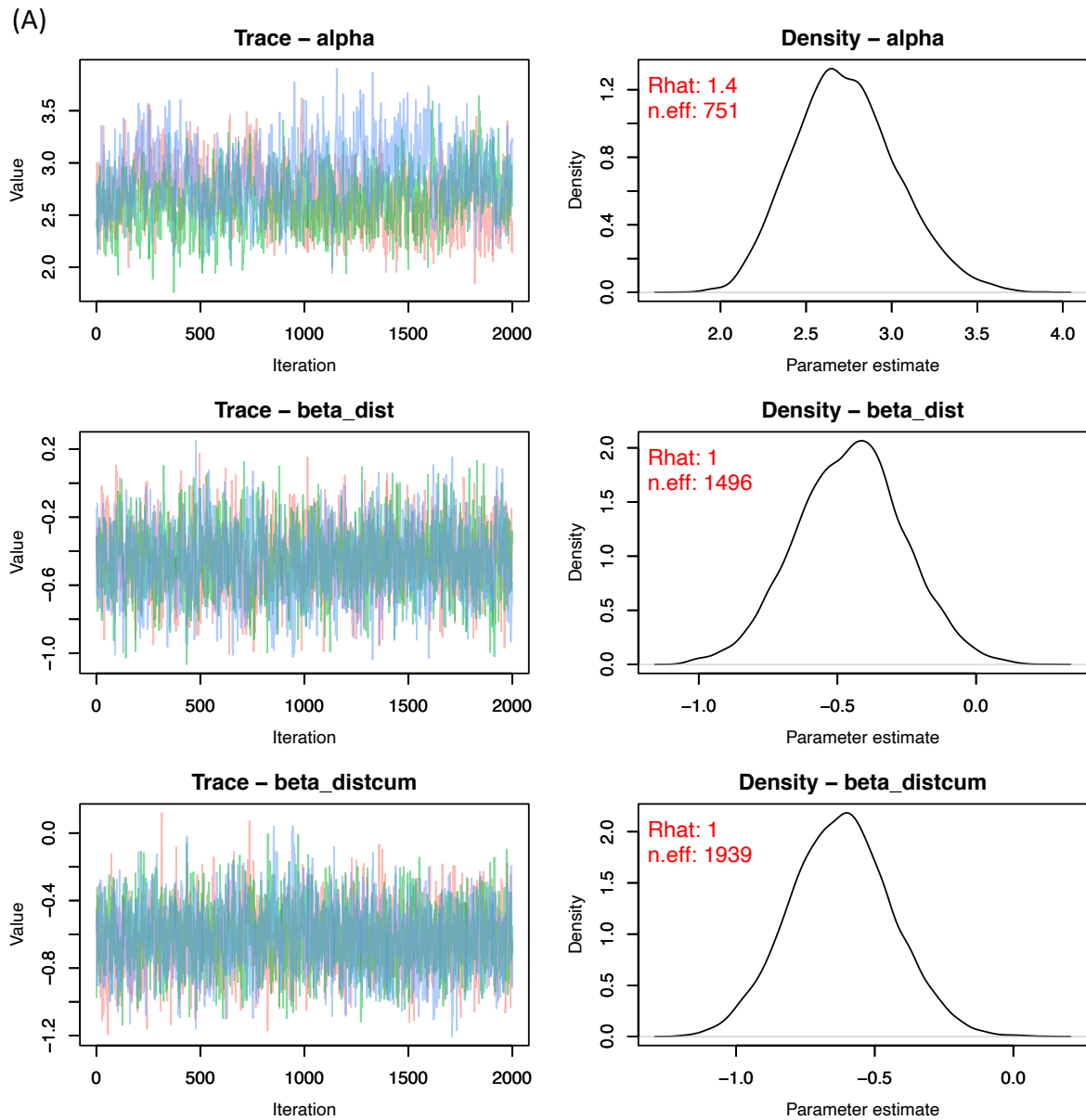
Fig. S1. Trace plots and posterior distribution of parameters estimated with (A) Model 2a and (B) Model 2b. Left panels showed the MCMC chains to check convergence of each parameter (named beta); panels on the right represent their posteriors with Gelman-Rubin value (Rhat) and effective sample size (n.eff)
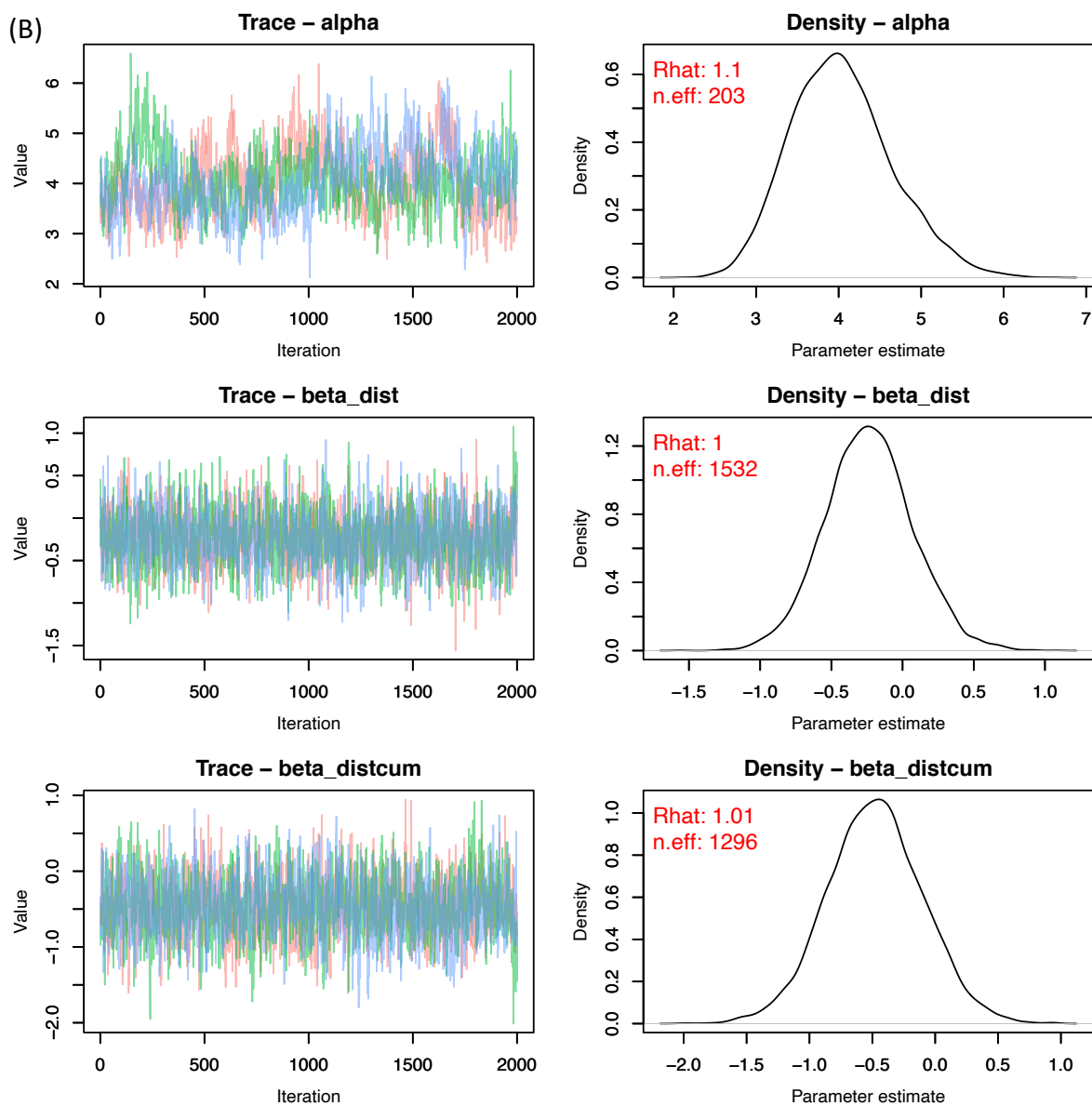
(B)

Fig. S1. (continued)