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Atlantic salmon survival during different life-stages: time to focus on improving marine survival to slow population declines

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Over the last five decades, the Atlantic salmon *Salmo salar* has suffered marked population declines across its distribution, attributed *inter alia* to overfishing, barriers to migration, climate change, aquaculture, and pollution. Conservation measures have been implemented to protect and recover this species, but little improvement in its population status has been observed. Here, we used population monitoring data to estimate the abundance of Atlantic salmon originating from the River Frome in southern England. Subsequently, juvenile (parr-to-smolt) freshwater and adult marine (smolt-to-adult) survival estimates were used to understand associations with environmental and anthropogenic factors. Annual Atlantic salmon trapping and tagging data containing more than 148,000 juveniles were analysed from 2012 to 2024. Over the study period, juvenile freshwater survival varied without a significant temporal trend, whilst marine survival decreased. Annual juvenile freshwater survival rates ranged from 7.2% to 18.3% (mean 11.6%), with their between-year variation explained by mean winter river discharge (40%). In contrast, smolt-to-one- and two-sea-winter adult marine survival rates were significantly lower, varying between 0.4% and 6.1% (mean 2.2%). Sea ice extent within the Norwegian and Greenland Seas was the most important covariate that explained the greatest amount (60%) of variation in smolt-to-adult marine survival rates. Hitherto, Atlantic salmon conservation efforts have primarily focused on protecting juvenile life-stages in freshwater. This study revealed that smolt-to-adult marine survival was 81.6% lower than parr-to-smolt freshwater survival, so much greater emphasis should be given to understanding the factors affecting their mortality at sea to protect this important life-stage. At present, Atlantic salmon are afforded almost no protection at sea, unlike other threatened marine species, and despite population declines observed across their distribution. We discuss measures required to safeguard Atlantic salmon at sea.

KEYWORDS
abundance, Atlantic salmon, capture-mark-recapture model, conservation measures, environmental and anthropogenic pressures, life-stages, survival

1 Introduction

Migratory fish are some of the most threatened taxa in the world (McDowall, 2009; Costa et al., 2021), since they rely on multiple environments and resources to complete their life history (McDowall, 1992; Chaparro-Pedraza and de Roos, 2019). Threats to such species are exacerbated when there is spatial separation between the environments they use during different life-stages (McDowall, 1992; Chaparro-Pedraza and de Roos, 2019), as is the case for diadromous fish that migrate between freshwater and marine environments (McDowall, 1992, 2009). Along their outbound and return migrations, they face a multitude of threats from dams, pollutants, habitat deterioration, fishing (targeted and bycatch), non-native species, predation, climate change, sea-regime shifts, and aquaculture, etc. (Costa et al., 2021; Thorstad et al., 2021; Dadswell et al., 2022; Gillson et al., 2022).

The Atlantic salmon *Salmo salar* (hereafter salmon) is a threatened anadromous fish that has suffered population declines across its North Atlantic range (Darwall, 2023; ICES, 2024a; Sayer, 2024). This species reproduces in freshwater from Northern Portugal to Northwestern Russia on the Eastern Atlantic coast, and from Connecticut, USA, to Canadian waters on the Western Atlantic coast (Hansen and Quinn, 1998). Eggs laid in upper river reaches hatch as 'fry', and then these fish remain in freshwater for 1–8 years to feed and grow as 'parr'. They emigrate from rivers to the sea as 'smolts', typically in spring, to their feeding grounds around Greenland and Norway (Hansen and Quinn, 1998; Klemetsen et al., 2003; Gilbey et al., 2021) for one to four 'sea winters' (winters at sea), before returning to their natal rivers to spawn (Hansen and Quinn, 1998). The timing of their migration varies latitudinally, but salmon populations mix extensively whilst at sea (Strøm et al., 2018; Rikardsen et al., 2021). Although the species continues to be commercially exploited in many areas of the North Atlantic, exploitation rate controls have been implemented to reduce fishing pressure substantially (Bull et al., 2022; Gillson et al., 2022; ICES, 2024a).

Salmon is among the most studied fish species in the world owing to its economic, recreational, and historical value (Hansen and Quinn, 1998; Thorstad et al., 2021; Gillson et al., 2022). Although recognition of the threats to the marine life-stages of salmon has received research attention relatively recently, large empirical research gaps on the factors driving variation in their survival at sea remain (Olmos et al., 2020; Thorstad et al., 2021; Utne et al., 2022). This is largely because it is difficult to observe changes in the numbers and biological characteristics of the fish at sea (Rikardsen et al., 2021; Utne et al., 2022; Artero et al., 2023; Lilly et al., 2023). It has been thought that protecting juvenile stages is the most practical strategy for the recovery of threatened salmon populations (Zabel et al., 2006; Thorstad et al., 2021). Factors influencing survival in freshwater are easier to manage than factors affecting survival at sea (Russell et al., 2012; Thorstad et al., 2021; Gillson et al., 2022). Furthermore, early life experiences in freshwater can also have carry-over effects on adult survival later in life (Nislow and Armstrong, 2012; Russell et al., 2012; Gregory et al., 2019). Nonetheless, increasingly, evidence points towards reduced marine survival as the most important contributory factor to the observed salmon population declines, given the sharp declines in returns that have occurred since the 1990s (ICES, 2024a). With this, slower growth and delayed maturation have also been observed (Bal et al., 2017; Tréhin et al., 2023). Improved understanding of their survival at sea is therefore paramount (Olmos et al., 2020; Thorstad et al., 2021; Gillson et al., 2022).

Despite the protections afforded through the North Atlantic Salmon Conservation Organisation (NASCO) and the establishment of national and international legal frameworks (e.g., OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic, Habitats Directive 92/43/EEC, etc.), salmon numbers have continued to decline (ICES, 2024a). Gillson et al. (2022) reviewed the most important stressors impacting salmon during their marine phases and assessed their threats to English stocks. Few studies have, however, used salmon population monitoring data to compare survival rates during different life-stages and to understand the multiple factors potentially causing mortality, such as predation, fisheries exploitation, food availability, sea temperature, and other climatic effects (Crozier and Zabel, 2006; Strøm et al., 2019; Gillson et al., 2022; Tyldesley et al., 2024). Furthermore, as a result of the application of varying methods to assess salmon return rates from fishery-dependent (rod catches) and -independent (salmon traps, counters and capture-mark-recapture) data, varying estimations and biases are made (Chaput, 2012; ICES, 2024a; Elliott et al., 2026). Recent efforts have focused on improving salmon return rate estimates derived from rod catches (e.g., Gregory et al., 2023), but further work is required for mark-capture-recapture techniques. Accordingly, this study aimed to: 1) estimate parr-to-smolt and smolt-to-adult survival rates from abundance estimates obtained using capture-mark-recapture methods, and 2) evaluate the environmental and anthropogenic factors that explained the most variation in these survival rates.

2 Methods

2.1 Study site and salmon population monitoring

The River Frome in Dorset, southern England, is thought to be part of the Channel salmon populations group, which experiences similar marine environmental conditions that affect marine return rates (Tyldesley et al., 2024). Further, the Frome is a chalk stream river that provides relatively stable and unique environmental conditions for salmon compared to spate rivers (Beaumont et al., 1986; Gillson et al., 2020; Simmons et al., 2020). This is because chalk rivers are fed primarily by Cretaceous groundwater upwellings, which provide stable freshwater temperatures and reduced flood peaks that are conducive to early migration (Parry et al., 2018; Simmons et al., 2020).

Every year since 2005, approximately 10,000 juvenile fish (parr) have been electro-fished (DC with a square-wave waveform fished at 50 Hz, c.200 V, and 20–30% duty cycle) in annual standardised

surveys from some 398 sites between the end of August and mid-September. The fish are anaesthetised using 2-phenoxy-ethanol, their fork length (nearest mm) and weight (g) measured, a scale sample taken, and a Passive Integrated Transponder (PIT) tag inserted into their coelomic cavity (Simmons et al., 2021a). Following recovery, all fish are returned to the river at their site of capture. Fish are aged using site-specific fork-length frequency distributions, as 0+ (young-of-the-year that hatched in spring: 60–110 mm) and 1+ parr (fish that hatched the previous year and have not migrated: 140–180 mm), or by reading scales for fork lengths of 111–139 mm. Only fish >60 mm (fork length; 2015-2023) and >70mm (2024) were tagged to reduce potential tag-related mortality (Richard et al., 2013; Vollset et al., 2020).

Migrating salmon smolts moving downstream between March and May are diverted into a side channel (the Mill Stream) of the River Frome at East Stoke using a Bioacoustic Fish Fence (BAFF; Figure 1) to facilitate capture by a Rotary Screw Trap (2006-2022) or a Wolf trap (2023 to date; hereafter referred to as a smolt trap). Although autumn migrants (migrating juveniles in the autumn period) are known to be a source of returning adults in the river (Riley et al., 2009), this population component was not considered in this study since the smolt trap is crucial to the estimates and is not in use outside the spring period.

The smolt trap is checked every 30 minutes, all tagged fish captured are anaesthetised, checked for PIT tags, their fork length (mm) and weight (g) measured, then placed in a container for recovery before being released downstream of the trap. Owing to the quantity of fish trapped, untagged fish are not aged by scales or length. Tagged smolts are aged using their birth year, as determined during parr tagging, and designated as fish aged S1 (hatched the previous year) or S2 (hatched two years earlier).

An array of four PIT antennae (detectors) has been set up on the river between East Stoke (A0, AA and A3) and Bindon (B) to record the passage of PIT-tagged fish, both as smolts undertaking their downstream seaward migration and as adults returning to the river (Figure 1). The full array of detectors enabling the use of capture-recapture methods to estimate numbers was not in place until 2012. For this study, we have therefore analysed data from 2012 to 2024.

2.2 Statistical methods

Tagged smolts undertaking a downstream seaward migration pass through Bindon first and then East Stoke (Figure 1C). In a capture-recapture context, tagged fish recorded by the Bindon detector represent a first capture event, and those detected at East Stoke (at any of A0, AA and A3) represent a second capture event, corresponding to a closed-population single mark-release experiment from which it is possible to estimate the total number of tagged fish passing through Bindon (e.g., Seber, 1982). Tagged smolts fell into four categories: ones detected at Bindon, ones detected at East Stoke, ones in common at the two locations, and ones not detected (missed). The number of tagged smolts in each category except the last one was known. We used a multinomial distribution to evaluate the number of missed tagged fish and constructed a 95% confidence interval around the abundance estimate based on a log-normal distribution of the odds-ratio, following Sadinle (2009).

Sadinle (2009) showed through simulation that these confidence intervals around the estimated number of tagged fish

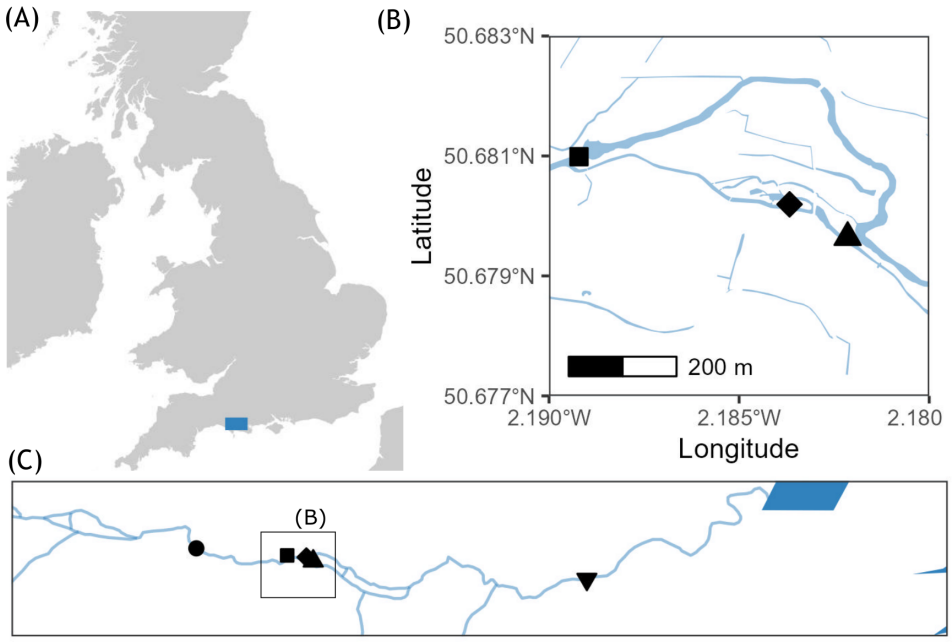

FIGURE 1
Map of the River Frome detectors and trapping locations. **(A)** Map of the UK with the study area depicted by the blue box. **(B)** Detector and trapping locations at East Stoke. East Stoke counter and detector (A0), both at the same location on the main river (black square), smolt trap and Millstream detector (AA), both at the same location on the Millstream (diamond), Downstream of Millstream detector (A3; triangle). **(C)** River Frome: Bindon detector (B, circle), East Stoke detectors (A0, AA and A3), tidal limit (inverted triangle), the upper reach of Poole harbour (the blue trapezoid).

were near the nominal level even for small samples, which was not the case for those obtained through maximum likelihood, Chapman's, or Bailey's methods (Bailey, 1951; Chapman, 1951). Moreover, the lower bound of the confidence interval is never smaller than the actual number of tagged fish that were recorded. We estimated the total number of tagged fish as the number of observed tagged fish plus the number estimated to have been missed. Empirically, estimates from this method matched the Chapman (1951) estimates when the latter were unbiased according to the criteria in Robson and Regier (1964). All statistical methods were carried out in R, version 4.4.1.

2.2.1 Estimating smolt numbers

2.2.1.1 Tagged smolts at Bindon

On average, only six S2 smolts were recorded per year, which was too few to estimate numbers. For S1 smolts, the annual total number of tagged smolts passing Bindon (TTS_B) was estimated from the annual number of individual tagged smolts aged S1 recorded by any of the three detectors A0, AA and A3 at East Stoke (TS_{ES}), those detected at Bindon (TS_B) and those detected in common at both sites ($TS_{B,\ ES}$) during the smolt period, 1 March to 31 May (Equation 1).

$$TTS_B = TS_B + TS_{ES} - TS_{B,ES} + \max\left(\frac{(TS_B - TS_{B,ES} + 0.5)\ (TS_{ES} - TS_{B,ES} + 0.5)}{(TS_{B,ES} + 0.5)} - 0.5,\ 0\right) \quad (1)$$

where $TS_B + TS_{ES} - TS_{B,ES}$ is the annual total number of tagged S1 smolts detected across Bindon and East Stoke, $\frac{(TS_B - TS_{B,ES} + 0.5)\ (TS_{ES} - TS_{B,ES} + 0.5)}{(TS_{B,ES} + 0.5)} - 0.5$ is the annual number of tagged S1 smolts estimated to have never been detected that year (Sadinle, 2009).

The lower and upper 95% confidence limits $LCL(TTS_B)$ and $UCL(TTS_B)$, respectively, of TTS_B are calculated from $SE(lnOR)$, the standard error of the annual log odds-ratio, according to Equations 2–4 (Sadinle, 2009).

$$SE(lnOR) = \sqrt{\frac{1}{TS_B - TS_{B,ES} + 0.5} + \frac{1}{TS_{B,ES} + 0.5} + \frac{1}{TS_{ES} - TS_{B,ES} + 0.5} + \frac{(TS_{B,ES} + 0.5)}{(TS_B - TS_{B,ES} + 0.5)(TS_{ES} - TS_{B,ES} + 0.5)}} \quad (2)$$

$$LCL(TTS_B) = TS_B + TS_{ES} - TS_{B,ES} + \left(\frac{(TS_B - TS_{B,ES} + 0.5)(TS_{ES} - TS_{B,ES} + 0.5)}{(TS_{B,ES} + 0.5)} e^{-1.96SE(lnOR)} - 0.5\right) \quad (3)$$

$$UCL(TTS_B) = TS_B + TS_{ES} - TS_{B,ES} + \left(\frac{(TS_B - TS_{B,ES} + 0.5)(TS_{ES} - TS_{B,ES} + 0.5)}{(TS_{B,ES} + 0.5)} e^{1.96SE(lnOR)} - 0.5\right) \quad (4)$$

2.2.1.2 Proportion of smolts tagged

The annual proportion of S1 smolts that were tagged ($PropTS_1$) was estimated as the proportion of smolts captured in the smolt trap that were tagged (Equation 5), together with its binomial standard error $SE(PropTS_1)$ (Equation 6). Although this calculation included S2 smolts, fewer than 3% of smolts were S2 on average, so any bias was minimal.

$$PropTS_1 = \frac{TS_{SmoltTrap}}{S_{SmoltTrap}} \quad (5)$$

$$SE(PropTS_1) = \sqrt{\left(\frac{PropTS_1(1 - PropTS_1)}{S_{SmoltTrap}}\right)} \quad (6)$$

where $TS_{SmoltTrap}$ is the number of tagged smolts captured in the smolt trap and $S_{SmoltTrap}$ is the total number of smolts (tagged and untagged) captured in the smolt trap. We assume that the parr-to-smolt survival is the same for tagged and untagged fish for the sizes of parr tagged (Richard et al., 2013).

2.2.2 Estimating the number of S1 smolts leaving the river

The estimated annual total number of S1 smolts at Bindon (S_B) was obtained by dividing the annual total number of tagged S1 smolts passing Bindon by the annual proportion of S1 smolts that were tagged. The lower and upper 95% confidence limits of S_{ES} ($LCL(S_B)$ and $UCL(S_B)$ respectively) were approximated using Taylor Series Linearisation ("delta method", Seber, 1982) applied separately to the lower and upper branches of the 95% confidence interval of TTS_B, treating each branch as being derived from a half-normal distribution and extracting the corresponding approximate lower and upper standard errors $LSE(TTS_B)$ and $USE(TTS_B)$ (Equations 7–13).

$$S_B = \frac{TTS_B}{PropTS_1} \quad (7)$$

$$LSE(TTS_B) = \frac{TTS_B - LCL(TTS_B)}{1.96} \quad (8)$$

$$USE(TTS_B) = \frac{UCL(TTS_B) - TTS_B}{1.96} \quad (9)$$

$$LSE(S_B) = S_B\sqrt{\left(\frac{LSE(TTS_B)}{TTS_B}\right)^2 + \left(\frac{SE(PropTS_1)}{PropTS_1}\right)^2} \quad (10)$$

$$USE(S_B) = S_B\sqrt{\left(\frac{USE(TTS_B)}{TTS_B}\right)^2 + \left(\frac{SE(PropTS_1)}{PropTS_1}\right)^2} \quad (11)$$

$$LCL(S_B) = S_B - 1.96\ \ LSE(S_B) \quad (12)$$

$$UCL(S_B) = S_B + 1.96\ \ USE(S_B) \quad (13)$$

2.2.3 Estimating the number of adults returning to the river

2.2.3.1 Tagged adults at East Stoke

Similar to smolts, the detections of returning adults heading upstream also constituted a closed-population single mark-release experiment. The difference was one of directionality, with the first detection being at East Stoke (either on the main river or the Mill stream) and the second at Bindon. The estimated annual total number of tagged adults (TTA_{ES}) per sea winter returning was calculated from Equation 14 (the sea winter of an adult was determined by the number of years spent at sea since it was detected as a smolt). We restricted abundance estimates to one-sea-winter (1SW) and two-sea-winter (2SW) adults because only five 3SW fish were recorded between 2012 and 2024.

$$TTA_{ES} = TA_B + TA_{ES} - TA_{B,ES} \tag{14}$$

$$+ \max\left(\frac{(TA_B - TA_{B,ES} + 0.5)(TA_{ES} - TA_{B,ES} + 0.5)}{TA_{B,ES} + 0.5} - 0.5,\ 0\right)$$

where TA_B and TA_{ES} were the number of returning tagged adults per sea winter detected at Bindon and East Stoke, respectively, while $TA_{B,ES}$ was the number in common across the two sites.

The lower and upper 95% confidence limits $LCL(TTA_{ES})$ and $UCL(TTA_{ES})$ around TTA_{ES} follow Equations 2–4, replacing tagged smolts with tagged returning adults.

2.2.3.2 Total number of returning adults at East Stoke

The annual total number of returning adults per sea winter at East Stoke (A_{ES}) was obtained by dividing the annual total number of tagged adults at East Stoke by the annual proportion of tagged smolts in the corresponding smolt year (Equation 15). We assume that smolt-to-SW1 and smolt-to-SW2 survival is the same for tagged and untagged fish.

$$A_{ES} = \frac{TTA_{ES}}{PropTS_1} \tag{15}$$

Where $PropTS_1$ is the proportion of tagged in the cohort of S1 smolts to which the returning SW1 or SW2 adults belonged (section 2.2.1.2). The lower and upper confidence limits for returning adults per sea winter were constructed in the same way as for smolts (Equations 8–13).

2.2.4 Survival estimates

2.2.4.1 Survival from 0+ parr to S1 smolt

Annual survival from 0+ parr to S1 smolt (s_S) was calculated as the ratio of the estimated total number of tagged S1 smolts passing through Bindon (TTS_B) to the total number of 0+ parr tagged (TTP) the year before (Equation 16), noting that the latter was a straight count with no error attached to it (for 0+ parr abundance estimates refer to Supplementary Figure S1). Its 95% confidence limits $LCL(s_S)$ and $UCL(s_S)$ were obtained from the 95% confidence limits of TTS_B in the same way (Equations 17, 18).

$$s_S = \frac{TTS_B}{TTP} \tag{16}$$

$$LCL(s_S) = \frac{LCL(TTS_B)}{TTP} \tag{17}$$

$$UCL(s_S) = \frac{UCL(TTS_B)}{TTP} \tag{18}$$

2.2.4.2 Survival from smolt to returning adult

Return rates were used as a proxy for overall smolt-to-adult survival, and from here on we refer to this as smolt-to-1SW and -2SW survival. Survival from smolt to adult per sea winter (s_A) was calculated as the ratio of the estimated annual total number of returning adults per sea winter (A_{ES}), to the estimated annual total number of smolts for the matching smolt year (S_B; Equation 19), assuming that all fish return to their natal river. The 95% confidence limits were calculated using Taylor Series Linearisation (Seber, 1982) applied separately to the lower and upper branches of the 95% confidence intervals of A_{ES} and S_B, treating each branch as being derived from a half-normal distribution and using the corresponding lower and upper standard errors (Equations 20–23).

$$s_A = \frac{A_{ES}}{S_B} \tag{19}$$

$$LSE(s_A) = s_A\sqrt{\frac{LSE(A_{ES})^2}{A_{ES}^2} + \frac{LSE(S_B)^2}{S_B^2}} \tag{20}$$

$$USE(s_A) = s_A\sqrt{\frac{USE(A_{ES})^2}{A_{ES}^2} + \frac{USE(S_B)^2}{S_B^2}} \tag{21}$$

$$LCL(s_A) = s_A - 1.96\ \ LSE(s_A) \tag{22}$$

$$UCL(s_A) = s_A + 1.96\ \ USE(s_A) \tag{23}$$

2.3 Environmental variables

2.3.1 Choice of environmental variables

Environmental and anthropogenic variables with the potential to explain variation in Frome salmon survival during both parr-to-smolt and smolt-to-adult life-stages were chosen based on a review of the literature (Table 1). These included temperature-related variables (river temperature, sea-surface temperature (SST) surrounding Poole harbour, river-to-sea temperature differential, and temperatures in known salmon feeding areas in the Norwegian sea); winter river discharge; distance travelled from sites where parr were caught to smolt traps; parr and smolt mean length; climatic variables (sea-ice extent acting as a thermal front, North Atlantic Oscillation (NAO) and Atlantic Multi-decadal Oscillation (AMO),

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TABLE 1 Covariates retained to explore the survival of salmon during their parr-to-smolt and smolt-to-adult life-stages: measurement method, quantitative description, data source, years(s) imputed and justifying literature.

Variable	Method used	Shorthand	Variable characteristic	Source	Imputation year	Reference
Parr-to-smolt survival covariates						
River discharge (m^3/s^{-1})	Daily river discharge averaged over the parr tagging period (August-September) to the end of smolt migration (31 May).	Discharge	Mean: 7.73 Range: 4.36-11.03	Environment Agency	2024	(Crozier and Zabel, 2006; Nislow and Armstrong, 2012; Gillson et al., 2020; Simmons et al., 2021b)
	The monthly standard deviation of river discharge between parr tagging and the end of smolt migration (variation).	Discharge V	Mean:0.48 Range: 0.36-0.66			
Freshwater temperature (°C)	Daily freshwater temperature averaged between 15/08 - 31/05.	Temp	Mean: 11.20 Range: 10.10-11.92	Temperature loggers	None	(Simmons et al., 2021b)
	Variation in the freshwater temperature between 15/08 and 31/05.	Temp V	Mean: 0.26 Range: 0.18-0.34			
	Daily freshwater temperature averaged over the autumn, winter and spring seasons from parr tagging to smolt trapping	Au Temp 16/10 - 30/11	Mean: 10.41 Range: 9.25-11.46			(Crozier and Zabel, 2006)
		Wi Temp 01/12 - 14/03	Mean: 8.57 Range 7.78-9.63			
		Sp Temp 15/03-31/05	Mean: 11.76 Range 10.36-12.57			
Parr length (mm)	Yearly average length of parr when tagged.	Parr length	Mean: 93 Range: 88-100	Frome parr tagging	None	(Gregory et al., 2017, 2020)
Freshwater migration distance (km)	Distance between East Stoke and the tagging site.	Distance	Mean: 15.08 Range: 12.21-18.13	Frome parr tagging	None	(Artero et al., 2023; Simmons et al., 2021a)
Smolt-to-adult survival covariates						
Temperature (°C)	Difference in monthly water temperature between the lower river and nearshore from March to June.	River-SST	Mean: 1.48 Range: 0.78-2.30	Temperature loggers and NOAA	None	(Simmons et al., 2021a; Tyldesley et al., 2025)
	Monthly SST averaged across the smolt period outside Poole harbour.	P SST	Mean: 12.89 Range: 11.94-13.67	NOAA		(Beaugrand et al., 2003; Rikardsen et al., 2002; Strøm et al., 2018, 2019; Gilbey et al., 2021)
	Monthly SST averaged across the year within thermal fronts identified as being a salmon key feeding area in the Norwegian Sea (Supplementary Figure S2).	M TF SST	Mean: 3.81 Range: 3.26-4.46			
	Variation in the SST within the thermal fronts in the Norwegian Sea (Supplementary Figure S2).	TF SST V	Mean: 0.61 Range: 0.56-0.73			
Arctic water	An index of cold Arctic water flowing northeast of Iceland and into the Norwegian Sea.	Arctic water	Mean: 0.32 Range: 0.01-0.79	ICES, 2024b	None	(Skagseth et al., 2022; Utne et al., 2022)
Sea ice extent (km)	Quantity of winter sea ice off Eastern Greenland and within the Norwegian Sea predicted winter-feeding grounds recorded January 1 each year (Supplementary Figure S3).	Sea ice extent	Mean: 12.71 Range: 2.64-36.11	met.no/en	None	(Strøm et al., 2018, 2019; Copeland et al., 2024)
Sub-polar gyre index	The first Principal Component (PC1) of an Empirical Orthogonal Function Analysis (EOFA) of the sea level anomaly field in the North Atlantic recorded on an annual basis.	SPGI	Mean: -0.48 Range: -46-1.02	ICES, 2024b	2024	(Hátún et al., 2009; 2016; ICES, 2024b)

(Continued)

TABLE 1 Continued

Variable	Method used	Shorthand	Variable characteristic	Source	Imputation year	Reference
Smolt-to-adult survival covariates						
North Atlantic Oscillation	The mean annual index of changes in strength of two pressure patterns over the North Atlantic Ocean, a low near Iceland and a high near the Azores (recorded monthly).	M NAO	Mean:0.13 Range: -0.42-1.01	NOAA	None	(Crozier and Zabel, 2006; Hátún et al., 2016; ICES, 2024b)
Atlantic Multi-decadal Oscillation	An area average of detrended low pass filtered North Atlantic monthly SST anomalies.	M AMO	Mean: 0.70 Range: 0.41-1.21	NOAA	None	(Friedland et al., 2009)
Poole harbour water quality during the smolt period	First principal component from a PCA of Ammonia, BOD, Chlorophyll acetone, Iron, N, dissolved and saturated and chemical oxygen demand, pH, suspended solids (Supplementary Figure S4).	Water quality	Mean: -0.20 Range: -4.47-1.53	Environment Agency	None	(Alabaster and Lloyd, 1982; Cabral et al., 2019)
Pelagic commercial landings (t)	Marine pelagic fisheries landings thought to be a bycatch risk during the post-smolt migration year within areas where Frome smolts migrate (Supplementary Figure S5).	Pelagic fisheries	Mean: 476, 302 Range: 383, 344-587, 862	ICES	2023 used for 1SW covariates	(Elliott et al., 2023; ICES, 2023a)
Predation on leaving the river	Great cormorant numbers during the smolt period on the lower Frome and Poole harbour. Insufficient data were available for other predatory bird species.	Cormorant	Mean: 94 Range: 12-475	British Trust for Ornithology – Wetland Bird Survey	None	(Dieperink, 2002; ICES, 2023b)
Smolt Length (mm)	Average length of tagged smolts.	Smolt length	Mean: 139 Range: 136-144	GWCT data	None	(Gregory et al., 2018; Simmons et al., 2021a)

Sub-Polar Gyre Index (SPGI)); river and estuarine water quality; commercial fishery landings; predation (numbers of great cormorant *Phalacrocorax carbo* - both in the river and Poole harbour, and European seabass *Dicentrarchus labrax*); and competitors (numbers of pink salmon *Oncorhynchus gorbuscha* whilst Atlantic salmon are in their feeding areas in the Norwegian and Greenland seas).

The average monthly river-to-sea temperature differential and SST outside Poole harbour during the smolt period (March-May) incorporated data to the end of June since it may take a few weeks for smolts to migrate out to sea (Table 1; Artero et al., 2023). Commercial landings from marine pelagic fisheries were examined as a proxy for bycatch of salmon at sea (Elliott et al., 2023; ICES, 2023a). SST within the Norwegian Sea (M TF SST) and sea ice extent along the east coast of Greenland, both thought to be thermal front areas which may be key feeding areas, were identified from the literature.

For covariates missing data from one year (e.g., from 2020, the year of COVID-19 pandemic), a value for the missing year was imputed using the impSeqRob function in the R package 'rrcovNA' (Todorov et al., 2011). Covariates missing more than one year of data were not considered for further analysis and removed from Table 1. These included parr-to-smolt period river water quality, predators, except the great cormorant (European seabass (Riley et al., 2011; Simmons et al., 2021a) and avian predators on the river (British Trust for Ornithology – Wetland Bird Survey; Dieperink, 2002), and competitors [pink salmon (ICES, 2018; Sandlund et al., 2019)].

The commercial exploitation of salmon by directed fisheries in the marine environment was not considered in this study, because it has decreased drastically since the 1990s (ICES, 2024a) and is not regarded as currently significantly impacting English salmon stocks (Gillson et al., 2022). The Faroese salmon fishery has been closed since 1991 (Jacobsen et al., 2012). A salmon fishery is in operation along the coast of West Greenland, but the exploitation rate has been low since the mid-1990s (ICES, 2024a). Further, the exploitation rates for salmon originating from southern Europe have been 0-3% since 1993 (ICES, 2024a).

Too few years of data were available to fit interactions among covariates. We disregarded parr density and their dependence (Milner et al., 2003; Einum et al., 2006) and site-specific habitat variables because density estimates and habitat mapping were undertaken at only 25 of the 398 sites where fish tagging takes place.

2.3.2 Relating survival to environmental variables

To improve the normality of the error distribution, annual survival estimates s of parr-to-smolt and smolt-to-adult were logit-transformed ($z = \log\left(\frac{s}{1-s}\right)$) before analysis (Crozier and Zabel, 2006). For parr-to-smolt survival, the analysis took into account the magnitude of the error attached to each survival estimate by weighting each point by a quantity $w = \frac{1}{SE(z)^2}$ where $SE(z) =$

$\frac{1}{2}\frac{LSE(s)+USE(s)}{s(1-s)}$ approximated the standard error of z. For smolt-to-adult survival, since the $USE(s)$ was so large, weighting was undertaken using $\frac{1}{USE(z)^2}$ where $USE(z) = \frac{USE(s)}{s(1-s)}$ approximated the standard error (upper branch) of z.

The logit-transformed annual survival rates z with weights w were then used as a response variable and modelled against the covariates using a General Linear Model (GLM). All covariates were standardised to have a mean of 0 and a variance of 1 before modelling. Given the small nature of the dataset, variables with a Variance Inflation Factor >5 and absolute value of Pearson's correlation coefficient >0.5 were removed to ensure no collinearity, using the 'corrplot' package in R (Dormann et al., 2013). All models were checked for temporal autocorrelation using 'ACF plots' and for normality of residuals using a Durbin-Watson Test using the CAR package.

First, a weighted Pearson's correlation coefficient was used to find variables significantly related to the survival of salmon (Supplementary Tables S1, S2). The significant variables were then modelled jointly in a stepwise GLM with an entry and remove criterion of partial correlation > 0.5 to avoid Type 1 errors caused by multiple testing. For adult survival, the GLM included sea winter age (as a categorical variable) for a unified analysis of 1SW and 2SW survival in relation to the covariates. After selection, interations between sea winter age and the selected covariates were included in the model to check that regression slopes did not differ according to sea winter age.

3 Results

3.1 Smolt abundance and parr-to-smolt survival estimates

Table 2 shows the numbers of tagged 0+ parr, S1 and S2 smolts detected, and total smolts trapped the following year, and corresponding 1SW and 2SW adult salmon detected. Using the Sadinle (2009) abundance estimates, between 2012 and 2024, annual smolt numbers were estimated to range from 4164 (2017) to 23,092 (2024), with a mean of 10,113 ± 1361 SE (mean UCL = 11, 586 and LCL = 8719; Figure 2A).

Mean parr-to-smolt survival was estimated to be 11.57% ± 0.82% SE (range = 7.23-18.30%; Figure 3B). No overall increase or decrease in parr-to-smolt survival estimates was observed over the period analysed (Supplementary Table S1). However, variation in survival among years was observed, with the 2020 and 2024 survival of parr-to-smolts the highest (above 14%), and 2012 and 2019 survival the lowest (below 9%; Figure 2B).

Since only discharge was significantly correlated with survival, collinearity between variables was not a problem (Figure 3A; Supplementary Table S1). The slope of mean river discharge (on the logit scale) was 0.15 ± 0.05 SE, P<0.05, with an R^2 of 0.40 ($F_{1,\ 11} = 7.28$, P<0.05; Figure 4).

3.2 Adult return estimates and smolt-to-adult survival

The number of tagged returning adults varied between 4 and 42 individuals for 1SW fish and 6 and 24 individuals for 2SW fish (Table 2). Using the Sadinle (2009) estimates, between 2012 and 2024, the average number of returning 1SW adults was 248 ± 61 SE (mean UCL = 2023 and mean LCL = 151, range: 40-860; Figure 5A) and 133 ± 15 SE (mean UCL = 475 and mean LCL = 101, range: 73-243) for 2SW adults. Extremely large UCL values for 1SW adults were obtained in 2014 (15,407) and 2022 (5,120), when there were no tags in common between East Stoke and Bindon. The combined abundance estimate of 1SW and 2SW fish is in line with salmon counter estimates (Supplementary Figure S5; $R^2 = 0.546$, P = 0.015, slope = 0.62 ± 0.20 SE).

There appears to be a shift in the relative proportions of returning 1SW and 2SW fish, with 1SW fish outnumbering 2SW fish in nine out of ten years from 2012 to 2021, but the reverse from

TABLE 2 The numbers of 0+ parr tagged, S1 and S2 smolts detected, total smolts trapped the following year, and the subsequent detections of 1SW and 2SW adults returning to the River Frome.

Parr tagging year	0+ parr tagged	S1 detected	S2 detected	Total smolts	1SW	2SW
2011	5597	224	20	2673	9	6
2012	8498	342	4	4251	10	13
2013	10,244	464	3	2508	12	11
2014	8607	226	1	1812	42	17
2015	8353	236	1	2859	31	11
2016	4632	148	12	1108	15	11
2017	10,444	144	1	1615	12	13
2018	10,024	127	5	1672	30	8
2019	9998	181	2	1672	29	24
2020	7855	173	11	1597	10	9
2021	10,027	227	5	2305	4	6
2022	8318	193	10	1942	5	NA
2023	9591	179	0	2355	NA	NA

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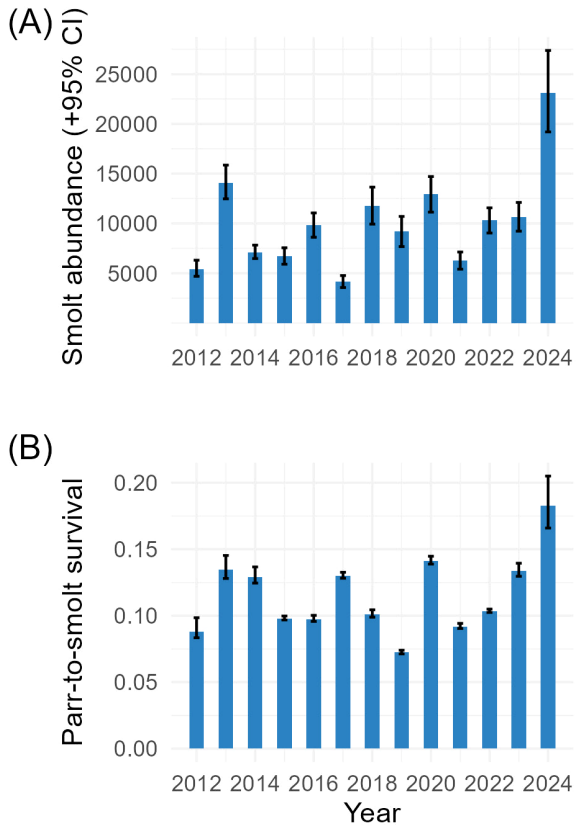

FIGURE 2
Bar plots of **(A)** smolt abundance and **(B)** parr-to-smolt survival estimates, with 95% confidence intervals. Year corresponds to the smolt migration year.

2022 onwards. Mean smolt-to-adult survival for 1SW fish was estimated to be 2.82% ± 0.52 SE (range = 0.39-6.12%) between 2013 and 2024. Mean smolt-to-adult survival for 2SW fish was estimated to be 1.57% ± 0.14 SE (range = 0.71-2.27%; Figure 5B) between 2014 and 2024. A significant decline in smolt-to-adult survival was observed over the period of data collection (Supplementary Table S2).

The individual means for each smolt-to-adult cohort (1SW and 2SW) survival estimates were 75.57% and 87.56% (average 81.57%) lower than the mean of parr-to-smolt survival, showing a much higher rate of mortality, albeit over a longer time-span. Taking average time-spans (from data collection) as 303 days for parr-to-smolt survival (September to June the following year), 426 days (July to September the following year) for 1SW survival, and 730 days (1 year and 11 months later) for 2SW survival, the corresponding annualised rates are 7.44%, 4.70% and 12.53% respectively.

The minimum adequate model for smolt-to-adult survival, considering sea winter age, included just sea ice extent with a negative coefficient (slope = -0.43 ± 0.08 SE on the logit scale; $F_{2,\ 20} = 76.12$, $P<0.001$) and a partial R^2 accounting for just sea ice extent of 0.60 (Figure 6). Initially, correlation coefficients (Supplementary Table S2) were also significant for SPGI and Arctic water. However, these variables were collinear with sea ice extent, so were subsequently removed (VIF > 5; Figure 3B; Supplementary Table S3). There was no significant interaction between sea ice and sea winter age ($F_{1,\ 19} = 1.59$, $P>0.05$).

4 Discussion

We aimed to obtain accurate salmon abundance estimates using PIT-tag capture-mark-recapture data adapted to small sample sizes. Subsequently, we used those estimates to derive survival rates during freshwater (parr-to-smolt) and subsequent (smolt-to-adult) life-stages and identify associations between those survival rates and a range of external factors. Despite large confidence intervals on smolt-to-adult survival estimates due to low numbers of returns, we identified several variables that explained variation in the survival rate estimates of salmon from the River Frome. Our

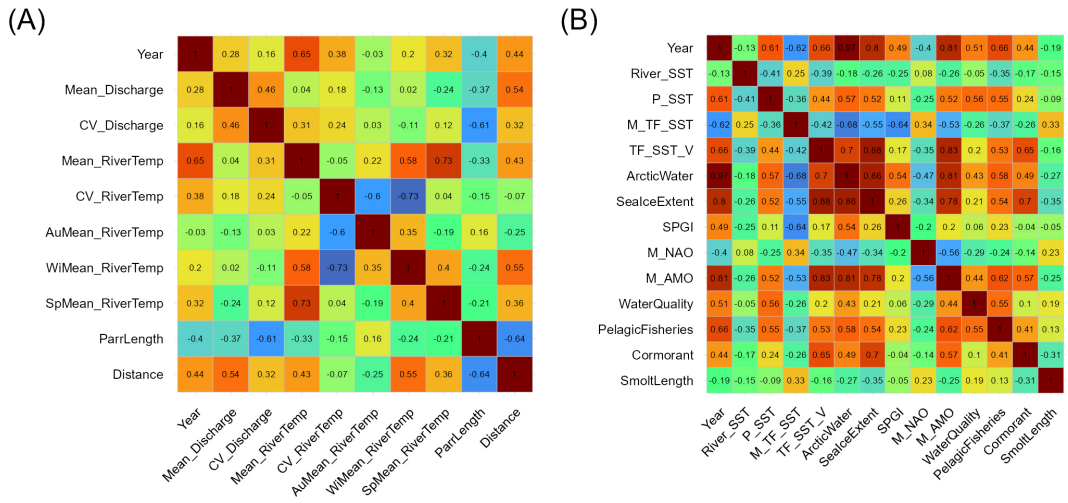

FIGURE 3
(A) Parr-to-smolt and **(B)** smolt-to-adult covariate correlation matrices used to identify collinearity. See Table 1 for covariate abbreviations.

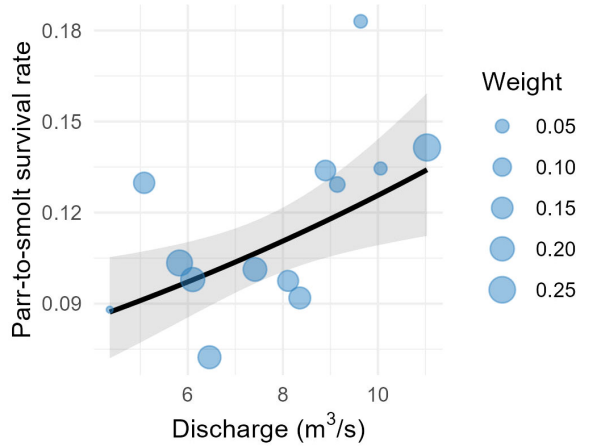

FIGURE 4
Parr-to-smolt survival model of best fit with mean river discharge (back-transformed from logit scale). The shaded area represents the 95% confidence interval of the fitted values. The size of the blue circles reflects the error-derived weights associated with each survival estimate.

findings have implications for future salmon stock assessment due to the application of a statistically robust method to improve the quantification of salmon survival estimates from capture-mark-recapture data, and the empirical identification of important factors affecting their survival.

4.1 Survival from parr to smolt

Out of nine covariates explored, only mean river discharge was significantly associated with parr-to-smolt survival. Higher parr-to-smolt survival estimates were observed in years with high river discharge (e.g., smolt years 2020 and 2024), and lower parr-to-smolt survival estimates were evident in years with lower river discharge (e.g., smolt years 2012 and 2019). Discharge is thought to be a master variable influencing environmental factors in rivers (Arthington, 2012), with high flows positively affecting salmon migrations and survival (Nislow and Armstrong, 2012). High river discharges may have increased parr-to-smolt survival by enabling juveniles to access additional food and territory in otherwise inaccessible areas (which are more prevalent in groundwater-fed rivers) of the catchment under elevated water levels (Moir et al., 2004; Nislow and Armstrong, 2012; Parry et al., 2018). The low survival rate observed in 2019 may also be because of below average parr length, which is known to affect their survival (Gregory et al., 2018). Although other variables have been shown to influence juvenile abundance and migration timing (e.g., temperature and parr length; Gregory et al., 2020; Simmons et al., 2021b), we worked at the whole catchment scale and at the annual level (2012-2024) of just 0+ parr to S1 smolt survival. This may have led to fine-scale associations being lost in this analysis because of averaging variables across the river and year.

Poor salmon recruitment in many European rivers occurred in 2016 (Gregory et al., 2020). Gregory et al. (2020) showed that this recruitment crash coincided with warmer spawning temperatures and higher flood frequencies during pre-emergence, which could have inhibited reproductive success and washed-out eggs. Smolt abundance in the River Frome was also low in 2017 following the 2016 recruitment crash (Supplementary Figure S1). However, survival was higher, possibly due to density-dependent effects lowering competition among parr for food and territory in the river (Milner et al., 2003; Einum et al., 2006; Gregory et al., 2020).

4.2 Survival from smolt to returning adult

Even though juvenile stages are thought to be most important for population persistence (Zabel et al., 2006; Einum et al., 2008; Nislow and Armstrong, 2012), we found that the survival rate estimates for smolt-to-1SW and -2SW-adults were on average 81.6% lower than the parr-to-smolt survival estimate, and within the range of the return rates recorded for other rivers (~3-7%; Chaput, 2012; ICES, 2024a). This lower return rate corroborates other research (e.g., Hansen and Quinn, 1998; Olmos et al., 2020; Thorstad et al., 2021) and highlights the importance of

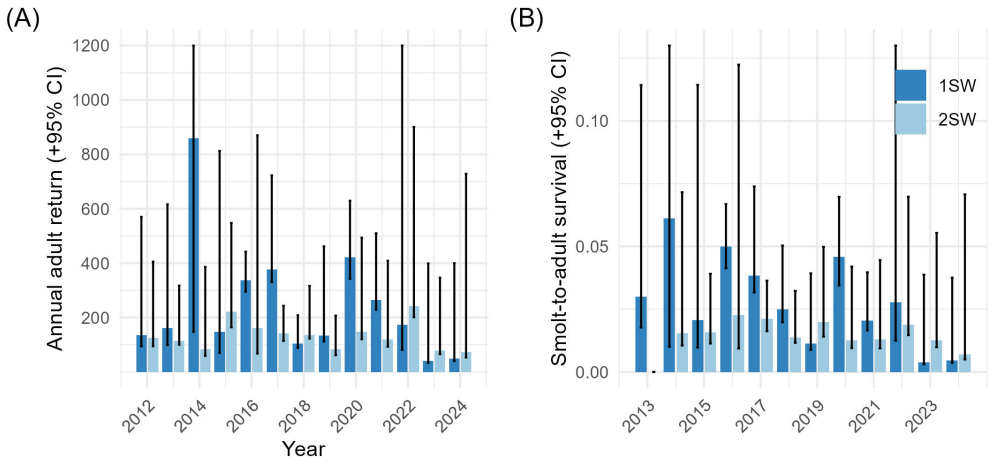

FIGURE 5
Bar plots of **(A)** annual numbers of returning adults and **(B)** smolt-to-adult survival estimates, with 95% confidence intervals. Dark blue bars represent 1SW adults, and light blue ones denote 2SW adults. Note: the UCL values for 1SW adult returns in 2014 and 2022 are off the scale. Year corresponds to the adult return year.

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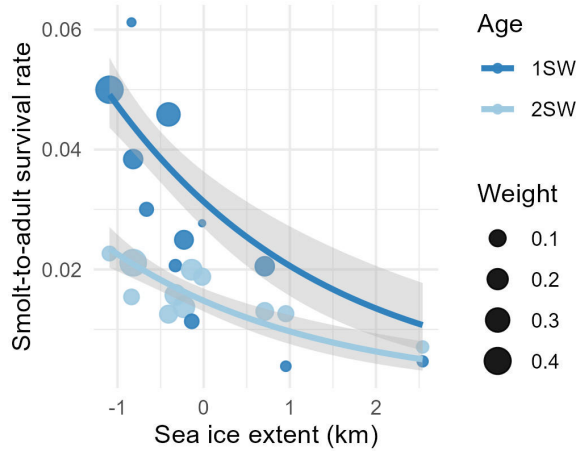

FIGURE 6
Smolt-to-adult survival in relation to sea ice extent (back-transformed from the logit scale). The shaded area represents the 95% confidence interval of the fitted values. The size of the circles reflects the error-derived weights associated with each survival estimate.

understanding marine return rates in salmon conservation. Although the period between smolt-to-adult survival (~14 months for 1SW and ~23 months for 2SW salmon) is much greater than that of parr-to-smolt survival (~9 months), the annualised survival rate for 1SW salmon is 4.7% versus 7.4% for parr-to-smolt (37% lower than that for parr-to-smolt). This low survival highlights the perils of the first year at sea for salmon regardless of the time-span (Artero et al., 2023; Thorstad et al., 2012).

Marine return rates are not always a good proxy for survival at sea because they can be confounded by differences in the homing ability of adult salmon returning to their natal rivers (straying rate is thought to range from 2.2-6%; Potter and Russell, 1994; Jonsson et al., 2003) and variation in maturation (Chaput, 2012). Survival rates here were estimated from tagged smolts to returns by sea-age, rather than combining multiple cohorts into a multi-sea-winter fish category (e.g., ICES, 2024a). The length of time salmon spend out at sea varies depending on sex and population-specific maturation norms and on environmental conditions (Bal et al., 2017; Tréhin et al., 2023). The lack of incorporation of 3SW fish would also not have affected the results since only five 3SW individuals were detected between 2012 and 2024. Although our estimations were in line with the resistivity counter estimates, differences observed may be because of over-estimations and biases of counter methods, given the difficulty in distinguishing between salmon and trout, and their age (Elliott et al., 2026). Further, the estimated annual return rates per sea winter shown here include large UCL error bars. Unfortunately, at present, counter estimates do not include uncertainty estimates (ICES, 2024b). If the return estimates are lower than those used in the annual salmon stock assessments, then stock status could be worse than thought. Further work is required to confirm this.

Despite a wide range of possible covariates (13) explored to understand factors affecting smolt-to-adult survival, the variables explaining the most variation were climate-related, as reported by Gillson et al. (2022). Not all variables were able to be considered owing to their incompleteness or availability (e.g., some salmon predators, salmon prey, and competitors). The model of best fit for both 1SW and 2SW return rates was sea ice extent within the Norwegian and Greenland Seas, which is affected by global temperatures. Associations between smolt-to-adult survival and sea ice extent have not been directly reported in the literature before, and several underlying mechanisms could exist. Firstly, feeding conditions east of Greenland and in the western Norwegian Sea may be poorer during periods of high sea ice cover, and as it melts, immediately cooler sea water temperatures lead to better feeding conditions (Martin and Mitchell, 1985; Beaugrand and Reid, 2003; Tyldesley et al., 2024). Secondly, there could be increased overlap with predators in cold years (Suuronen and Lehtonen, 2012). Seal predation on salmon in this region has not been documented, and whether interactions occur is still an untested hypothesis. Lastly, sea ice extent may be correlated with another factor not yet tested.

Key 1SW salmon feeding areas have been seen along oceanic fronts in the western Norwegian Sea (Strøm et al., 2018, 2019; Rikardsen et al., 2021). These oceanic fronts can shift geographically, and the quantity and quality of prey available to salmon within these front areas probably have interannual variations that influence trophic energy transport (Jonsson et al., 2016; Gilbey et al., 2021; Tyldesley et al., 2024). This may have led to variation in SST within the Norwegian Sea thermal front (TF SST V) feeding areas not being statistically important. Sea ice extent may, however, be acting as a thermal front further west (Sloth and Buch, 1988). Alternatively, the Frome stock may migrate further west than previously thought or migrate to different frontal areas according to different environmental conditions (Gilbey et al., 2021).

Negative associations between smolt-to-adult survival and SPGI and Arctic water were observed, however, to a lesser extent than that of sea ice extent. Our results corroborate previous studies, which have shown that salmon experience climate-induced changes in marine survival (Friedland et al., 1998; Limburg and Waldman, 2009; Robinson et al., 2009; Utne et al., 2022). Climate change is not only known to alter and shift species distribution, but also the timings of migration and spawning, potentially causing a phenological mismatch and thereby affecting feeding opportunities and growth (Limburg and Waldman, 2009; Robinson et al., 2009; Perry et al., 2010; Thorstad et al., 2021).

Between 2012 and 2021, adult returns to the River Frome predominantly comprised 1SW fish. In the past few years (2022 to date), relatively more 2SW fish have been observed returning to the river. Such shifts in the sea age composition of salmon stocks have been reported in the past (Bielak and Power, 1986; Heddell-Cowie, 2005), and this shift to a smaller proportion of 1SW returns has been observed more recently (since 2000) across Northeast Atlantic stocks (ICES, 2024a). The apparent shift to more time spent at sea and a reduction in returning fish is thought to be because of worsening conditions (Utne et al., 2021; Gillson et al., 2022), leading to slower growth and delayed maturation (Bal et al., 2017; Tréhin et al., 2023).

4.3 Conservation measures

Despite declines in salmon being widespread across their distribution (ICES, 2024a) and being largely attributed to reduced marine survival, little progress has been made to protect salmon whilst at sea. Much greater emphasis needs to be given to salmon conservation measures at-sea "to support and promote urgent and transformative actions" at regional, national and international levels (NASCO, 2024). It is common to believe that little can be done to mitigate large-scale anthropogenic pressures at sea (Russell et al., 2012; Thorstad et al., 2021). However, marine conservation measures are applied to other threatened and commercially important species (e.g., the bluefin tuna, and a range of chondrichthyan species; Heffernan, 2014; Lascelles et al., 2014). Measures during both salmon's freshwater and marine life-stages can be implemented to help protect and restore them (e.g., Thorstad et al., 2012; Gregory et al., 2018; Verhelst et al., 2021; Utne et al., 2022). Here we list a series of measures that consider the results from this research and other studies, which could help slow the decline of salmon populations when considering their full migratory paths.

1. Implementation of national and international climate mitigation measures: Tackling climate change impacts requires both national and international action, and measures to reduce greenhouse gas emissions are critical (IPCC, 2024). Since 2021, climatic conditions have become more variable, with records for the driest and wettest seasons being set regionally (Schneider et al., 2013; IPCC, 2024). Given previously observed carry-over effects from freshwater to marine environments (Gregory et al., 2019; Crozier et al., 2021), buffers to protect and restore salmonid freshwater environments need to be introduced. For example, judicious tree planting can help stabilise freshwater temperatures, reduce sedimentation, minimise habitat deterioration, and increase water retention (Crozier and Zabel, 2006; Thorstad et al., 2021). Good freshwater, estuarine and marine water quality and habitat heterogeneity promote biodiversity and limit the impacts of temperature fluctuations (Thorstad et al., 2021; Gillson et al., 2022; Marsh et al., 2022).
2. Implementing spatial and temporal protection measures at sea: Eighteen salmon rivers in England and Wales, including the River Frome, have been designated as freshwater Special Areas of Conservation (SACs) under the Habitats Directive (92/43/EEC), providing salmon protection (NASCO, 2009). Protecting salmon through Marine Protected Areas (MPAs) in the Northeast Atlantic is an OSPAR commission requirement (https://www.ospar.org/work-areas/bdc/species-habitats/implementation-of-species-and-habitat-recommendations; OSPAR, 2017). Despite this, no MPA or spatial measure has been implemented at sea or across salmon migration corridors (including estuarine migratory passages) in the UK to protect the species, despite the benefits of protecting these pelagic habitats and the effects of high marine mortality on population persistence being known. At present, the current network of MPAs largely protects benthic features (Defra, 2025). Mortality rates within estuarine habitats are also known to be high for diadromous fish (McDowall, 1992; Artero et al., 2023; Elliott et al., 2023). Greater protection should be given to salmon in these transitional waters and the high seas feeding areas.

   Salmon of European origin are known to migrate to Norwegian and Greenlandic waters (Hansen and Quinn, 1998; Gilbey et al., 2017). Although the bycatch of salmon in marine pelagic fisheries operating in these waters appears to be low (Elliott et al., 2023), protecting key feeding areas and reducing catch (Dadswell et al., 2022; including bycatch) within those waters at specific periods and depths could improve feeding conditions and salmon return rates (Limburg and Waldman, 2009). In addition to temporal and spatial closures of fisheries overlapping with salmon migration, fishing gear modifications and incentives for bycatch avoidance could be implemented (Hilborn, 2011; Blasco et al., 2020).
3. Improve freshwater, estuarine, and seawater quality: Reducing anthropogenic threats and promoting strong, healthy and productive ecosystems in the salmon's freshwater, transitional estuarine, and marine habitats as set out within various national and international legislation (e.g., Marine Strategy Framework Directive 2008/56/EC, OSPAR Convention, Water Framework Directive 2000/60/EC) is essential to population recovery (McDowall, 1992; Limburg and Waldman, 2009; Hilborn, 2011; McQuatters-Gollop et al., 2022).

   Further, although smolt-to-adult survival of Frome fish was found to be much lower than parr-to-smolt survival, carry-over effects from previous life-stages may influence the performance later in life (Nislow and Armstrong, 2012; Gregory et al., 2019; Crozier et al., 2021). Salmon production in freshwater should therefore be maximised (Thorstad et al., 2021; Gillson et al., 2022).

5 Conclusion

Although many fish species are currently declining in abundance throughout the globe (Halpern et al., 2015; Pauly and Zeller, 2016; McQuatters-Gollop et al., 2022), species on the brink of extinction (including marine fish) have been observed to recover with appropriate and adaptive management actions (Lichatowich et al., 1995; Worm et al., 2009; Elliott et al., 2020). Hitherto, salmon conservation efforts have primarily concentrated on protecting juveniles in freshwater, due to their tractable nature compared with subsequent marine life-stages. Given the decline in salmon across their range and the low smolt-to-adult survival for salmon originating from the River Frome, conservation measures that address factors affecting their survival at sea are urgently required. We propose that the following measures be undertaken to slow declines in salmon across their range: 1) implement national and international climate mitigation measures to safeguard salmon

in both their freshwater and marine environments; 2) introduce spatial and temporal measures at sea to reduce harmful pressures across salmon's migratory pathways; and, 3) improve freshwater, estuarine and seawater quality to support and build population resilience to anthropogenic pressures.

Data availability statement

The datasets presented in this article are not readily available because they contain privately owned data which we are not able to share publicly, Table 2 includes raw summarised data. Requests to access the datasets should be directed to s.elliott-16@kent.ac.uk.

Ethics statement

The animal study was approved by GWCT's Animal Welfare and Ethical Review Body and conducted under a UK Home Office Animals (Scientific Procedures) Act 1986 licence (Project licence: PP9506723 (2020 – 2025), 30/3277 (2015 – 2020), 30/2732 (2010 – 2015). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

SE: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. NA: Methodology, Supervision, Validation, Writing – review & editing. JG: Writing – review & editing. KU: Data curation, Writing – review & editing. WB: Data curation, Writing – review & editing. KB: Data curation, Writing – review & editing. DR: Funding acquisition, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Alabaster, J. S., and Lloyd, R. S. (1982). *Water quality criteria for freshwater fish. 2nd edn* (London: Butterworths).

Artero, C., Gregory, S., Beaumont, W., Josset, Q., Jeannot, N., Cole, A., et al. (2023). Survival of Atlantic salmon and sea trout smolts in transitional waters. *Mar. Ecol. Prog. Ser.* 709, 91–108. doi: 10.3354/meps14278

Arthington, A. H. (2012). *Environmental flows: Saving rivers in the third millennium* (Berkeley, CA: University of California Press).

Bailey, N. T. J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika* 38, 293–pp.306. doi: 10.2307/2332575

Bal, G., Montorio, L., Rivot, E., Prévost, E., Baglinière, J.-L., and Nevoux, M. (2017). Evidence for long-term change in length, mass and migration phenology of anadromous spawners in Atlantic salmon. *Salmo salar. J. Fish Biol.* 90, 2375–2393. doi: 10.1111/jfb.13314

Beaugrand, G., Brander, K. M., LJ, A., Souissi, S., and Reid, P. (2003). Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664. doi: 10.1038/nature02164

Beaugrand, G., and Reid, P. C. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob Chang Biol.* 9, 801–817. doi: 10.1046/j.1365-2486.2003.00632.x

Beaumont, W., Mills, C., and Williams, G. (1986). Use of a microcomputer as an aid to identifying objects passing through a resistivity fish counter. *Aquac Res.* 17, 213–226. doi: 10.1111/j.1365-2109.1986.tb00105.x

Bielak, A. T., and Power, G. (1986). Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec 1859–1983. *Can. J. Fish Aquat Sci.* 43, 281. doi: 10.1139/f86-036

Blasco, G. D., Ferraro, D. M., Cottrell, R. S., Halpern, B. S., and Froehlich, H. E. (2020). Substantial gaps in the current fisheries data landscape. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.612831

Bull, C. D., Gregory, S. D., Rivot, E., Sheehan, T. F., Ensing, D., Woodward, G., et al. (2022). The likely suspects framework: the need for a life cycle approach for managing Atlantic salmon (*Salmo salar*) stocks across multiple scales. *ICES J. Mar. Sci.* 79, 1445–1456. doi: 10.1093/icesjms/fsac099

Cabral, H., Fonseca, V., Sousa, T., and Costa Leal, M. (2019). Synergistic effects of climate change and marine pollution: an overlooked interaction in coastal and estuarine areas. *Int. J. Environ. Res. Public Health* 16, 2737. doi: 10.3390/ijerph16152737

Chaparro-Pedraza, P. C., and de Roos, A. M. (2019). Environmental change effects on life-history traits and population dynamics of anadromous fishes. *J. Anim. Ecol.* 88, 1178–1190. doi: 10.1111/1365-2656.13010

Chapman, D. G. (1951). Some properties of the hypergeometric distribution with applications to zoological cens. *Univ. Calif. Publ. Stat.* 1, 131–159.

Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J. Mar. Sci.* 69, 1538–1548. doi: 10.1093/icesjms/fss013

Copeland, W., Wagner, P., Hughes, N., Everett, A., and Robertsen, T. (2024). The MET Norway Ice Service: a comprehensive review of the historical and future evolution, ice chart creation, and end user interaction within METAREA XIX. *Front. Mar. Sci.* 11. doi: 10.3389/fmars.2024.1400479

Costa, M. J., Duarte, G., Segurado, P., and Branco, P. (2021). Major threats to European freshwater fish species. *Sci. Total Environ.* 797, 149105. doi: 10.1016/j.scitotenv.2021.149105

Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L., and Zabel, R. W. (2021). Climate change threatens Chinook salmon throughout their life cycle. *Commun. Biol.* 4, 222. doi: 10.1038/s42003-021-01734-w

Crozier, L. G., and Zabel, R. W. (2006). Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *J. Anim. Ecol.* 75, 1100–1109. doi: 10.1111/j.1365-2656.2006.01130.x

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., et al. (2022). The decline and impending collapse of the Atlantic Salmon (*Salmo salar*) population in the North Atlantic Ocean: a review of possible causes. *Rev. Fisheries Sci. Aquaculture* 30, 215–258. doi: 10.1080/23308249.2021.1937044

Darwall, W. R. T. (2023). *Salmo salar* (The IUCN Red List of Threatened Species). doi: 10.2305/IUCN.UK.2023-1.RLTS.T19855A67373433.en

Defra (2025). *Marine Protected Areas Network Report 2019–2024*. Available online at: https://assets.publishing.service.gov.uk/media/67601b1fb745d5f7a053ef97/Marine_Protected_Areas:MPA:Network_Report_2019-2024_Web_Accessible:002_.pdf (Accessed 03/10/2025).

Dieperink, C. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *J. Fish Biol.* 61, 848–852. doi: 10.1006/jfbi.2002.2090

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Einum, S., Nislow, K. H., Reynolds, J. D., and Sutherland, W. J. (2008). Predicting population responses to restoration of breeding habitat in Atlantic salmon. *J. Appl. Ecol.* 45, 930–938. doi: 10.1111/j.1365-2664.2008.01464.x

Einum, S., Sundt-Hansen, L., and H. Nislow, K. (2006). The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113, 489–496. doi: 10.1111/j.2006.0030-1299.14806.x

Elliott, S. A. M., Acou, A., Beaulaton, L., Guitton, J., Réveillac, E., and Rivot, E. (2023). Modelling the distribution of rare and data-poor diadromous fish at sea for protected area management. *Prog. Oceanogr* 210, 102924. doi: 10.1016/j.pocean.2022.102924

Elliott, S. A. M., Bearup, D., Carpentier, A., Larivain, A., Trancart, T., and Feunteun, E. (2020). Evaluating the effectiveness of management measures on skates in a changing world. *Biol. Conserv.* 248, 108684. doi: 10.1016/j.biocon.2020.108684

Elliott, S. A. M., Boraiah, K., Tham, C. K., Beaumont, W. R. C., Elsmere, P., Scott, L., et al. (2026). Deep learning models used to detect fish movement over resistivity counters. *Ecol. Inf.* 94, 103606. doi: 10.1016/j.ecoinf.2026.103606

Friedland, K. D., Hansen, L. P., and Dunkley, D. A. (1998). Marine temperatures experienced by postsmolts and the survival of Atlantic salmon, Salmo salar L., in the North Sea area. *Fish Oceanogr* 7, 22–34. doi: 10.1046/j.1365-2419.1998.00047.x

Friedland, K. D., MacLean, J. C., Hansen, L. P., Peyronnet, A. J., Karlsson, L., Reddin, D. G., et al. (2009). The recruitment of Atlantic salmon in Europe. *ICES J. Mar. Sci.* 66, 289–304. doi: 10.1093/icesjms/fsn210

Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., et al. (2021). The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis. *Fish Fisheries* 22, 1274–1306. doi: 10.1111/faf.12587

Gilbey, J., Wennevik, V., Bradbury, I. R., Fiske, P., Hansen, L. P., Jacobsen, J. A., et al. (2017). Genetic stock identification of Atlantic salmon caught in the Faroese fishery. *Fish Res.* 187, 110–119. doi: 10.1016/j.fishres.2016.11.020

Gillson, J. P., Bašić, T., Davison, P. I., Riley, W. D., Talks, L., Walker, A. M., et al. (2022). A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. *Rev. Fish Biol. Fish* 32, 879–919. doi: 10.1007/s11160-022-09714-x

Gillson, J. P., Maxwell, D. L., Gregory, S. D., Posen, P. E., Riley, W. D., Picken, J. L., et al. (2020). Can aspects of the discharge regime associated with juvenile Atlantic salmon (*Salmo salar* L.) and trout (S. trutta L.) densities be identified using historical monitoring data from five UK rivers? *Fish Manag Ecol.* 27, 567–579. doi: 10.1111/fme.12456

Gregory, S. D., Armstrong, J. D., and Britton, J. R. (2018). Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival. *J. Fish Biol.* 92, 579–592. doi: 10.1111/jfb.13550

Gregory, S. D., Bewes, V. E., Davey, A. J. H., Roberts, D. E., Gough, P., and Davidson, I. C. (2020). Environmental conditions modify density-dependent salmonid recruitment: Insights into the 2016 recruitment crash in Wales. *Freshw. Biol.* 65, 2135–2153. doi: 10.1111/fwb.13609

Gregory, S. D., Gillson, J. P., Whitlock, K., Barry, J., Gough, P., Hillman, R. J., et al. (2023). Estimation of returning Atlantic salmon stock from rod exploitation rate for principal salmon rivers in England & Wales. *ICES J. Mar. Sci.* 80, 2504–2519. doi: 10.1093/icesjms/fsad161

Gregory, S. D., Ibbotson, A. T., Riley, W. D., Nevoux, M., Lauridsen, R. B., Russell, I. C., et al. (2019). Atlantic salmon return rate increases with smolt length. *ICES J. Mar. Sci.* 76, 1702–1712. doi: 10.1093/icesjms/fsz066

Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R. C., Jeannot, N., Lauridsen, R. B., et al. (2017). Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshw. Biol.* 62, 1117–1129. doi: 10.1111/fwb.12929

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6, 1–7. doi: 10.1038/ncomms8615

Hansen, L. P., and Quinn, T. P. (1998). The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Can. J. Fisheries Aquat. Sci.* 55, 104–118. doi: 10.1139/d98-010

Hátún, H., Lohmann, K., Matei, D., Jungclaus, J. H., Pacariz, S., Bersch, M., et al. (2016). An inflated subpolar gyre blows life toward the northeastern Atlantic. *Prog. Oceanogr* 147, 49–66. doi: 10.1016/j.pocean.2016.07.009

Hátún, H., Payne, M. R., and Jacobse, J. A. (2009). The North Atlantic subpolar gyre regulates the spawning distribution of blue whiting (*Micromesistius poutassou*). *Can. J. Fisheries Aquat. Sci.* 66, 759–770. doi: 10.1139/F09-037

Heddell-Cowie, M. (2005). Importance of the River Teviot to Atlantic salmon, *Salmo salar*, rod catches in the River Tweed, Scotland. *Fish Manag Ecol.* 12, 137–142. doi: 10.1111/j.1365-2400.2004.00435.x

Heffernan, J. P. (2014). Dealing with Mediterranean bluefin tuna: A study in international environmental management. *Mar. Policy* 50, 81–88. doi: 10.1016/j.marpol.2014.05.014

Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal perspective. *Fish Res.* 108, 235–239. doi: 10.1016/j.fishres.2010.12.030

ICES (2018). *Report of the Working Group on North Atlantic Salmon (WGNAS)* (Woods Hole, MA, USA: ICES CM 2018/ACOM), 386.

ICES (2023a). Working group on north atlantic salmon (WGNAS). *ICES Sci. Rep.* :41, 478. doi: 10.17895/ices.pub.22743713

ICES (2023b). The Second ICES/NASCO Workshop on Salmon Mortality at Sea (WKSalmon2; outputs from 2022 meeting). *ICES Sci. Rep.* 36, 69. doi: 10.17895/ices.pub.22560790

ICES (2024a). Working group on north atlantic salmon (WGNAS). *ICES Sci. Rep.* 36, 415. doi: 10.17895/ices.pub.25730247

ICES (2024b). Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR; outputs from 2023 meeting). *ICES Sci. Rep.* 33, 71. doi: 10.17895/ices.pub.25526548

IPCC (2024). *Assessment report* (Reports — IPCC). Availble online at: https://www.ipcc.ch/reports/NASCO: https://nasco.int/wp-content/uploads/2020/02/HabitatFAR_EnglandWales.pdf (Accessed September 30, 2025).

Jacobsen, J. A., Hansen, L. P., Bakkestuen, V., Halvorsen, R., Reddin, D. G., White, J., et al. (2012). Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the

sea around the Faroe Islands based on analysis of historical tag recoveries. *ICES J. Mar. Sci.* 69, 1598–1608. doi: 10.1093/icesjms/fss115

Jonsson, B., Jonsson, N., and Albretsen, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *J. Fish Biol.* 88, 618–637. doi: 10.1111/jfb.12854

Jonsson, B., Jonsson, N., and Hansen, L. P. (2003). Atlantic salmon straying from the River Imsa. *J. Fish Biol.* 62, 641–657. doi: 10.1046/j.1095-8649.2003.00053.x

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., et al. (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. Freshw. Fish* 12, 1–59. doi: 10.1034/j.1600-0633.2003.00010.x

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., et al. (2014). Migratory marine species: their status, threats and conservation management needs. *Aquat. Conservation: Mar. Freshw. Ecosyst.* 24, 111–127. doi: 10.1002/aqc.2512

Lichatowich, J., Mobrand, L., Lestelle, L., and Vogel, T. (1995). An approach to the diagnosis and treatment of depleted pacific salmon populations in pacific northwest watersheds. *Fisheries (Bethesda)* 20, 10–18. doi: 10.1577/1548-8446(1995)020<0010:AATTDA>2.0.CO;2

Lilly, J., Honkanen, H. H., Rodger, J. R., del Villar, D., Boylan, P., Green, A., et al. (2023). Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 12 rivers through the coastal zones around the Irish Sea. *J. Fish Biol.* 104, 0–1. doi: 10.1111/jfb.15591

Limburg, K. E., and Waldman, J. R. (2009). Dramatic declines in north atlantic diadromous fishes. *Bioscience* 59, 955–965. doi: 10.1525/bio.2009.59.11.7

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Kratina, P., Scott, L. J., Cooling, D., et al. (2022). High summer macrophyte cover increases abundance, growth, and feeding of juvenile Atlantic salmon. *Ecol. Appl.* 32, e02492. doi: 10.1002/eap.2492

Martin, J. H. A., and Mitchell, K. A. (1985). Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). *Can. J. Fisheries Aquat. Sci.* 42, 1513–1521. doi: 10.1139/f85-189

McDowall, R. M. (1992). Particular problems for the conservation of diadromous fish. *Aquat Conserv.* 2, 351–355. doi: 10.1002/aqc.3270020405

McDowall, R. M. (2009). Making the best of two worlds : diadromy in the evolution, ecology, and conservation of aquatic organisms. *Am. Fisheries Soc. Symposium* 69, 1–22.

McQuatters-Gollop, A., Guérin, L., Arroyo, N. L., Aubert, A., Artigas, L. F., Bedford, J., et al. (2022). Assessing the state of marine biodiversity in the Northeast Atlantic. *Ecol. Indic* 141, 109148. doi: 10.1016/j.ecolind.2022.109148

Milner, N., Elliott, J., Armstrong, J., Gardiner, R., Welton, J. S., and Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Res.* 62, 111–125. doi: 10.1016/S0165-7836(02)00157-1

Moir, H. J., Gibbins, C. N., Soulsby, C., and Webb, J. (2004). Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology* 60, 21–35. doi: 10.1016/j.geomorph.2003.07.014

NASCO (2009). *Protection, Restoration and Enhancement of Salmon Habitat Focus Area Report, EU-UK (England & Wales)*. Available online at: https://nasco.int/wp-content/uploads/2020/02/HabitatFAR_EnglandWales.pdf (Accessed August 16, 2025).

NASCO (2024). Report of the forty second annual meeting of the council. Wales. *CNL2580rev_Report-of-the-Forty-Second-Annual-Meeting-of-the-Council.pdf*.

Nislow, K. H., and Armstrong, J. D. (2012). Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. *Fisheries Manage. Ecol.* 19, 451–463. doi: 10.1111/j.1365-2400.2011.00810.x

Olmos, M., Payne, M. R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., et al. (2020). Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Glob Chang Biol.* 26, gcb.14913. doi: 10.1111/gcb.14913

OSPAR (2017). *OSPAR Recommendation 2016/3 on furthering the protection and conservation of the Atlantic salmon (*Salmo salar*) in Regions I, II, III and IV of the OSPAR maritime area*.

Parry, E. S., Gregory, S. D., Lauridsen, R. B., and Griffiths, S. W. (2018). The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015. *Ecol. Freshw. Fish* 27, 128–137. doi: 10.1111/eff.12330

Pauly, D., and Zeller, D. (2016). Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 7, 1–9. doi: 10.1038/ncomms10244

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. (2010). Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *J. Mar. Syst.* 79, 427–435. doi: 10.1016/j.jmarsys.2008.12.017

Potter, E. C. E., and Russell, I. C. (1994). Comparison of the distribution and homing of hatchery-reared and wild Atlantic salmon, *Salmo salar* L., from north-east England. *Aquaculture Res.* 25, 31–44. doi: 10.1111/are.1994.25.s2.31

Richard, A., O'Rourke, J., Caudron, A., and Cattanéo, F. (2013). Effects of passive integrated transponder tagging methods on survival, tag retention and growth of age-0 brown trout. *Fish Res.* 145, 37–42. doi: 10.1016/j.fishres.2013.03.001

Rikardsen, A. H., Righton, D., Strøm, J. F., Thorstad, E. B., Gargan, P., Sheehan, T., et al. (2021). Redefining the oceanic distribution of Atlantic salmon. *Sci. Rep.* 11, 12266. doi: 10.1038/s41598-021-91137-y

Rikardsen, A. H., Woodgate, M., and Thompson, D. A. (2002). A comparison of Floy and soft VIalpha tags on hatchery Arctic charr, with emphasis on tag retention, growth and survival. *Environ. Biol. Fishes* 64, 269–273. doi: 10.1023/A:1016037921211

Riley, W. D., Ibbotson, A. T., and Beaumont, W. R. (2009). Adult returns from Atlantic salmon, *Salmo salar*, parr autumn migrants. *Fisheries Manage. Ecology.* 1, 16(1). doi: 10.1002/aqc.1184

Riley, W. D., Ibbotson, A. T., Beaumont, W. R. C., Pawson, M. G., Cook, A. C., and Davison, P. I. (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. doi: 10.1002/aqc.1184

Robinson, R., Crick, H., Learmonth, J., Maclean, I., Thomas, C., Bairlein, F., et al. (2009). Travelling through a warming world: climate change and migratory species. *Endanger Species Res.* 7, 87–99. doi: 10.3354/esr00095

Robson, D. S., and Regier, H. A. (1964). Sample size in Petersen mark–recapture experiments. *Trans. Am. Fish Soc.* 93, 215–226. doi: 10.1577/1548-8659(1964)93[215:ssipme]2.0.co;2

Russell, I. C., Aprahamian, M. W., Barry, J., Davidson, I. C., Fiske, P., Ibbotson, A. T., et al. (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. doi: 10.1093/icesjms/fsr208

Sadinle, M. (2009). Transformed logit confidence intervals for small populations in single capture–recapture estimation. *Commun. Stat. Simul Comput.* 38, 1909–1924. doi: 10.1080/03610910903168595

Sandlund, O. T., Berntsen, H. H., Fiske, P., Kuusela, J., Muladal, R., Niemelä, E., et al. (2019). Pink salmon in Norway: the reluctant invader. *Biol. Invasions* 21, 1033–1054. doi: 10.1007/s10530-018-1904-z

Sayer, C. (2024). Salmo salar *(Europe assessment)* (The IUCN Red List of Threatened Species). doi: 10.2305/IUCN.UK.2024-2.RLTS.T19855A212864916.en

Schneider, C., Laizé, C. L. R., Acreman, M. C., and Flörke, M. (2013). How will climate change modify river flow regimes in Europe? *Hydrol Earth Syst. Sci.* 17, 325–339. doi: 10.5194/hess-17-325-2013

Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters. 2nd edn* (London: Charles Griffin & Co.).

Simmons, O. M., Britton, J. R., Gillingham, P. K., and Gregory, S. D. (2020). Influence of environmental and biological factors on the overwinter growth rate of Atlantic salmon Salmo salar parr in a UK chalk stream. *Ecol. Freshw. Fish* 101, 665–678. doi: 10.1111/eff.12542

Simmons, O. M., Britton, J. R., Gillingham, P. K., Nevoux, M., Riley, W. D., Rivot, E., et al. (2021a). 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.*, 1–11. doi: 10.1111/jfb.14946

Simmons, O. M., Gregory, S. D., Gillingham, P. K., Riley, W. D., Scott, L. J., and Britton, J. R. (2021b). Biological and environmental influences on the migration phenology of Atlantic salmon Salmo salar smolts in a chalk stream in southern England. *Freshw. Biol.* 66, 1581–1594. doi: 10.1111/fwb.13776

Skagseth, Ø., Broms, C., Gundersen, K., Hátún, H., Kristiansen, I., Larsen, K. M. H., et al. (2022). Arctic and atlantic waters in the norwegian basin, between year variability and potential ecosystem implications. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.831739

Sloth, P., and Buch, E. (1988). *Correlation Between Winter Ice Coverage in the Greenland Sea and the Summer Temperatures at Fylla Bank, West Greenland? Northwest Atlantic Fisheries Organisation* (West Greenland?: NAFO SCR 88/49/) Available online at: https://www.nafo.int/Portals/0/PDFs/sc/1988/scr-88-049.pdf (Accessed June 23, 2025).

Strøm, J. F., Rikardsen, A. H., Campana, S. E., Righton, D., Carr, J., Aarestrup, K., et al. (2019). Ocean predation and mortality of adult Atlantic salmon. *Sci. Rep.* 9, 7890. doi: 10.1038/s41598-019-44041-5

Strøm, J. F., Thorstad, E. B., Hedger, R. D., and Rikardsen, A. H. (2018). Revealing the full ocean migration of individual Atlantic salmon. *Anim. Biotelemetry* 6, 2. doi: 10.1186/s40317-018-0146-2

Suuronen, P., and Lehtonen, E. (2012). The role of salmonids in the diet of grey and ringed seals in the Bothnian Bay, northern Baltic Sea. *Fish Res.* 125–126, 283–288. doi: 10.1016/j.fishres.2012.03.007

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., et al. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquat Conserv.* 31, 2654–2665. doi: 10.1002/aqc.3624

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., and 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. doi: 10.1111/j.1095-8649.2012.03370.x

Todorov, V., Templ, M., and Filzmoser, P. (2011). Detection of multivariate outliers in business survey data with incomplete information. *Adv. Data Anal. Classif* 5, 37–56. doi: 10.1007/s11634-010-0075-2

Tréhin, C., Rivot, E., Santanbien, V., Patin, R., Gregory, S. D., Lamireau, L., et al. (2023). A multi-population approach supports common patterns in marine growth and maturation decision in Atlantic salmon (*Salmo salar* L.) from southern Europe. *J. Fish Biol.* 104, 125-138. doi: 10.1111/jfb.15567

Tyldesley, E., Banas, N. S., Diack, G., Kennedy, R., Gillson, J., Johns, D. G., et al. (2024). Patterns of declining zooplankton energy in the northeast Atlantic as an indicator for marine survival of Atlantic salmon. *ICES J. Mar. Sci.* 81, 1164–1184. doi: 10.1093/icesjms/fsae077

Tyldesley, E., Banas, N., Kennedy, R., Diack, G., and Bull, C. (2025). River–sea thermal differential experienced by salmon post-smolts is not a proximal driver of marine survival. *J. Fish Biol.* 81, 1411-1419. doi: 10.1111/jfb.70134

Utne, K. R., Pauli, B. D., Haugland, M., Jacobsen, J. A., Maoileidigh, N., Melle, W., et al. (2021). Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES J. Mar. Sci.* 78, 2844–2857. doi: 10.1093/icesjms/fsab163

Utne, K. R., Skagseth, Ø., Wennevik, V., Broms, C. T., Melle, W., and Thorstad, E. B. (2022). Impacts of a changing ecosystem on the feeding and feeding conditions for atlantic salmon during the first months at sea. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.824614

Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., and Moens, T. (2021). Toward a roadmap for diadromous fish conservation: the Big Five considerations. *Front. Ecol. Environ.* 19, fee.2361. doi: 10.1002/fee.2361

Vollset, K. W., Lennox, R. J., Thorstad, E. B., Auer, S., Bär, K., Larsen, M. H., et al. (2020). Systematic review and meta-analysis of PIT tagging effects on mortality and growth of juvenile salmonids. *Rev. Fish Biol. Fish* 30, 553–568. doi: 10.1007/s11160-020-09611-1

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., et al. (2009). Rebuilding global fisheries. *Sci. (1979)* 325, 578–585. doi: 10.1126/science.1173146

Zabel, R. W., Scheuerell, M. D., Mcclure, M. M., and Williams, J. G. (2006). The interplay between climate variability and density dependence in the population viability of chinook salmon. *Conserv. Biol.* 20, 190–200. doi: 10.1111/j.1523-1739.2006.00300.x