

On the edge of the abyss: modelling the early marine migration of Atlantic salmon post-smolts

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Abstract

Atlantic salmon (*Salmo salar*) populations have suffered declines across their range in recent decades, largely attributed to decreasing marine survival rates. The first few months at sea are thought to be a time of particular vulnerability, but the drivers of mortality during this period are not yet fully understood. Characterising the conditions experienced by salmon at sea is challenged by a lack of knowledge of full migration paths, with empirical approaches limited to specific locations. Additionally, the mechanisms shaping migration paths and the extent of variability in migrations between years are unclear. To address knowledge gaps, the movement of juvenile salmon over the first three months at sea is simulated for a group of Irish, Northern Irish and Scottish rivers using a Lagrangian particle tracking model coupled with an active swimming model that is dependent on ocean currents, salinity, and compass direction. Differences in the speed of migrations, the proportion of time spent in different oceanographic regions, and the proportion of migrations reaching the Norwegian Sea are seen between years. These differences are related to changes in local ocean conditions: years with lower on-shelf salinity, stronger on-shelf northwest currents, and stronger shelf-edge currents were associated with greater migration success.

Motivated by the observed interannual variability, the value of behavioural variability in dampening interannual variance in modelled migration success is investigated. The migration model is expanded and parameterised for 38 rivers around the British Isles, with different parameter sets representing different navigation behaviours. Portfolios of behaviours were selected for each river by maximising a version of the Sharpe index, which balances portfolio return (mean migration success rate) and risk (interannual variability in migration success). For simulated salmon from some rivers, a single swimming behaviour is found to be optimal, while other river populations benefit from up to 24 behaviours. The use of an optimal portfolio of swimming behaviours for each river minimises stock-level variation (when considering all 38 rivers together). These findings highlight the importance of behavioural diversity both within and between salmon populations, which may be supported by the conservation of genetic diversity.

To aid future research into the bycatch risk of juvenile salmon, a potential driver of mortality at sea, the exposure of juvenile Atlantic salmon to pelagic fisheries during their first few months at sea is determined. Landings (taken as a proxy for fishing intensity) of six commercially important pelagic finfish species (mackerel, herring, horse mackerel, capelin, sardine, chub mackerel) were quantified from 2000 to 2022 within salmon migration regions. Pelagic fisheries for herring and

mackerel present the highest total exposure along the migration corridor between April and August. Additionally, there is potential for Atlantic salmon bycatch in the horse mackerel and sardine fisheries in April. Future investigations using Environmental DNA (eDNA) analysis and/or landings port observations of the fisheries identified in this study could quantify bycatch rates, which may be combined with the exposure values developed here to quantify bycatch risk to Atlantic salmon stocks.

Two applications of the juvenile salmon migration model are presented in the final chapters. First, zooplankton energy derived from the Continuous Plankton Recorder (CPR) is used as a measure of energy in the juvenile salmon food chain (prey-of-prey energy), and occupancy-weighted zooplankton energy estimates are generated using gridded densities of modelled juvenile salmon. CPR sampling is found to be highly variable within specific migration space-time regions, so time-mean energy over multiple years is considered within the spatial migration regions. Slower migrations allow access to more energy resources, but there may be a tradeoff between moving slowly and feeding, versus making it to the Norwegian Sea by a suitable time.

Finally, a metric of similarity between modelled migrations from different rivers is developed and used to estimate marine survival rates for rivers where they are unknown, assuming that similarity in modelled migration densities drives similarity in experienced prey and predation conditions, and hence survival patterns. Estimated marine survival rates accurately depict known interannual trends, though some uncertainty is generated by differences in the absolute values of marine survival rates between rivers. The estimated marine survival rates are used in a decision support tool which visualises the life-cycle wide effects of changing river and ocean conditions, helping to inform appropriate management action.

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Contents

Abstract	i
1 Atlantic salmon ecology and migrations in the northeast Atlantic	1
1.1 Overview	1
1.2 Anadromous lifecycle	2
1.3 Methods for collecting data on salmon migrations	5
1.4 Characteristics of the post-smolt migration	9
1.5 Movement modelling	13
1.6 Oceanographic conditions and variability in the northeast Atlantic	17
1.7 Management of salmon stocks	19
1.8 Thesis overview	22
2 Modelled marine migrations of Atlantic salmon post-smolts from Irish, Northern Irish and Scottish rivers vary interannually with local currents and salinity	24
2.1 Introduction	24
2.2 Methods	27
2.3 Results	41
2.4 Discussion	47
2.5 Conclusion	53
3 Movement modelling of migrating Atlantic salmon post-smolts reveals the value of a portfolio of behavioural strategies	54
3.1 Introduction	54
3.2 Methods	56
3.3 Results	62
3.4 Discussion	69
3.5 Conclusion	74
4 Quantifying the exposure of migrating Atlantic salmon to pelagic fisheries in the northeast Atlantic to reveal potential bycatch hotspots	75
4.1 Introduction	75
4.2 Methods	78

4.3	Results	83
4.4	Discussion	85
4.5	Conclusion	90
5	Zooplankton energy available to forage fish	92
5.1	Introduction	92
5.2	Methods	95
5.3	Results	96
5.4	Discussion	103
6	Using similarity in modelled migration densities to estimate marine survival rates	108
6.1	Introduction	108
6.2	Methods	110
6.3	Results	111
6.4	Discussion	114
	Overall conclusion and future outlook	118
	Appendices	122
Appendix A	Modelled post-smolt migrations from Scottish, Northern Irish and Irish rivers	123
A.1	Model assumptions	123
A.2	Subpolar gyre and North Atlantic Oscillation indices	125
A.3	Annual particle concentrations 1993-2019	125
Appendix B	Migration behaviour portfolio analysis	127
B.1	Ranges of optimal portfolio sizes	127
B.2	Portfolio component examples	128
B.3	Coefficients of variation without rivers 4-7	129
B.4	Optimal portfolio components with migration distance	130
Appendix C	Fisheries exposure analysis	131
C.1	Fisheries overview	131
C.2	Estimation of pelagic landings from Russia and the Faroe Islands	132
C.3	Spatial overlap of pelagic fishing activity with monthly post-smolt migration regions	138
	Bibliography	138

List of Figures

1.1	PIT tagging salmon parr on the River Laxford in northwest Scotland. Parr were collected using electrofishing, which briefly immobilises fish and attracts them to the equipment, allowing them to be collected in a net, without causing any harm to the fish (Bohlin <i>et al.</i> , 1989).	6
2.1	Summer feeding grounds of Atlantic salmon post-smolts (<i>Salmo salar</i>), the Scottish Shelf Model domain, and the rivers where migrations are modelled (orange). Isobaths at 200m and 400m indicate the location of the continental shelf-edge. . .	26
2.2	Schematic of salinity gradient calculation. Quadrants q_1, q_2, q_3, q_4 are shown, with dots representing points in the salinity field on the irregular Scottish Shelf Model (SSM) grid.	31
2.3	Salinity gradient magnitude calculated with: (a) $\epsilon = 5$ km, (b) $\epsilon = 10$ km, and (c) $\epsilon = 50$ km. (d)-(f) show the same salinity gradient magnitude with $\epsilon = 5$ km, $\epsilon = 10$ km, and $\epsilon = 50$ km respectively, but with the saturation function in Equation 2.4 for $\mathbf{g}_s$ applied.	32
2.4	(a) the top 10 % of domain exit rates for the parameter optimisation runs. The top 10 % was determined from the means across each of the five years. The optimal solution (greatest mean across the five years) is shown in purple. (b) Boxplots showing the spread of values of parameters w_c, w_s , and consequently w_d in the top 10 % of runs. (c) Boxplot showing the values of s in the top 10 % of runs. . . .	37
2.5	Domain exit rates are displayed for all cases where: (a) $w_c = 0$; (b) $w_s = 0$; (c) $w_d = 0$. The purple line again depicts the optimal solution, in which all weights were non-zero ($w_c = 0.3, w_s = 0.8, w_d = 0.52$).	38
2.6	Changes in domain exit rates when varying the parameters θ_{bias} , ϵ , and the threshold depth at which R is set to 1 (Equation 2.5) by $\pm 10\%$	38
2.7	Density of modelled Atlantic salmon post-smolts (<i>Salmo salar</i>) from all releases of all years, measured as the total number of incidences of particles per 30 km ² bin. Modelling start points (river mouths) are shown as black circles. The domain exit region, used for calculating domain exit rates, is also displayed.	41

2.8	(a) simulated Atlantic salmon post-smolt (<i>Salmo salar</i>) density (total number of particles per 30 km ² bin) from 2008 within ± 1 week of all observations from the SALSEA-Merge project (http://salmonatsea.com/the-salsea-merge-project/ ; Utne <i>et al.</i> , 2020), which are marked as black dots. The general migration track following the continental shelf edge is shown as a black line. (b) Distance along this general migration track with time for simulated post-smolts and observations, again marked as black dots. The black dashed line displays particle release locations and timing.	42
2.9	Scottish Shelf Waters Reanalysis Service (SSW-RS) conditions averaged over April-June each year for the shelf region (blue) and the shelf-edge region (orange): (a) shelf salinity; (b) shelf eastward currents; (c) shelf northward currents; (d) shelf-edge salinity; (e) currents along the shelf-edge; (f) currents perpendicular to the shelf-edge (on-shelf positive). Lines show conditions averaged over 1st April - 30th June each year. Dots show conditions averaged over 2-week periods from 1st April - 24th June.	43
2.10	(a), (c), (e): heatmaps displaying metrics of modelled Atlantic salmon (<i>Salmo salar</i>) migrations per river per year (including both releases). (b), (d), (f): metrics of modelled migrations (mean taken across rivers) for the earlier and later (2 weeks later) particle releases, and the combined mean (both releases).	44
2.11	Correlation matrix between: (a) on-shelf salinity and currents, (b) shelf-edge salinity and currents, (c) large-scale climate indices (subpolar gyre SPG and North Atlantic Oscillation NAO), (d) modelled Atlantic salmon (<i>Salmo salar</i>) migration metrics. Pearson correlation coefficients (r) between each combination are shown via the colour scale. Significant correlations ($p^* < 0.05$) are denoted by white dots.	45
2.12	Time series of grouped one-sea-winter (1SW) normalised return rates from western populations (blue line; Tyldesley <i>et al.</i> , 2024, normalisation was by z-scores across whole time series, 1980-2019) and modelled domain exit rates (green). Correlation coefficients between the time series are shown.	47
2.13	A summary of the beneficial oceanographic conditions for simulated Atlantic salmon (<i>Salmo salar</i>) post-smolt migrations, based on the correlations displayed in Figure 2.11. Faster shelf-edge currents and faster on-shelf northwest currents are both associated with a negative North Atlantic Oscillation (NAO) index. Lower on-shelf salinity is associated with a stronger subpolar gyre (SPG) index.	51
3.1	The 38 salmon rivers included in this study, coloured and labelled according to their geographical location, and the Scottish Shelf Model domain (blue).	57
3.2	Density of modelled Atlantic salmon post-smolts (total number of occurrences per 20 km ² bin) from all rivers, 1993-2019. Modelled migrations were weighted so that each river had the equivalent number of particles as the river with the largest portfolio size. Black dots denote river mouth start points.	63

3.3	Monthly densities of modelled Atlantic salmon post-smolts, compared with: (a)-(c) telemetry detections between April and June (Rodger <i>et al.</i> , 2025; Adams <i>et al.</i> , 2025); and (d) epipelagic trawl data in May (Newton <i>et al.</i> , 2026).	64
3.4	Intervals of the parameters in the selected optimal portfolio of each river. Intervals are displayed for the continuous parameters: (a) w_c ; (b) w_s ; (c) w_d ; and (d) s . Probabilities are displayed for the discrete parameters: (e) the threshold for $R=1$; and (f) θ_{bias} . Probabilities are indicated by circle size, with a probability of 1 corresponding to all solutions within the optimal portfolio taking the same value.	65
3.5	Rivers grouped according to the relative weights of the three navigation cues w_c^2 , w_s^2 , and w_d^2 : (a) rivers with parameter sets solely in the upper third of the ternary plot (i.e. predominant use of currents to navigate); (b) those only in the lower right third (i.e. predominant use of salinity); (c) those only in the lower left third (i.e. predominant use of direction); and (d) those spanning wide ranges of navigational cues.	66
3.6	The selected bearings within the optimal portfolio for each river (-45° , 0° , 45° , or a combination; shown by colour and arrow direction).	67
3.7	The optimal number of swimming behaviours (i.e. parameter sets) for each river, determined by the maximum Sharpe ratio.	68
3.8	Domain exit rate time series for: individual parameter sets (only those selected in the optimal portfolios); aggregated river portfolios; aggregated for all rivers (stock-level). Coefficients of variation (CV) are displayed for each level.	68
3.9	The coefficient of variation (CV) on individual-, river- and stock-levels for: $n = 1$, i.e. the single best swimming behaviour per river; the selected optimal portfolio per river; and $n = 25$, i.e. the set of all modelled swimming behaviours per river.	69
4.1	Salmon rivers in the northeast Atlantic (blue) and monitored rivers with time series of marine return rates available for analysis (black). Isobaths at 200m and 400m indicate the location of the continental shelf-edge.	79
4.2	ICES rectangle scale (0.5° latitude x 1° longitude) locations and concentrations of surveyed post-smolts (Gilbey <i>et al.</i> , 2021) for: (a) April to August; (b) April; (c) May; (d) June; (e) July; and (f) August. Defined post-smolt migration regions are displayed (southwest, west, east, common). Isobaths at 200 m and 400 m in (a) indicate the location of the continental shelf-edge.	80
4.3	Normalised marine return rates for one-sea-winter (1SW) salmon for individual populations (thin blue lines) and combined means per region (thick orange lines) from 2000-2021 for: (a) the southwest region (including the Scorff, Oir, Bresle, Tamar, and Frome); (b) west region (Corrib, Burrishoole, Bush, and Dee); and (c) east region (North Esk and Imsa).	82
4.4	Total landings of all species (mackerel, herring, horse mackerel, capelin, chub mackerel, sardine) by ICES rectangle within the post-smolt regions (outlined in black) per month across 2000-2022.	84

4.5	Time series from 2000-2022 of all landings (in tonnes per square kilometre) per region and per month, coloured by the proportional contribution of each species.	85
4.6	The mean landings (tonnes/km ²) per fishery and month within the regions occupied by post-smolts (SW = southwest, W = west, E = east, C = common) between 2000 and 2022. Boxes are shaded according to lower values of mean landings (blue = less than 0.002 tonnes/km ²), moderate values (yellow = between 0.002 and 0.02 tonnes/km ²), and higher values (orange = greater than 0.02 tonnes/km ²). The black box displays the cells where the landings are known to be a lower bound due to missing data from some nations (Appendix C).	86
4.7	Correlations (with at least moderate evidence, $p < 0.05$) between pelagic landings in the post-smolt regions and grouped 1SW return rates. Correlations between common region landings and return rates were not considered due to missing data relevant to this region (Appendix C). Negative correlations are denoted by purple shaded text and positive correlations by orange shaded text. NSC = no significant correlation. Strong evidence is denoted by *.	87
5.1	All CPR transects. The Scottish Shelf Model (SSM) domain is outlined.	94
5.2	Between March and September 1993-2019: (a) the total number of Continuous Plankton Recorder (CPR) samples per box; (b) the coefficient of variation (CV) in the number of samples taken each year; (c) the mean energy per box.	98
5.3	(a) Total CPR samples between March and September each year summed over the area spanned by the modelled migrations of river 12 (southern North Sea); (b) CPR samples per box March-September 1994; (c) CPR samples per box March-September 2001. Black outlines in (b) and (c) indicate the area spanned by the simulated migrations.	99
5.4	Simulated post-smolt occupancy (left) and occupancy-weighted zooplankton energy (right) between March and October from 1993 to 2019 for: (a)-(b) river 5 (Ugie) in the northern North Sea; (c)-(d) river 8 (Tyne) in the mid North Sea; (e)-(f) river 12 (Thames) in the southern North Sea.	100
5.5	Simulated post-smolt occupancy weighted zooplankton energy between March-October from 1993 to 2019 for: (a) river 5 (Ugie) in the northern North Sea; (b) river 8 (Tyne) in the mid North Sea; (c) river 12 (Thames) in the southern North Sea.	101
5.6	Simulated post-smolt occupancy and occupancy-weighted zooplankton energy between March and October 1993 to 2019 for: (a)-(b) the parameter set giving the lowest summed occupancy-weighted energy for river 12 (Thames) in the southern North Sea; (c)-(d) the parameter set with the highest summed occupancy-weighted energy for river 12 (Thames).	102
5.7	Summed occupancy-weighted energy for river 12 (Thames) against: (a) the weight of the current-following behaviour w_c ; (b) the weight of the salinity-gradient-following behaviour w_s ; (c) the weight of the directional swimming behaviour w_d .	103

5.8	Mean time taken to exit the SSM domain against summed occupancy-weighted energy for the River Thames.	105
6.1	The seven monitored salmon rivers around the British Isles: North Esk, Frome, Tamar, Dee, Corrib, Burrishoole, Bush.	109
6.2	(a) Mean annual similarity between each combination of the 38 rivers and the 7 indexed rivers, (b) dissimilarity for each of the 38 rivers with the 7 indexed rivers combined.	112
6.3	The most similar indexed rivers to each region, based on the similarity matrix for the modelled rivers and generalised to cover the areas between the modelled rivers. Areas with the highest dissimilarities to all of the indexed rivers are highlighted with thin dashed white lines.	113
6.4	Estimated return rates, using the similarity-weighted sum, for the river Bharp (number 36), in the Outer Hebrides in Scotland: (a) year-by-year estimates; (b) decadal estimates. Each of the return rates time series is displayed (grey lines), with the line thicknesses weighted by their proportional contribution to the estimate, such that the more ‘important’ time series stand out clearly.	114
6.5	Estimated return rates for the Burrishoole, calculated using the other indexed rivers are shown in (a) year-by-year and (b) decadal formats. The yellow line in both indicates the real Burrishoole return rates. Correlation coefficients (r^2 and p) in (a) indicate the linear relationship between the estimated and real Burrishoole return rates. Each of the return rates time series is displayed (grey lines), with the line thicknesses weighted by their proportional contribution to the estimate, such that the more ‘important’ time series stand out clearly.	115
6.6	The mean 1SW return rate for each monitored salmon river across the whole period when return rates were measured: North Esk (1981-2009, with a few years unavailable inbetween); Frome (2002-2019); Tamar (2002-2019); Dee (1993-2019); Corrib (1980-2019); Burrishoole (1980-2019); Bush (1986-2019).	116
A.1	Subpolar gyre (SPG) index annual mean from 1993-2018. North Atlantic Oscillation (NAO) index annual mean and April-June mean from 1993-2019.	125
A.2	Density of modelled Atlantic salmon (<i>Salmo salar</i>) post-smolts (total number per 30 km ² bin) for all timesteps of modelled migrations each year (1993-2019).	126
B.1	The range of portfolio sizes per river giving a Sharpe ratio within 5% of the optimal. The optimal portfolio size is shown by a black square. In the case of infinite Sharpe ratios (as for river 1), the interval of portfolio sizes giving infinite Sharpe ratios is displayed.	127
B.2	Standard deviation σ_n and mean return μ_n of different portfolio sizes for (a) river 27 and (b) river 28. A vertical black dashed line indicates the value of n for the optimal Sharpe ratio.	128

B.3	Domain exit rate for each component of portfolios (thin lines) and the combined portfolio means (thick line) for river 27 and river 28 for: (a), (d) $n = 1$; (b), (e) $n = 4$, the optimal portfolio size for river 27; (c), (f) $n = 23$, the optimal portfolio size for river 28.	129
B.4	The coefficient of variation (CV) on individual-, river- and stock-levels, calculated without the domain exit rates of rivers 4-7, for: $n = 1$, i.e. the single best swimming behaviour per river; the selected optimal portfolio per river; and $n = 25$, i.e. the set of all modelled swimming behaviours per river.	130
B.5	Standard deviation σ_n and mean return μ_n for the optimal portfolio for each river against the minimum migration distance to the domain exit region.	130
C.1	Fishing hours of Russian fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.	132
C.2	Fishing hours of Faroese fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.	133
C.3	Fishing hours of Norwegian fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.	133
C.4	Fishing hours of Icelandic fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.	134
C.5	Region excluding waters less than 400m deep used for summing Global Fishing Watch (GFW) effort and pelagic landings.	135
C.6	Hours of Norwegian fishing effort from Global Fishing Watch (blue) and Norwegian pelagic landings (orange) over the region defined in Figure S5. Correlation coefficients r^2 and p are displayed where there is at least moderate evidence of a relationship ($p < 0.05$).	136
C.7	Hours of Icelandic fishing effort from Global Fishing Watch (blue) and Icelandic pelagic landings (orange) over the region defined in Figure S5. Correlation coefficients r^2 and p are displayed where there is at least moderate evidence of a relationship ($p < 0.05$).	137
C.8	Linear models fitted to monthly Icelandic fishing effort (from Global Fishing Watch) and landings in the central Norwegian Sea region per month, with the gradient of these being the estimated CPUE in tonnes per hour. Fishing hours axes are on a square root scale.	138

C.9	Estimated pelagic landings of the Faroese/Russian fleets (red/yellow line with circles, shaded confidence interval) per month alongside the summed annual Faroese/Russian mackerel, herring, and blue whiting landings (red/yellow dashed line) from ICES (2023g). Total monthly landings across the same area in the Norwegian Sea from the other nations considered in this study (all species, including blue whiting) are displayed as a dashed blue line.	139
C.10	Landings of mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	139
C.11	Landings of herring by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	140
C.12	Landings of horse mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	140
C.13	Landings of sardine by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	141
C.14	Landings of capelin by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	141
C.15	Landings of chub mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.	142

List of Tables

2.1	Mean 25th and 75th percentile Atlantic salmon (<i>Salmo salar</i>) smolt migration timing from six monitored rivers around the British Isles (Diack, 2021, https://doi.org/10.5063/F1HQ3XD1). River numbers are provided for the Burrishoole and the Bush, as displayed in Figure 2.1. *data were not available 1998-2000 and 2002-2003.	34
2.2	Linear relationships between the mean migration metrics per river and the minimum distance from each river to the continental shelf-edge, or the total minimum migration distance.	46
3.1	Prior distributions of the movement model parameters. *Note that these are minimum straight-line speeds between telemetry detections, and they are expressed in speed relative to the ground, rather than speed relative to the post-smolt (i.e. Eulerian rather than Lagrangian), so are not directly comparable with s	60
6.1	A summary of potential future research opportunities based on expanding the post-smolt movement model developed in this thesis.	120
A.1	Assumptions used in the development of the Atlantic salmon post-smolt (<i>Salmo salar</i>) migration model.	124
C.1	A summary of the target species, gear types, and operational fishing depths of the pelagic fisheries considered in this study. Cells are left blank where the information was not available within any ICES Scientific Reports.	131

Chapter 1

Atlantic salmon ecology and migrations in the northeast Atlantic

1.1 Overview

Atlantic salmon (*Salmo salar*; referred to as salmon throughout this thesis) inhabits temperate and subarctic regions around the North Atlantic (Aas *et al.*, 2010). Salmon are migratory fish, dividing their lifecycle between freshwater and marine environments. Their ability to return to their home river after a long-distance marine migration has been recorded since the 16th century, and measured since the early 20th century with mark and recapture studies (Stabell, 1984). Salmon have been considered important both culturally and as subsistence for thousands of years, and the annual return of salmon to their home rivers has been widely celebrated (Gunther, 1926; Mink, 2013; Kurlansky, 2020). Fishing has the potential to overexploit salmon, so conservation measures, in the form of limitations on salmon fishing methods and seasonality, have been applied in Scotland since the 18th century to prevent overfishing and to ensure that no single fisher took a large proportion of a river's stock (Robertson, 2001). However, fishing reductions are no longer sufficient to protect salmon. At present, there is negligible at-sea exploitation of salmon and most in-river angling is conducted using catch-and-release methods (ICES, 2024a). Despite this, since the 1960s, large declines in salmon population sizes have been observed across both the northeast and northwest Atlantic (Parrish *et al.*, 1998; Lehnert *et al.*, 2019), with salmon now being classified as 'near threatened' according to the International Union for the Conservation of Nature (IUCN) Red List Assessment (Darwall, 2023; Sayer, 2024).

Declines in marine survival rates of salmon are thought to largely explain the stock-wide population declines (Friedland *et al.*, 2009; Olmos *et al.*, 2020; Pardo *et al.*, 2021). While it is challenging to partition the marine survival rates of salmon to particular periods of time, it is thought that the first few months spent at sea by juvenile salmon is a period of particular vulnerability to mortality, likely due to their small body size and vulnerability to multiple predators (Thorstad *et al.*, 2012). This thesis focuses on the initial marine migration of juvenile salmon (the *post-smolt* life stage, as defined below). We focus on salmon originating from rivers around the British Isles,

but relevant information is included from other regions, such as the northwestern Atlantic. This introductory chapter begins with information applicable to all life stages of salmon, covering their lifecycle (Section 1.2) and methods used to collect data on migration traits (Section 1.3). Details on the juvenile marine migration stage are discussed, including migration phenology, pathways, behaviours, feeding, and predation (Section 1.4). Previous studies simulating marine migrations of juvenile salmon are discussed (Section 1.5), and the marine environment relevant to salmon in the northeast Atlantic is summarised (Section 1.6). Finally, information is provided on the current management and conservation measures applied to salmon stocks (Section 1.7). An overview of the remaining chapters of this thesis is provided in Section 1.8.

1.2 Anadromous lifecycle

Atlantic salmon is an anadromous species, returning from the sea to freshwater to reproduce (Myers, 1949). Mature adult salmon typically spawn in rivers between September and February, with more northerly populations spawning earlier in this period (Aas *et al.*, 2010). Spawning females select a suitable habitat and then use tail movements to create a depression for their eggs (Aas *et al.*, 2010). The eggs hatch the following spring as alevins, equipped with a yolk sac which contains all the nutrients required to sustain the first 3-8 weeks of life (Aas *et al.*, 2010). Following this, the fish emerge from the gravel and begin feeding in the river, employing a visual sit-and-wait foraging method. After further growth, the young salmon are known as parr. They remain in freshwater, feeding and growing, for 1-8 years in total (Aas *et al.*, 2010). Small-scale migrations are undertaken between preferred stream habitats, driven by temperature and resource requirements.

After achieving a threshold size and level of energy stores, maturation is triggered and salmon undergo a process known as smoltification to prepare for their life at sea. Physiological changes include the development of osmo-ionoregulation in seawater (Aas *et al.*, 2010), cardiovascular and respiratory adaptations for increased exercise demands (Høgåsen, 1998), and retinal changes to adapt to the differing optic environment of the sea (Jonsson & Jonsson, 2011). Visual and morphological changes include silvering, a slimmer and more streamline body, and darkened fins (Aas *et al.*, 2010; McCormick, 2024). Behavioural changes include a switch from positive to negative rheotaxis (i.e. swimming against currents to swimming in the direction of currents, facilitating downstream movement; McCormick *et al.*, 1998; Veselov *et al.*, 1998), a reduction in territorial and aggressive behaviour, and an increase in schooling behaviour (Jonsson & Jonsson, 2011). Smolts migrating downriver towards the sea are vulnerable to predation and challenges associated with migration barriers, such as dams (Flávio *et al.*, 2021).

Upon entering the sea, and until the end of their first winter at sea, salmon are termed post-smolts (Allan & Ritter, 1977). This life stage is a time of low and variable survival rates, which may drive large-scale trends in declining abundances of salmon (Thorstad *et al.*, 2012). Salmon spend 1-4 years at sea (Aas *et al.*, 2010), feeding and increasing in size greatly, before returning to their home river to spawn. River entry may occur at any time of the year (Lucas & Baras,

2008). It is believed that returning adult salmon identify their natal river using olfactory cues which they learned during their downriver migration (Aas *et al.*, 2010). Before entering the river, adults cease feeding. This transition is thought to occur once they have gained enough weight, particularly lean mass (Kadri *et al.*, 1995).

Atlantic salmon is an iteroparous species (Klemetsen *et al.*, 2003), meaning some individuals spawn more than once. A proportion of adult salmon return to the sea post-spawning to continue feeding and are known as kelts. Having used up most of their energy reserves during the upstream migration and spawning process, kelts are prone to mortality due to their poor body condition (Jonsson *et al.*, 1997). Kelts contribute little to the spawning population in some rivers (Hubley *et al.*, 2008), but are an important contribution in other rivers (Ducharme, 1969). Kelts can contribute more eggs than first-time spawners, due to their larger body size (Aas *et al.*, 2010).

Competition for resources, including food and shelter, is an important mechanism regulating salmon populations in freshwater (Finstad *et al.*, 2009; Aas *et al.*, 2010), and survival is density-dependent in the juvenile freshwater life-stages (Jonsson *et al.*, 1998; Einum & Nislow, 2011). Stock-recruitment curves typically increase steeply at lower egg densities, then plateau or begin to decline at higher densities, indicating that the population size is constrained by the carrying capacity of the river (Cushing, 1973; Buck & Hay, 1984; Jonsson *et al.*, 1998). Contrastingly, in the marine life-phase, salmon are distributed widely among a more abundant environment and therefore are not believed to be subject to density-dependent mortality (Jonsson *et al.*, 1998; Milner *et al.*, 2003).

There are several sources of plasticity in the salmon life cycle. Life-history variation can be driven by differing choices in resource allocation (for growth, reproduction, and maintenance) and differing environmental conditions (which influence physiological traits and behavioural choices) (Dammhahn *et al.*, 2018). The variable amount of time spent in the river by juvenile salmon (1-8 years) is an example of life history variability. In the late summer or autumn prior to their potential smolt migration, the salmon's energetic status (size, condition, and energy reserves; both the values at that point in time and the gradient of change) is thought to determine whether they will spend another year in fresh water or migrate in the following spring (Thorpe *et al.*, 1998). The threshold energetic status which must be reached is likely to be genetically determined (Thorpe *et al.*, 1998), and so will vary among individuals and populations. Individuals preparing to smolt the following spring will maintain a high appetite throughout the winter and continue to grow in body size, while those spending another year in freshwater display reduced appetite and little growth as an optimised survival strategy (Bull *et al.*, 1996).

A similar energetic-threshold based decision is made during the marine migration to determine when to return to freshwater to spawn. The growth of post-smolts during the first summer spent at sea may explain their probability of returning after spending one winter at sea (known as a one sea winter, or 1SW, fish; Tréhin *et al.*, 2021). Others delay maturation and may return after two sea winters (2SW) or more (multiple sea winters, MSW). Empirical evidence and modelling studies suggest that ongoing declines in marine growth rates (discussed further in Section 1.4.5) may drive increases in the proportion of 2SW and MSW returning adults (compared to 1SW),

as salmon need to spend more time at sea to grow sufficiently (Piou & Prévost, 2013; Tréhin *et al.*, 2021; Harvey *et al.*, 2022).

The decision of when to commence the return migration is also sex-specific (Tréhin *et al.*, 2021). Female fecundity increases with body length and condition (Jonsson *et al.*, 1996; Bacon *et al.*, 2012; Hanson *et al.*, 2020), so the spawning capacity of a salmon population is highly dependent on the growth of females at sea. Female salmon may need to spend more time at sea than males, particularly under increasingly poor growth conditions (Piou & Prévost, 2013). Reduced marine growth may hence decrease the overall return rates of female fish as opposed to males, if they are subject to the risk of marine mortality over an additional year (Piou & Prévost, 2013). Furthermore, female salmon do not mature before going to sea (aside from a small number of landlocked salmon populations; Hutchings *et al.*, 2019), but a proportion of male parr mature in the river and sneakily fertilise eggs ('precocious parr'; Aas *et al.*, 2010). These parr may mature again the following year as precocious parr, or migrate to sea as smolts and then return to spawn again as adults (i.e. they can be repeat spawners). Using an individual-based full lifecycle model of salmon, Piou & Prévost (2013) predicted that rising river temperatures will increase the proportion of mature male parr. Similarly, Adams *et al.* (2022) suggested that, if the present high costs of marine migration continue, salmon population sizes will continue to decline unless there is a shift in the expression of migration (e.g. a partial migration where males predominantly lose anadromy, but the females continue to migrate to the sea).

Life history diversity in salmonids can stabilise populations. Within a cohort, if fish spend a variable amount of time in the river, then a variable amount of time at sea, then the impact of poor environmental conditions at some point in space and time will be dampened across the cohort (Schindler *et al.*, 2010). This is an example of the portfolio effect, which describes how a varied portfolio of assets (here, life-histories) is likely to produce more stable returns (Schindler *et al.*, 2015). The portfolio effect is discussed in relation to behavioural variability of post-smolts in Chapter 3.

The anadromous lifecycle of salmon means they are exposed to both freshwater and marine pressures. Both environments are changing with ongoing global climate change (IPCC, 2021), and both environments can pose challenging conditions to various life-stages of salmon (Piou & Prévost, 2013). However, marine survival rates have seen particularly large declines over recent decades (Olmos *et al.*, 2019; ICES, 2024a), and it is believed that these are the main driver of population declines (Friedland *et al.*, 2009; Chaput, 2012; Friedland *et al.*, 2012; Pardo *et al.*, 2021). Marine survival rates of salmon are typically inferred from 'return rates', measured in some monitored rivers by trapping some or all of the migrating salmon as they leave and return (ICES, 2023e). Return rates are the proportion of salmon returning from the marine migration (of all those that exited the river in a given year), and are generally aggregated by the number of winters spent at sea. Recent return rates (2018-2022) of European salmon stocks ranged between 0.5-7%; between 1975-1985, return rates of 15-26% were not uncommon (ICES, 2024a). Understanding the mechanisms behind these declines in marine return rates is vital for effective future management actions (Bull *et al.*, 2022). The use of marine return rates to identify factors

impacting marine survival rates, and the uncertainties associated with this type of analysis, are discussed in Chapter 6.

1.3 Methods for collecting data on salmon migrations

Empirical data on salmon migrations, including counts, locations, timing, and swimming speeds, can be used to infer spatial-temporal distributions of salmon and their migration traits, helping to inform analyses of mechanisms driving marine survival (e.g. Gilbey *et al.*, 2021; Rodger *et al.*, 2025). These data are typically obtained through telemetric methods (i.e. tagging) or direct capture in surface trawls in the marine environment.

1.3.1 Telemetry

The main types of tag used for salmon of various life-stages are described below. They are listed in order of increasing size, which is important as tag size governs the minimum body size of salmon to be tagged. Battery size (and hence duration) is typically the limiting factor in tags (Thorstad *et al.*, 2013).

Passive integrated transponder (PIT) tags: these are the smallest electronic tags, with a minimum length of 9 mm and weight of 0.1 g (Thorstad *et al.*, 2013). PIT tags do not contain a battery and are activated by a radio signal when they pass close to a scanner. Each tag has a unique code so that individual fish can be identified. PIT tags are implanted in fish using a syringe implanter, or by making a small incision and inserting it (Thorstad *et al.*, 2013). The small size of PIT tags means they are suitable for salmon parr (Larsen *et al.*, 2013; Foldvik & Kvingedal, 2018), and they have a lifetime of up to several decades, so can provide information throughout the life-cycle (Thorstad *et al.*, 2013). However, PIT tags are greatly limited by their detection distance (around 1 m), so are typically only useful in small rivers or fish passes (Thorstad *et al.*, 2013).

PIT tags are sometimes used for capture-mark-recapture (CMR) studies, which can be used to estimate mortality (or specifically predation) rates (Anderson *et al.*, 2005; Gregory *et al.*, 2018). However, tag detections are imperfect in real systems and may be impacted by traits such as fish behaviour, size, and environmental conditions, meaning CMR results will exhibit some degree of bias (Gregory *et al.*, 2018).

Acoustic tags: commonly used for tracking smolts and post-smolts (e.g. Økland *et al.*, 2006; Thorstad *et al.*, 2013; Barry *et al.*, 2020; Newton *et al.*, 2021; Lilly *et al.*, 2022, 2023; Rodger *et al.*, 2025). Acoustic tags are surgically implanted into the abdominal cavity of salmon and may be up to 22 mm long and up to a weight of 2 g (Lilly *et al.*, 2023). Due to the non-trivial size of these tags, typically only individuals passing a minimum length and/or weight threshold will be tagged (e.g. 130 mm and 20 g; Lilly *et al.*, 2023); still, a tag may weigh up to 10% of the body weight of the salmon. The possibility of reduced fitness or survival of salmon due to the tag implantation surgery or the tag burden (weight or length of tag in relation to weight or length of fish) cannot be dismissed (Chavarie *et al.*, 2022), but some studies indicate that the survival of



Figure 1.1: PIT tagging salmon parr on the River Laxford in northwest Scotland. Parr were collected using electrofishing, which briefly immobilises fish and attracts them to the equipment, allowing them to be collected in a net, without causing any harm to the fish (Bohlin *et al.*, 1989).

tagged salmon smolts is not decreased with tags up to 12% of the body weight (Newton *et al.*, 2016; Lothian *et al.*, 2024).

Acoustic tags transmit signals to receivers placed in the water over distances of up to several kilometres (Thorstad *et al.*, 2013). The locations and approximate movements of salmon can be inferred from receiver detections. Detection rates depend on local conditions; a detection efficiency of 75% at 200 m distance has been measured in Scottish coastal waters (Newton *et al.*, 2021). Individual fish are detected at receivers via different frequencies or sequences of pulses (Thorstad *et al.*, 2013). Sensors recording environmental variables can also be combined with acoustic tags, such as temperature, depth of pH tags (Daniels *et al.*, 2019). The expected battery life of acoustic tags depends on the transmission rates. In a low transmission scenario, the battery can last for up to 500 days (Lilly *et al.*, 2023), however this will lower the detection rate of fish, and may not provide useful information. More typical transmission rates lead to an expected battery life of 75-90 days (Newton *et al.*, 2021; Lilly *et al.*, 2022).

Due to the limited battery life, and the required proximity to receivers, acoustic telemetry is generally used as a method for tracking smolts and post-smolts through the estuarine and nearshore marine migration. This method cannot provide information on the full migratory paths of salmon. Less commonly, acoustic tags may be implanted into smolts and then programmed to switch on after a given period of time, hence tracking the return migration of adult salmon in nearshore environments (e.g. Kennedy *et al.*, 2023), but this method requires an estimation of the return migration timings of adults, which is hard to estimate in systems where return timings are variable.

Data storage tags (DST): also known as archival tags, these tags store sensor data (such as temperature and depth) rather than transmitting it to a receiver, and hence must be recaptured to obtain the data (Thorstad *et al.*, 2013). They come in a range of sizes, with smaller sizes

suitable for implantation in smolts (25 mm length and 2.5 g; Guðjónsson *et al.*, 2015) and larger sizes suitable only for adult salmon (46 mm length and 19 g; Hedger *et al.*, 2022). The usability of this method is hindered by the necessity to recover tags, with data returned for a much smaller number of fish than were tagged (e.g. recovery rates of 1-5%; Guðjónsson *et al.*, 2015; Hedger *et al.*, 2022).

Pop-up satellite archival tags (PSAT): attached externally to salmon, these tags are programmed to detach after a pre-determined period of time, when they float to the surface and transmit stored sensor data and location at detachment to satellites (Thorstad *et al.*, 2013). They are large (115-125 mm length; Godfrey *et al.*, 2015), and hence can only be used for adult salmon. Unlike DSTs, they do not need to be collected; however, the transmission of data to satellites requires sufficient battery to remain after detachment, which can sometimes limit the amount of data obtained (Thorstad *et al.*, 2013).

Neither data storage nor pop-up satellite archival tags explicitly measure location (aside from the final location transmitted to satellites by PSATs), but post-process light-based geolocation methods can use day lengths measured by light sensors on the tags to estimate location. This method requires sufficient diel light variation to work accurately and hence is less effective in polar regions (Strøm *et al.*, 2018).

Interpreting telemetry data

In telemetry studies, the sample sizes are usually relatively small. For acoustic tags implanted in smolts, larger individuals may be selected to meet the minimum length or weight requirements. This means that the group of tagged fish may not be representative of the entire population, and particularly may be biased towards larger fish, which tend to have higher survival rates (Dieperink *et al.*, 2002; Gregory *et al.*, 2019). Additionally, the possibility of reduced fitness due to tag burden or the implantation surgery should not be overlooked, though the effect of tagging on survival rates has recently been shown to be minimal (Newton *et al.*, 2016; Lothian *et al.*, 2024).

Survival or migratory ‘success’ rates of smolts and post-smolts are often inferred from acoustic telemetry, based on loss rates (i.e. the count of tagged fish which were detected at one point in time and were then not subsequently detected). A number of these studies will be referenced in upcoming sections of this thesis: they are highly informative, but it must be noted that tag detections are not equivalent to survival. Tags may fail to be detected, or may be expelled (e.g. Brunsdon *et al.*, 2019; Lawrence *et al.*, 2023).

The identification of smolt and post-smolt migration traits based on acoustic telemetric data can also be biased by the detection of salmon with predators’ stomachs (Daniels *et al.*, 2019; English *et al.*, 2023; Waters *et al.*, 2024). If predated smolts are assumed to be swimming smolts, then estimates of swimming speeds, mortality rates, or migration pathways will be biased. It is sometimes possible to identify such predation events by unusual movements (e.g. Daniels *et al.*, 2018), but sensor tags (measuring pH, depth, or temperature) provide a more definitive measure

of predation. Unfortunately, these tags are not commonly used (or are only used for a small proportion of the tagged smolts) due to their greater cost.

1.3.2 Post-smolt surface trawls

After exiting coastal regions, where data on migratory movements can be obtained through acoustic telemetry, post-smolt locations are less clear. Previously, data were obtained through catches in commercial fisheries, but these data are no longer available with the now negligible at-sea salmon fisheries (ICES, 2024a). At-sea sampling of post-smolts can be undertaken using surface trawling methods (e.g. Shelton *et al.*, 1997; Turrell, 1997). These data typically provide the location and timing of a relatively small number of post-smolts. The river of origin, time spent at sea, and growth since entering the sea can also be inferred if tagged salmon are recaptured (Shelton *et al.*, 1997; Thorstad *et al.*, 2012). Alternatively, DNA samples can be collected from captured post-smolts, and genetic stock identification methods can be used to identify the river or region of origin (Gilbey *et al.*, 2021; Newton *et al.*, 2026).

1.3.3 Scale growth analysis

A growth record is stored in the scales of fish. Salmon scales are characterised by circuli, which are concentric ridges (Peyronnet *et al.*, 2007), much like growth layers in a tree trunk. The distance between circuli indicates growth conditions, with bigger gaps implying better growth (Peyronnet *et al.*, 2007). Growth can be partitioned into freshwater and marine growth, and further into post-smolt growth, or even monthly indices of post-smolt growth (McCarthy *et al.*, 2008; Vollset *et al.*, 2022). Scale samples can be collected nonlethally (Power *et al.*, 2023).

1.3.4 Otolith analysis

Otoliths are structures composed of calcium carbonate found in the inner ear of teleost fish that play a role in hearing and balance (Hanson *et al.*, 2013; Schulz-Mirbach *et al.*, 2019). They grow incrementally throughout the entire lifetime of fish, displaying ‘banding’ relevant to daily and annual growth (Hanson *et al.*, 2013). Like scales, otolith growth can be used to calculate the growth rates of fish (Sturrock *et al.*, 2020). Analysis of stable isotope ratios in otoliths can also reveal properties of the environment inhabited by fish, allowing for reconstruction of migratory movements and behaviours (Sturrock *et al.*, 2015). For example, the abundance of one stable oxygen isotope in otoliths is related to water temperature; using this, Hanson *et al.* (2022) reconstructed the temperatures experienced by individual salmon and then used this to inform a probability-based movement model (a hidden Markov model) and then estimate the locations of salmon at sea throughout their entire marine migration.

While stable isotope analysis of otoliths provides a promising approach to identifying migration pathways of salmon, it provides a large-scale and coarsely resolved result, not precise migration paths (Hanson *et al.*, 2022). A further drawback is that, unlike tagging or scale sampling, otolith extraction requires killing the fish (Lux, 1971).

1.4 Characteristics of the post-smolt migration

1.4.1 Migration phenology

The downriver migration of smolts is initiated in response to environmental cues, including river flow, photoperiod, and river temperature (McCormick *et al.*, 1998; Otero *et al.*, 2014; Lilly *et al.*, 2023; Adams *et al.*, 2025). Smolt migration timing varies among different regions and populations, with both west-east and south-north gradients in timing observed (Otero *et al.*, 2014; Vollset *et al.*, 2021). A trend towards earlier migration has been identified in many rivers, possibly driven by increasing freshwater temperatures (Russell *et al.*, 2012; Otero *et al.*, 2014; Tyldesley *et al.*, 2025).

McCormick *et al.* (1998) suggested that the migratory timing of smolts should coincide with both a physiological and an environmental ‘window’. They argue that smoltification is a reversible process, with osmoregulatory ability decreasing with time and exposure to high temperatures, and hence they defined the physiological window as the period of optimal physiological readiness for migration. The environmental window was defined as the period when physical and biological conditions (including temperature, food availability, and predator abundance or distribution) are optimal for smolt survival (McCormick *et al.*, 1998). When these two windows coincide, smolt survival rates are thought to be high. Other studies provide evidence towards the smolt window hypothesis: Hvidsten *et al.* (2009) found both sea temperature at marine entry and abundance of fish larvae to be positively correlated with return rates; Hansen & Jonsson (1989) found marine survival of hatchery smolts released in spring was higher than at other times of the year; Antonsson *et al.* (2010) found that later migrating smolts from two Icelandic rivers had higher survival rates than earlier migrating smolts.

The environmental smolt window hypothesis encompasses the more widely known ‘match-mismatch hypothesis’, where fish production depends on the phenology of juvenile development ‘matching’ the timing of peak plankton production (Cushing, 1990). For anadromous salmonids, the match-mismatch hypothesis implies that the timing of sea entry should match the timing of optimal prey availability (the diet of post-smolts is discussed in Section 1.4.5). Wilson *et al.* (2021) investigated this hypothesis for steelhead trout (*Oncorhynchus mykiss*), finding that there was an interannually-varying optimal migration date that maximised survival. Furthermore, they found that particular years with a great phenological mismatch between migration timing and increased zooplankton abundance had notably low marine survival rates. It is likely that similar relationships between Atlantic salmon migration timing, prey abundance, and marine survival exist, particularly as prey availability for post-smolts has been linked to overall marine survival rates (Tyldesley *et al.*, 2024).

Whether or not smolts migrate within the optimal environmental window will depend on the in-river environmental cues (including flow and temperature) that prime their downstream migration. Trends towards earlier migration have protected smolts against increasingly high river temperatures (Tyldesley *et al.*, 2025), but if the abundance of prey items is lower at the now-earlier point of marine entry, then there may be a phenological mismatch.

1.4.2 The estuarine migration of smolts

Studies using acoustic telemetry have characterised the migration qualities of smolts in estuaries. Smolts migrate actively (Martin *et al.*, 2009; Jensen *et al.*, 2022) and measured ground speeds range between 0.17-13.8 km/day and 0.2-3 BL/s, with differences observed between individuals, years and regions (Gudjonsson *et al.*, 2005; Halfyard *et al.*, 2012; Lilly *et al.*, 2022; Barry *et al.*, 2024). Barry *et al.* (2024) observed that smolts from an Irish river swam faster in the estuary than the lower river, possibly indicating a predator avoidance behaviour. Similarly, Lilly *et al.* (2022) measured faster smolt speeds in the outer Clyde estuary, as opposed to the inner estuary (note that the outer estuary speeds were almost double those of the inner estuary, so could not be accounted for by an increase in body length, and hence swimming speed). Evidence to support this predation-evasion hypothesis was provided by Flávio *et al.* (2020), who found that predation pressure was higher in the final 3.5 km of the river Bush in Northern Ireland than further upriver. Other studies have also found high mortality rates in estuaries (determined from telemetric detections, with limitations as discussed previously), but the specific values fluctuate between years and systems, ranging between 11 and 39% (Hvidsten & Møkkelgjerd, 1987; Dieperink *et al.*, 2002; Koed *et al.*, 2006; Flávio *et al.*, 2020; Lilly *et al.*, 2022; Barry *et al.*, 2024).

Smolts typically migrate nocturnally within estuaries, likely as a strategy to avoid predation by visual predators (Lothian *et al.*, 2018; Main, 2021; Lilly *et al.*, 2022; Barry *et al.*, 2024). However, later-migrating smolts are sometimes observed to migrate through both day and night (Thorstad *et al.*, 2012; Tétard *et al.*, 2019). Estuarine movement has been related to the tidal cycle in some systems, with smolts displaying passive reversal movements with the flood tide (Martin *et al.*, 2009; Lilly *et al.*, 2022). In other estuaries, smolt movements appear to be unrelated to tidal phase (Barry *et al.*, 2024).

Estuaries are often developed and industrialised, with high levels of human activity (Hodgson *et al.*, 2020; Dreujou *et al.*, 2023). As such, smolts may experience additional challenges, including pollution, low dissolved oxygen, artificial light and sound (Hodgson *et al.*, 2020), which may induce negative effects such as increased predation risk (McCormick *et al.*, 2009; Lerner *et al.*, 2012; Riley *et al.*, 2012; Ross *et al.*, 2013; Oppedal *et al.*, 2025).

1.4.3 The coastal migration of post-smolts

Upon entering coastal waters, post-smolts lose their nocturnal preference and migrate through the day (Lacroix & McCurdy, 1996; Lilly *et al.*, 2023). They are sometimes found to migrate faster in coastal waters than in estuaries, but estimated swimming speeds vary greatly between individuals and populations, ranging between 4-54 km /day (Lilly *et al.*, 2023; Rodger *et al.*, 2025). Migration success (based on tag detections) is also variable: Lilly *et al.* (2023) found that the minimum migration success of post-smolts in the Irish Sea ranged from 6-95% between rivers (in a single year), and Adams *et al.* (2025) found success rates of the coastal migration through the Moray Firth (Scotland) ranged from 37-100% between rivers (over two years).

Post-smolts may experience anthropogenically created challenges in coastal regions. For example, salmon aquaculture, common in sea lochs around the west coast of Scotland, exposes wild salmon to the risk of infestation by parasitic sea lice. Sea lice infestation is associated with reduced growth of salmon and increased predation risk (Thorstad *et al.*, 2012; Harvey *et al.*, 2022). Salmon mortality attributed to sea lice varies between locations and time periods (Johnsen *et al.*, 2021). Individual or population-specific migration behaviours are also likely to impact the exposure of salmon to sea lice (and hence their mortality risk): post-smolts that spend longer close to the coast are more likely to be infested by sea lice (Thorstad *et al.*, 2012), and post-smolts swimming at moderate swim speeds (around 1 BL/s) have been found to have higher modelled exposure rates to sea lice (Murray & Moriarty, 2021). Concern has also been expressed about the interactions between salmon post-smolts and marine energy structures (e.g. Thorstad *et al.*, 2012; Gillson *et al.*, 2022). Marine structures can encourage aggregations of fish, which in turn attract predators (Bicknell *et al.*, 2025), possibly increasing the predation risk of salmon near energy structures (Malcolm *et al.*, 2010). Additionally, artificial electromagnetic fields are introduced by energy structures and their connecting cables (Gillson *et al.*, 2022). As salmon are thought to use magnetic fields to navigate (Minkoff *et al.*, 2020), it is possible that electromagnetic fields affect their migratory behaviour.

1.4.4 The open ocean migration of post-smolts

As mentioned previously, recent data collection on the open ocean distribution of salmon post-smolts is generally limited to surface trawls. Using this method, post-smolts have been identified near the continental shelf-edge west of the British Isles in May and June (Holst *et al.*, 1996; Shelton *et al.*, 1997). Interannual variation in migration routes was also identified by Holst *et al.* (1996). Gilbey *et al.* (2021) conducted a comprehensive analysis of a large number of surface trawls, where post-smolts were genetically assigned to stock groups so that their migration routes could be better understood. Similar to the earlier studies, Gilbey *et al.* (2021) identified a relatively high number of post-smolts in the shelf-edge current in May and June, and a smaller number in April. By July, most of the post-smolts were residing in the Norwegian Sea, where they remained for the following months. Post-smolts were found in the northern North Sea (near Shetland) in June and July (Gilbey *et al.*, 2021). More recently, Newton *et al.* (2026) used pelagic trawls and genetic stock identification techniques to infer the distribution and migration patterns of post-smolts from eastern Scottish and northeast English rivers draining into the North Sea. They found that post-smolts were constrained to specific migration regions, or ‘corridors’, but the spatial distribution of post-smolts varied between rivers.

Even with the knowledge gained from these studies, there are many gaps in the knowledge of post-smolt migration paths in the open ocean. None of these studies widely sampled the North Sea, meaning the distribution of post-smolts there is still not fully understood. There was also no sampling by Gilbey *et al.* (2021) south of Shetland in July and later months. It is therefore not possible to confirm that slower-moving or later-exiting migrants were not still in the seas surrounding the British Isles at this point.

1.4.5 Feeding and growth

Smolt body size has been found to be positively related to eventual marine return probability (Friedland *et al.*, 2009; Gregory *et al.*, 2018; Armstrong *et al.*, 2018; Chaput *et al.*, 2019). Upon entering the sea, post-smolts must continue to grow rapidly to escape the “risk size window” where they are highly likely to be preyed upon (Aas *et al.*, 2010). However, there is evidence to suggest that post-smolt marine growth rates have declined. Tréhin *et al.* (2021) found that growth rates of post-smolts from a French river during the first summer at sea had declined between 1987 and 2017, while Harvey *et al.* (2022) found that growth during the first year at sea of a Norwegian salmon population had declined over the past four decades. Maoiléidigh (2018) found that the lengths of 1SW salmon from several European rivers had declined significantly between 1960 and 2010. Growth declines may be climate-driven, with Todd *et al.* (2021) finding a link between increasing sea surface temperatures and growth patterns. Using the scale circuli spacing of 1SW Atlantic salmon, they found decreases in periods of fast growth, increases in slow growth periods and increases in growth pauses. These changes were significantly linked to warming sea surface temperatures. Similarly, Todd *et al.* (2008) found a negative correlation between sea surface temperature anomalies in January and the total marine growth of 1SW salmon.

As their body length increases, it is also crucial that salmon gain enough weight to maintain energy reserves, such as lipids (Todd *et al.*, 2008; Smith *et al.*, 2009). The ‘condition factor’ of fish, typically defined as weight divided by length cubed, is often used as a marker for growth quality (Todd *et al.*, 2008; Aine *et al.*, 2011; Utne *et al.*, 2021b). To obtain necessary length and mass growth, post-smolts consume a range of prey items, including fish larvae, amphipods, decapods and euphausiids (Utne *et al.*, 2021a,b). The feeding ecology of post-smolts is discussed further in Chapter 5.

1.4.6 Predation

In estuarine and coastal regions, predators of smolts include birds (cormorants, goosanders, herons, corvids, gannets, gulls), pinnipeds (harbour and grey seals), piscivorous fish (cod, halibut, saithe) and otters (Reitan *et al.*, 1987; Metcalfe *et al.*, 1987; Carss *et al.*, 1990; Koed *et al.*, 2006; Butler *et al.*, 2006; Jepsen *et al.*, 2006; Sharples *et al.*, 2009; Falkegård *et al.*, 2023; Säterberg *et al.*, 2023; Sortland *et al.*, 2023). In the open ocean, salmon are preyed on by toothed whales, large endothermic fish such as tuna and porbeagle, and large ectothermic fish such as blue sharks (Strøm *et al.*, 2018; Falkegård *et al.*, 2023).

Predation is a clear, visible driver of mortality, but it is not independent of other drivers. Predation might be the ultimate cause of mortality, when a healthy individual is taken and predation is the only cause of death, or the proximate cause of mortality, when predation was not the primary cause of death as the individual was less fit in some way (Falkegård *et al.*, 2023). Predation as a proximate driver of mortality is inextricably linked to other factors that reduce the fitness of salmon, including anthropogenically driven factors such as pollution and artificial structures that disrupt migration in rivers or at sea (Ross *et al.*, 2013; Falkegård *et al.*, 2023). Furthermore,

predation might disproportionately affect populations that are already compromised (Falkegård *et al.*, 2023).

Controlling predator populations has been suggested by some as a possible management strategy to aid salmon populations. However, the evidence for the benefit of this strategy is weak, and reducing predators can create a gap which may instead be filled by a less dominant predator or an invasive species (Falkegård *et al.*, 2023). A more viable option might be to focus on the restoration of other species that predators of salmon eat, consequently reducing the pressure on salmon (Falkegård *et al.*, 2023).

1.5 Movement modelling

While empirical methods such as telemetry and surface trawls have revealed a lot about the migration of post-smolts, both of these approaches leave gaps. For example, acoustic telemetry is useful in estuaries, sea lochs, and coastal regions, but provides little to no data on the open-ocean migration of salmon, while surface trawls provide a single location of post-smolts, but not the path taken before or after the detection. Modelling approaches are typically used to fill gaps, both literally by joining together known points of occupancy (e.g. Booker *et al.*, 2008), or to fill less visible knowledge gaps, such as the navigation mechanisms used to guide post-smolts (e.g. Burke *et al.*, 2016a; Newton *et al.*, 2021).

1.5.1 Particle tracking and active swimming models

Individual-based models (IBMs), also known as agent-based models, are a common modelling approach for the simulation of post-smolt migrations. IBMs are a type of mechanistic model where processes are simulated for a large number of individuals, each of which may display slightly different traits (through different model parameterisations or a stochastic element in the model) (DeAngelis & Grimm, 2014). Population-scale results are obtained by combining the results of all modelled individuals.

Particle tracking models are an example of an IBM. These models use a Lagrangian approach to simulate the advection and diffusion of particles in a flow, and are useful for simulations such as larval dispersal (Garnier *et al.*, 2025). A further sub-class of model consists of a particle tracking model coupled with an active movement component. This type of model is relevant to organisms that move actively and are also passively transported (advected) in a flow, such as migratory fish. IBMs combining particle tracking and active movement have been used to simulate fish migrations on a range of scales, from small-scale vertical movements of brown shrimp (*Crangon crangon*; Daewel *et al.*, 2011) to the long-distance migration of blue whiting (*Micromesistius poutassou*; Dolmaire, 2022). More specifically, several relevant studies have applied these methods to simulate the marine migration of salmon post-smolts. These studies are summarised chronologically below. Each of these studies developed swimming behavioural models based on empirical evidence regarding the navigational cues and responses of post-smolts in the ocean; the evidence to support these behavioural models is discussed in Chapter 2.

Booker *et al.* (2008) developed a movement model for post-smolts migrating from the west coast of Ireland by testing several active swimming behaviours: random movement; rheotaxis (orientation to local currents; Coombs *et al.*, 2020); and thermotaxis (orientation to temperature gradients). The rheotactic behaviour used by Booker *et al.* (2008) was “negative”, meaning that movement was in the same direction as local currents (whereas positive rheotaxis is movement against the currents). The thermotactic behaviour was variable, with simulated post-smolts moving up or down temperature gradients to stay in a preferred water temperature of 4-8 °C, and moving randomly when within this temperature range. Booker *et al.* (2008) compared their modelled trajectories with the recapture locations of 15 salmon tagged in rivers on the west coast of Ireland and subsequently recaptured at sea. Both rheotaxis and thermotaxis led to simulated trajectories passing close to the known locations of post-smolts, while the randomly directed swimming behaviour did not. The authors noted that a combination of both rheotactic and thermotactic behaviours might be feasible, but they did not test this in their study.

Mork *et al.* (2012) expanded this work by simulating post-smolts migrations from two locations (west Ireland and southwest Norway) with two behaviours: rheotaxis, and rheotaxis combined with movement up or down temperature and salinity gradients to maintain preferred ranges (8-12 °C and ≥ 35 psu). The simulations were run for two years (2002 and 2008), selected by the authors due to their varying measures of the North Atlantic Oscillation index (discussed in Section 1.6). Different migration routes were observed between the two years, suggesting that environmental variability described by the NAO index may affect migrations. Mork *et al.* (2012) compared their model results with trawl survey data from 2008 and 2009, finding a generally good agreement between the modelled particle distributions and the known locations of post-smolts. However, the authors did not discuss whether one of the two swimming behaviours gave a better spatial and temporal overlap with the observations.

Across the Atlantic, Byron *et al.* (2014) used a particle tracking model combined with a bioenergetics model to investigate the impact of oceanographic variability on the migration of post-smolts in the Gulf of Maine across several years (2002-2007). The active swimming model consisted of movement towards a target point, with an element of stochasticity included in the direction. Byron *et al.* (2014) found that migration pathways were relatively consistent throughout years (which is unsurprising given the movement model was not dependent on environmental conditions), but success rates and timings varied, with surface currents having a notable impact on migrations. The coupled bioenergetics model assumed that feeding rate was constant, but the conversion of food to body mass was temperature dependent. This meant that a fish taking longer to migrate had more time to grow, and hence could be bigger (though there was a risk of an “unsuccessful” migration if fish took too long to migrate). A trade-off was suggested between migrating quickly (but not having much time to grow) and migrating slowly, but potentially risking not making it there in time. Growth was therefore dependent on both temperature (directly) and surface currents (indirectly, through their impact on time taken to migrate).

Using the same time period and location as Byron *et al.* (2014), Moriarty *et al.* (2016) tested six swimming behaviours: passive movement; directed movement towards a target point; positive

and negative rheotaxis; and temperature gradient following to within 8-15 °C, with either random or rheotactic movement when within the preferred range. Migration paths and "success" rates, defined by the proportion of simulated salmon reaching a defined point within 60 days, varied between behaviours, river start points and years. No comparisons with empirical data were made, and the authors did not select any behavioural model as the most effective or realistic.

Over in the Pacific, Burke *et al.* (2016a) simulated the migrations of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). With a differing location and study species, this study is not directly comparable with the others summarised here, but it is discussed as it complements the findings of the Atlantic studies. Burke *et al.* (2016a) compared simulated migrations with empirical data from marine surface trawls that collected juvenile Chinook salmon. Trawled fish were genetically assigned to stock units, and their marine growth rates were back-calculated from their otoliths. Then, a number of variations of a movement model (in which fish swam in a directed manner according to their internal compass and away from the river mouth) were compared with the observed Chinook salmon (in terms of modelled final location and growth rate). The authors concluded that to maintain the interannual consistency in the observed distribution of juvenile Chinook salmon, the salmon must adapt their migration behaviour in response to variation in ocean currents.

Ounsley *et al.* (2020) then provided the first simulations of post-smolts migrating from Scottish rivers. The authors tested a variety of simulated swimming behaviours: passive movement; negative rheotaxis; directed movement on northwest, north, and northeast bearings; and the swimming models of both Booker *et al.* (2008) and Mork *et al.* (2012). The model was assessed according to migration "success", defined as a simulated smolt exiting the Scottish continental shelf region for the Norwegian Sea within 100 days. Only the directed movement behaviours resulted in successful migrations, but the applicable swimming direction varied regionally.

On a smaller scale, Newton *et al.* (2021) simulated post-smolt movements in comparison with telemetry data in the Moray Firth in Scotland. They tested passive movement, directed swimming on different bearings, and negative rheotaxis, finding that directed swimming on a bearing of 70° from north gave the greatest similarity to the tracked fish (though this bearing did not provide the shortest route to the open ocean).

Utne & Mousing (2025) simulated the migrations of post-smolts from eighteen rivers in Norway. They tested eleven swimming behaviours, with navigational cues including surface currents, temperature and salinity gradients, prey gradients, depth gradients, and compass direction. A model was selected based on a comparison with the abundances of salmon from surveys in the Norwegian Sea; this model included following currents, avoiding low temperatures (<2°C), and following an increasing depth gradient. However, the optimal model was only slightly better performing (in comparison with the empirical data) than a model in which post-smolts followed an increasing depth gradient and a northward direction, suggesting that multiple swimming behaviours could recreate observed patterns. Utne & Mousing (2025) did not test different swimming behaviours for different rivers, nor did they examine interannual variation in simulated migrations. They did, however, consider simulated prey encounters and resulting post-smolt

growth rates; this is discussed further in Chapter 5.

1.5.2 Common themes and disparities in post-smolt movement models

Migration modelling studies cannot confirm the exact navigational behaviours of salmon, but they can rule out unlikely behaviours and deem others to be feasible (Byron & Burke, 2014). There are areas of similarity and dissimilarity between each of the studies above in terms of the behaviours found to be feasible. Passive movement was a point of agreement; it was ruled out as a feasible migration behaviour by all those who tested it. Rheotaxis, however, was found to be feasible by Booker *et al.* (2008) and Mork *et al.* (2012) but not by Ounsley *et al.* (2020) or Newton *et al.* (2021), even though the Irish river of focus in the Mork *et al.* (2012) study was relatively close to the Scottish rivers considered by Ounsley *et al.* (2020). Similarly, the temperature preference models of Booker *et al.* (2008) and Mork *et al.* (2012) were found to be unsuccessful by Ounsley *et al.* (2020) (i.e. these models did not successfully simulate migration northwards toward the Norwegian Sea). Though in a slightly different format to the Booker *et al.* (2008) and Mork *et al.* (2012) models, Utne & Mousing (2025) also tested combinations of behaviours following surface currents, temperature and salinity gradients, and found that these did not reproduce observed abundances of post-smolts in the Norwegian Sea. Both of the Scottish studies found that directed movement on a constant compass bearing was the only swimming behaviour that could replicate known migration patterns, yet different compass bearings were found to be required for different areas around Scotland (Ounsley *et al.*, 2020; Newton *et al.*, 2021). Furthermore, while Booker *et al.* (2008) and Mork *et al.* (2012) appear to agree on the temperature preference model being suitable for simulating post-smolt migrations, the preferred temperature ranges differed between the two studies (4-8 °C and 8-12 °C respectively).

The differences between these studies could be taken as evidence towards the requirement of specific regional migration strategies (Byron & Burke, 2014). Salmon populations from different locations will experience different ocean conditions, and populations are locally adapted to their environment, meaning their fitness is optimised for the environment they will experience (Taylor, 1991). Furthermore, empirical evidence suggests the existence of different migration behaviours in different regions (Lacroix, 2008, 2013). Local adaptation and behavioural differences between populations are discussed further in Chapter 3.

Differences in methods might also have driven some of the disparities between studies. Firstly, the assessment and selection of swimming behaviours varied between studies, with some using the spatial and temporal overlap between the model and empirical data (e.g. Mork *et al.*, 2012), and others defining ‘successful’ models by migrants reaching a location within a given time frame (e.g. Moriarty *et al.*, 2016; Ounsley *et al.*, 2020). The swimming speed varied between studies, and they did not all include a sensitivity analysis of this parameter, meaning the selection of feasible migration behaviours may have been affected by the selected speed. Furthermore, hydrodynamic ocean models differed between the studies. Burke *et al.* (2016a) used two different ocean models to run their Chinook salmon migration model, and found that ocean temperatures and currents experienced by simulated salmon were dependent on the ocean model selected. Additionally,

Burke *et al.* (2016a) found that the resulting modelled speed relative to the ground of migrations varied between the ocean models. Differences in ocean models might hence drive some of the differences between studies. Burke *et al.* (2016a) did not discuss differing grid resolutions between their two ocean models as they were fairly similar, however the grid resolution of the ocean models used in the studies summarised here ranged from 150 m (Newton *et al.*, 2021) to 27 km (Booker *et al.*, 2008). This might be another cause of the differences in results; movement models based on different scales of environmental cues will undoubtedly differ.

While conclusions on swimming behaviours varied, these studies collectively provide evidence that post-smolts might navigate by following currents, temperature gradients, salinity gradients, and magnetic cues.

1.6 Oceanographic conditions and variability in the northeast Atlantic

There are several pathways by which oceanographic variability will impact salmon post-smolts. If post-smolts use ocean currents and gradients to navigate (Dadswell *et al.*, 2010; Mork *et al.*, 2012; Utne & Mousing, 2025), then variability or long-term trends in oceanographic variables will alter their migrations. Independent of navigation cues, ocean currents will also impact post-smolts through advection (even if they swim against the currents). Changes in oceanographic conditions will indirectly alter the prey distribution and availability for post-smolts (e.g. Tyldesley *et al.*, 2026). Finally, temperature changes might have direct physiological effects on post-smolts (e.g. McCormick *et al.*, 1998; Vargas-Chacoff *et al.*, 2018). This thesis focuses on the migration of post-smolts from rivers around the British Isles, which lie on the northwest European shelf, with the shelf-edge being approximately 300 km from the west coast of Scotland. Shelf seas exhibit variable oceanographic conditions which vary over daily, seasonal, interannual and decadal timescales (Jones *et al.*, 2018). A discussion of the local and Atlantic-wide drivers of oceanographic variability on the shelf west of Scotland and Ireland is provided in Chapter 2. Here, a broader summary of oceanographic variability across the region is provided.

In the absence of mixing, surface heating drives stratification in shelf seas, meaning the water layers are discrete, with warm water at the top of the water column and cool water at the base (Simpson & Sharples, 2012). In the summer months, when wind stress tends to be lower, stratification is observed in the shelf seas around the British Isles, aside from a tidally-mixed region along the coastline (Sheehan *et al.*, 2017; Jones *et al.*, 2018). The annual onset of stratification is thought to cause the onset of the spring phytoplankton bloom (Simpson & Sharples, 2012). Reduced mixing over the thermocline (the transition between warmer surface water and cooler deeper water) constrains phytoplankton to the surface waters, where they experience high light levels, allowing for rapid growth. However, nutrients are quickly depleted in the stratified surface layer, as they are not replenished by mixing with the deeper waters, meaning the phytoplankton production drops after the initial bloom. During the autumn and winter, or other periods of high wind stress, the water column becomes more homogenous (Jones *et al.*, 2018). Surface salinity

is greatly influenced by wind stress, as the strength and direction of the wind drives the wider propagation of freshwater run-off from near the coastline (Jones *et al.*, 2018). For example, on the shelf west of Scotland, under easterly winds, surface waters on the shelf will be much fresher due to the spread of coastal water. Conversely, under westerly wind conditions, more Atlantic water will be transported onto and across the shelf, meaning surface salinity will be higher. The extent and timing of stratification or mixing might impact salmon indirectly through trophic-level changes. More directly, salmon will experience different temperature and salinity regimes in stratified versus mixed seas, which may impact their migration if they use these variables to navigate.

At the shelf-edge west of the British Isles, the bathymetry drops suddenly from less than 200 m to approximately 2000 m (Barton *et al.*, 2022). The abrupt transition generates a current flowing parallel to the isobaths (depth contours), known as the slope or shelf-edge current (Simpson & Sharples, 2012). A branch of the shelf-edge current flows southeast into the North Sea between Orkney and Shetland (Sheehan *et al.*, 2017). These prevailing currents, directed north-northeast and southeast respectively, have the potential to impact post-smolts migrating northwards to the Norwegian Sea.

Large-scale mechanisms alter oceanographic conditions off-shelf and at the shelf-edge. Slope current variability is related to the extent of the subpolar gyre, a rotating body of cold, low salinity, subpolar water in the northwest Atlantic (Hátún *et al.*, 2005; Holliday *et al.*, 2020; Clark *et al.*, 2022). An expanded, or strong, subpolar gyre drives subpolar water towards the northeast Atlantic, while a contracted subpolar gyre allows the transport of more warm, saline Atlantic water (Hátún *et al.*, 2009). The extent of the subpolar gyre has been linked to the abundances of zooplankton, blue whiting, and pilot whales in the northeastern Atlantic (Hátún *et al.*, 2016). A multidecadal decline in eastward water transport in the Atlantic (towards the shelf-edge), attributed to changes in density, has been seen (Clark *et al.*, 2022). A substantial increase in warm water inflow into the slope current has also been seen over recent decades (Clark *et al.*, 2022). These changes impact nutrient transport, and the warming waters may also impact species distributions.

1.6.1 Atmospheric and oceanographic indices

Several indices provide simple measures of large-scale variability in the north Atlantic.

SPG index: The strength of the subpolar gyre is measured by an empirical orthogonal function (EOF) decomposition of the sea surface height across the regions spanned by the subpolar and subtropical gyres in the north Atlantic (Hátún & Chafik, 2018).

NAO index: The North Atlantic Oscillation index is defined by the difference in sea-level pressure between the Azores (high pressure) and Iceland (low pressure) (Hurrell, 1995). It is related to the strength of westerly winds across the north Atlantic, which can alter water properties (Hátún *et al.*, 2009; Sheehan *et al.*, 2017). Temperature and rainfall are also linked to the NAO (Wakelin *et al.*, 2003).

AMO index: The Atlantic Multidecadal Oscillation index is the Atlantic-wide sea surface temperature anomaly, detrended from ongoing global climate change (Nye *et al.*, 2014). It describes some of the variability in sea surface temperature in the shelf seas around the British Isles (Sheehan *et al.*, 2017).

The NAO and AMO indices have been correlated with salmon marine return rates and growth (Jonsson & Jonsson, 2004; Peyronnet *et al.*, 2008; Friedland *et al.*, 2009). Relationships between these indices and metrics of salmon abundance, survival, and migratory success are discussed in Chapter 2. Sea surface temperature has also been (both positively and negatively) correlated with salmon marine survival and growth rates (Friedland *et al.*, 1998; Harvey *et al.*, 2022). However, the potential mechanisms behind these relationships are unclear. For example, it is not known whether temperature directly drives changes in survival and growth, or if it acts as a proxy for another variable (such as prey availability). The conflicting relationships between analyses suggest caution should be taken when correlating salmon metrics with sea surface temperature; additionally, we note that relationships between salmon metrics and temperature have commonly been found to break down with time (Klemetsen *et al.*, 2003).

1.7 Management of salmon stocks

Salmon pose a particular management challenge as their lifecycle is divided between freshwater and marine environments, yet conservation action is mainly constrained to the freshwater environment (Bull *et al.*, 2022). Post-smolts experience many challenges at sea, and these may be intensified or exacerbated by lagged ‘carryover’ effects from poor freshwater rearing conditions (McCormick *et al.*, 2009; Russell *et al.*, 2012). Most studies do not evaluate the lifecycle-wide effects of freshwater pressures (with the exception of full lifecycle models such as IBASAM, Piou & Prévost, 2012, or the Atlantic Salmon Trust Decision Support Tool, discussed in Chapter 6). However, given the lack of density-dependent mortality at sea, it is assumed that a larger number of smolts exiting rivers should lead to a larger number returning from the marine phase (Thorstad *et al.*, 2021). Migrating smolts must also be in good condition; larger (longer and heavier) smolts have a higher probability of returning (Armstrong *et al.*, 2018; Gregory *et al.*, 2019). Therefore, any factor that reduces the growth of salmon in the river (smolts and younger life stages) or increases mortality (through predation or otherwise) can be interpreted as eventually causing lowered numbers of adult returning salmon.

McCormick *et al.* (2009) reviewed the anthropogenic factors that can negatively influence smolts, leading to reduced marine survival rates. They suggest that exposure to high water temperatures or contaminants, including acids and heavy metals, over a period of time can inhibit osmoregulatory ability (linked to increased predation risk, Schreck *et al.*, 2006; Stich *et al.*, 2015). McCormick *et al.* (2009) also suggested that migration delays due to dams or other migration barriers would have a similar negative impact on osmoregulatory ability, and more so when combined with high water temperatures. Other studies have identified additional anthropogenic and climate-driven factors that negatively impact smolts. For example, low river flow rates can delay

the downstream migration of smolts (possibly because salmon smolts require a minimum flow of 0.5-0.9 m/s to swim in a rheotactic manner, Veselov *et al.*, 1998; Kundegorski *et al.*, 2025), with any migration delays increasing their risk of mortality (McCormick *et al.*, 1998; Hodgson *et al.*, 2020). Similarly, artificial light and sound can cause migration delays and physiological stress to juvenile salmonids, potentially increasing predation rates (Feist *et al.*, 1991; Tabor *et al.*, 2004; Nelson *et al.*, 2021; Vega *et al.*, 2024).

Similar challenges are posed to the other life stages of salmon. Low river flow rates and high water temperatures can cause migration delays to returning adult salmon, leading to reduced likelihood of successful river entry (Priede *et al.*, 1988; Solomon & Sambrook, 2004; Jonsson & Jonsson, 2009). Furthermore, exposure to high water temperatures increases the metabolic requirements of adult salmon, possibly leading to declines in spawning capacity (Lennox *et al.*, 2018). We note that periods of extreme (low or high) flow rates and high water temperatures are increasing in frequency with ongoing human-driven climate change (Watts *et al.*, 2015; IPCC, 2021), suggesting in-river conditions might become increasingly hazardous to salmon. Periods of high river flow, including floods, can redistribute substrate in rivers, changing the availability and quality of spawning habitat for salmon (Lennox *et al.*, 2021). All life stages of salmon require a physically complex river habitat, including substrate of different sizes, boulders, and woody structures (Floyd *et al.*, 2009; Finstad *et al.*, 2011). Harvesting of trees along rivers has caused a large decline in woody structures in rivers across the Atlantic and Pacific (Floyd *et al.*, 2009). Habitat simplification through the removal of riparian trees is an example of a local pressure, which might be relevant in some rivers but not all, or some stretches of any river (though we note that this is a very common situation), while increasing temperature is a global pressure which affects all rivers. Moore *et al.* (2025) suggested that salmon rivers are likely to experience both local and global pressures, and local pressures can exacerbate global pressures; this is true for tree harvesting, which can also increase river temperatures further due to the removal of shading.

Local river management can ease local pressures, consequently reducing the cumulative impact of local + global pressures. For example, reintroducing woody structures into rivers can increase habitat complexity, while replanting of riparian vegetation can improve shading, and eventually repopulate the river naturally with woody structures (van Zyll De Jong *et al.*, 1997; Moore *et al.*, 2025). Migration barriers, such as dams, can be removed, or bypass channels can be developed, to reduce migration challenges and delays (Koed *et al.*, 2020). Chemical pollutant input into rivers, including agricultural runoff, can be minimised (Koed *et al.*, 2020). Artificially straightened (channelised) rivers can be restored to their former meandering paths, poor water quality can be remediated, and gravel can be added to restore spawning habitat (Lennox *et al.*, 2021).

The above examples are of habitat restoration management actions. More active restoration of salmon population sizes in some rivers is undertaken by hatchery stocking, where salmon are artificially reared in hatcheries and then released into the river (Lennox *et al.*, 2021). This can be useful, or indeed necessary, to maintain some salmon populations (Lennox *et al.*, 2021). However, stocking can deteriorate the genetic structure and fitness of wild anadromous salmonid

populations (Koed *et al.*, 2020; May *et al.*, 2024). Additionally, hatchery-reared fish have been found to display different migratory behaviours and lower survival rates compared to wild fish (Stabell, 1984; Thorstad *et al.*, 2012; Lennox *et al.*, 2021; Nilsen *et al.*, 2022a). Hatchery stocking may boost population sizes, but the long-term population effects are often unclear.

The results of local management strategies vary greatly, with positive results recorded in some rivers, and neutral or negative results in others (Lennox *et al.*, 2021). This suggests that appropriate action is specific: it must be focused around the particular limiting factors for a river (e.g. spawning habitat availability may limit some rivers, while migration barriers will limit others by stopping the movement of smolts and adults downstream/upstream). With uncertainty surrounding the outcomes of interventions, Finstad *et al.* (2011) suggest the importance of an adaptive management approach, where the effects of actions are monitored, and then actions are modified as required. Additionally, Finstad *et al.* (2011) emphasise the importance of widely sharing findings to aid future management developments. Furthermore, it is vital that novel research findings are communicated in an accessible manner to river managers in order to drive effective management actions (Bull *et al.*, 2022). Communication across the science-management interface is discussed in Chapter 6.

1.7.1 Invasive pink salmon

Pink salmon (*Oncorhynchus gorbuscha*) are an invasive species which pose concern to Atlantic salmon. They have spread across the north Atlantic after they were intentionally released in northwest Russia between 1950 and 1999 (Skóra *et al.*, 2023; Thorstad *et al.*, 2025). Like Atlantic salmon, they are an anadromous species, undertaking a marine migration before returning to rivers to spawn (Thorstad *et al.*, 2025). In 2017, large numbers of pink salmon started appearing in Norway, and there are now 11 times more invasive pink salmon than Atlantic salmon in Norwegian rivers (Thorstad *et al.*, 2025). There have been fewer pink salmon recorded in British rivers, but evidence was recently found of successful spawning of pink salmon in two Scottish rivers (Skóra *et al.*, 2023). Furthermore, it was found that the pink salmon smolts were feeding in the river, contrasting with previous beliefs that pink salmon smolts migrate downriver shortly after hatching (Skóra *et al.*, 2023). This suggests that pink salmon could compete for food resources with Atlantic salmon fry and parr, with potential negative implications for native salmon stocks. If pink salmon continue to colonise British rivers, extensive removal may be required, as currently actioned in Norway (Thorstad *et al.*, 2025).

1.8 Thesis overview

Atlantic salmon populations have declined greatly across their range since the 1960s (Parrish *et al.*, 1998; Lehnert *et al.*, 2019), with this change attributed to declines in marine survival rates (Friedland *et al.*, 2009; Olmos *et al.*, 2020; Pardo *et al.*, 2021). However, the causes of reduced marine survival of salmon are still not fully understood. Drawing upon the literature on factors affecting Atlantic salmon survival across the lifecycle, Bull *et al.* (2022) identified six key drivers of marine mortality: reduced prey availability, predation, competition, marine fisheries, aquaculture, and climate change. These drivers are all candidates for explaining patterns in marine survival rates, both long-term declines and year-to-year or river-to-river fluctuations, and understanding them better will help inform management decisions to protect Atlantic salmon. The extent to which these drivers impact populations will depend on the migration routes taken, and it has been recognised that a clearer understanding of marine migration paths is required to examine these drivers along specific spatio-temporal migration regions (ICES, 2020; Bull *et al.*, 2022; ICES, 2023e). This thesis builds understanding of post-smolt marine migration paths, supporting the examination of these drivers, and we focus on two of the drivers identified by Bull *et al.* (2022): prey encounters and marine fisheries.

Firstly, we focus on variability in modelled post-smolt migration paths, aiming to evaluate the extent of variability, and then to consider whether such variability might alter the prey availability encountered by post-smolts. Following this, we focus on the hypothesis of marine fisheries driving reduced salmon survival rates. This work is centred around the following hypotheses:

H1: Interannually varying oceanographic conditions cause interannual variability in modelled post-smolt marine migration routes.

H2: Different post-smolt navigation behaviours are exhibited within and between salmon populations.

H3: Changes in modelled migration routes driven by oceanographic conditions (**H1**) and behavioural variation (**H2**) drive differences in experienced energy fields.

We note that **H3** could be extended to the other drivers identified by Bull *et al.* (2022), as it is likely that variability in migration paths will also drive variability in predation rates, competition, or fishery and aquaculture encounters, but this is beyond the scope of this thesis and is left for future work. Finally, we hypothesise that:

H4: The migration paths of southern European Atlantic salmon during their first 3-5 months at sea coincide with commercial pelagic finfish fisheries, subjecting post-smolts to a risk of bycatch.

1.8.1 Outline of chapters

To address **H1**, **Chapter 2** develops a post-smolt migration model consisting of an active swimming model coupled with a particle tracking model (FVCOM i-state Configuration Model). The model is developed and parameterised for a group of Irish, Northern Irish and Scottish rivers; other rivers are not included as it is expected that different migratory behaviours are required

from different regions. The model is driven by the reanalysis of a high-resolution ocean model (Scottish Shelf Waters Reanalysis Service), which is available over 27 years (1993 to 2019). Inter-annual variability in migrations is evaluated and potential oceanographic drivers are identified. This chapter is published in the *ICES Journal of Marine Science* (Borland *et al.*, 2025).

Chapter 3 expands this model to describe post-smolt migrations from other river populations around the British Isles. A range of navigation behaviours is selected for each river, using a portfolio-style analysis to identify groups of behaviours generating aggregate ‘success’ rates with a high mean and low variability. **H2** is addressed by considering whether the existence of a range of navigation behaviours within populations, rather than a single behaviour, is likely to be ecologically optimal. Furthermore, evidence of the portfolio effect at the salmon stock-level is considered.

Chapter 4 uses pelagic landings data to evaluate the exposure of migrating post-smolts to fisheries in the first months at sea, addressing **H4**. Data limitations impacted the methods and results of this chapter: fisheries effort data were unavailable (landings were used as a proxy; even so, they were not available from all relevant fishing nations), and bycatch levels per fishery and unit of fishing were unknown. As such, risk estimates could not be generated, but exposure to fisheries was considered as an indicator of risk. The modelled migrations considered in Chapters 2 and 3 were not used to inform this work, as this would have limited the spatial domain.

There are some points of minor repetition in the introductions of Chapters 2-4, as these chapters were each prepared as manuscripts for journal submission.

Chapter 5 generates river population-specific estimates of zooplankton energy along modelled migration paths, evaluating whether this could act as a useful indicator of salmon survival at sea. Using the results from Chapters 2-3, differences in modelled encountered zooplankton energy between years and between migration behaviours are considered, addressing **H3**.

Chapter 6 explores the extent to which the results of this thesis can be used to inform management action. A metric of similarity in modelled migration densities between each of the modelled rivers and the monitored salmon rivers (where return rates are counted) is used to estimate marine return rates for all of the modelled rivers, and these results are used to inform a salmon management decision support tool.

Finally, future research expanding the work in this thesis is discussed.

Chapter 2

Modelled marine migrations of Atlantic salmon post-smolts from Irish, Northern Irish and Scottish rivers vary interannually with local currents and salinity

2.1 Introduction

Atlantic salmon (*Salmo salar*) populations once thrived around Europe and North America, but in recent decades there have been declines in their numbers across the north Atlantic (ICES, 2024a), likely caused by decreasing marine growth and survival rates (Friedland *et al.*, 2009; Pardo *et al.*, 2021). However, the mechanisms behind these shifts remain uncertain, and a more comprehensive understanding of the marine migration routes is required to investigate these mechanisms (ICES, 2020, 2023e) and to help develop more effective future management strategies (Bull *et al.*, 2022). In particular, a better understanding of year-to-year changes in migrations is key to understanding year-to-year changes in marine survival rates, as the spatial and temporal variability in physical ocean conditions and in prey fields (Bartsch & Coombs, 1997; van Deurs *et al.*, 2013) mean that variability in migration pathways will likely influence the physical conditions and feeding opportunities encountered by salmon, factors which have been shown to influence survival (Friedland *et al.*, 1998, 2012; Furey *et al.*, 2015; Tyldesley *et al.*, 2024).

Atlantic salmon from Southern European populations (including Scotland and Ireland) enter the sea in April and May at around 10-20 cm in body length and spend up to 4 years at sea before returning to their natal rivers as adults to spawn (Aas *et al.*, 2010). Until the end of their first winter at sea, they are known as post-smolts (Allan & Ritter, 1977). Post-smolts

initially migrate towards feeding grounds in the Norwegian Sea (Gilbey *et al.*, 2021, Figure 2.1) and several targeted sampling studies have found relatively high concentrations of post-smolts at the European continental shelf-edge (Shelton *et al.*, 1997; Holm *et al.*, 2000; Utne *et al.*, 2020; Gilbey *et al.*, 2021). Telemetry (tagging) studies provide valuable information on the early migratory movements of salmon (e.g. Økland *et al.*, 2006; Thorstad *et al.*, 2013; Barry *et al.*, 2020; Newton *et al.*, 2021; Lilly *et al.*, 2022, 2023; Rodger *et al.*, 2025) or on the later movements of returning adult salmon (e.g. Kennedy *et al.*, 2023), but due to limitations on the various telemetric methods, this approach has not yet revealed a full marine migration pathway in Atlantic salmon post-smolts.

Modelling approaches that integrate environmental, physiological and behavioural elements to simulate migrations offer an opportunity to address knowledge gaps. Particle tracking models coupled with active swimming models have been used for this purpose in several cases (Booker *et al.*, 2008; Mork *et al.*, 2012; Byron *et al.*, 2014; Moriarty *et al.*, 2016; Ounsley *et al.*, 2020; Newton *et al.*, 2021). Varied swimming models were applied across these studies since migration behaviour is expected to vary regionally and with environmental conditions (Byron & Burke, 2014). With the exception of the 24-year modelling study by Moriarty *et al.* (2016) in the Northwest Atlantic, previous particle tracking studies have focused on simulating migrations in just one or two years (Booker *et al.*, 2008; Mork *et al.*, 2012; Ounsley *et al.*, 2020; Newton *et al.*, 2021). Interannual variation has therefore not been well-considered over extended periods of time in models of post-smolt migration from European rivers.

Here, we simulate the initial post-smolt migration towards the Norwegian Sea from a group of Scottish, Northern Irish and Irish rivers (Figure 2.1) over a 27-year period. Large-scale ocean and atmospheric processes influence physical conditions across this region. Expansion or contraction of the subpolar gyre (SPG) causes changes to large-scale advective pathways in the northeast Atlantic, influencing water salinity, temperature and productivity (Hátún *et al.*, 2009; Koul *et al.*, 2020). Changes in the North Atlantic Oscillation (NAO), measured by the sea-level pressure difference between a region of high pressure (the Subtropical High, in the Azores) and a region of low pressure (the Subpolar Low, in Iceland) relate to changes in westerly winds, which can impact circulation and water mass properties in the North Atlantic region (Hurrell, 1995; Sarafanov, 2009). The NAO index has also been correlated with salmon growth and survival (Jonsson & Jonsson, 2004; Peyronnet *et al.*, 2008).

Most of the region in Figure 2.1 lies on the European continental shelf. In addition to basin-scale ocean and atmospheric processes, shelf seas are influenced locally by surface warming and heat loss, freshwater input, tides and wind forcing (Simpson & Sharples, 2012). These processes drive small-scale spatial and temporal variability in water properties and circulation on the northwest European continental shelf (Holt *et al.*, 2012; Jones *et al.*, 2018). At the shelf-edge, the sudden change in bathymetry induces a current flowing parallel to the isobaths (Simpson & Sharples, 2012), i.e. parallel to the shelf-edge. The European shelf-edge current exhibits seasonal and interannual variability (Xu *et al.*, 2015), with much of the interannual variability explained by the North Atlantic Current (NAC; Houpert *et al.*, 2020). The NAC is itself related to the subpolar

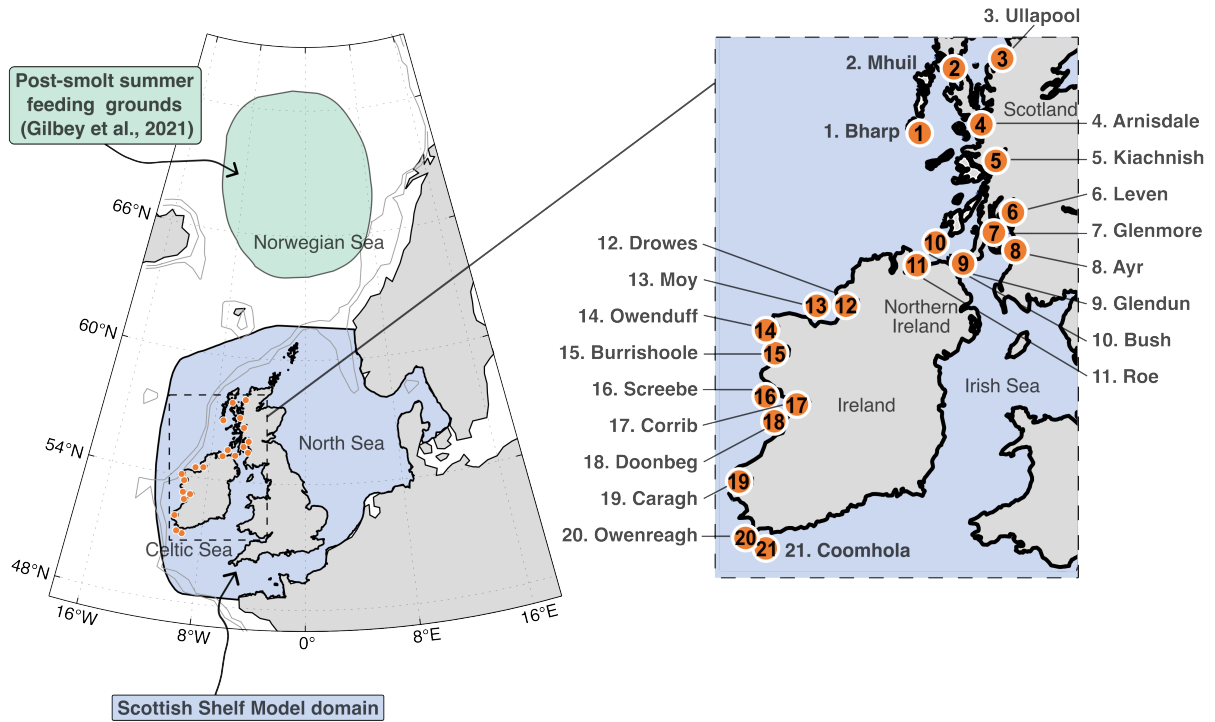


Figure 2.1: Summer feeding grounds of Atlantic salmon post-smolts (*Salmo salar*), the Scottish Shelf Model domain, and the rivers where migrations are modelled (orange). Isobaths at 200m and 400m indicate the location of the continental shelf-edge.

gyre: a faster and more eastward expanded NAC current pathway is seen in periods of a stronger subpolar gyre, causing a strengthened shelf-edge current (Marsh *et al.*, 2017; Holliday *et al.*, 2020; Clark *et al.*, 2022). A long-term decrease in the strength of the shelf-edge current has also been identified (Xu *et al.*, 2015; Clark *et al.*, 2022). Given there have been several recaptures of post-smolts at the continental shelf-edge, we hypothesise that this current is an important feature used by post-smolts during their migration towards the Norwegian Sea. Variability in this current might therefore influence migrations.

Simulating post-smolt migrations requires an understanding of the potential navigational cues employed. Migratory animals are known to use multiple navigational cues at once, or in sequence along their journey, with “signposts” in the form of magnetic cues or physical properties dictating the switch between behaviours (Kashetsky *et al.*, 2021). Gradients of environmental variables can be used to aid migration and even extrapolated beyond the area experienced by an individual (Kashetsky *et al.*, 2021). Intraspecific variation in how navigational behaviours are employed is found between and even within populations (Chapman *et al.*, 2014).

Several mechanisms have been suggested as potential navigational cues for Atlantic salmon. Firstly, salmon may use the vertical current shear between water layers to detect small changes in flow, a mechanism which could allow them to follow ocean currents (Døving & Stabell, 2003). Local currents have been identified as a navigational cue during estuarine migration, with post-smolts observed actively migrating primarily during ebb tides in acoustic telemetry

studies (Lacroix & McCurdy, 1996; Lacroix *et al.*, 2004; Main, 2021; Lilly *et al.*, 2022). On a larger scale, it has been suggested that post-smolts might use the North Atlantic subpolar gyre current to migrate (Dadswell *et al.*, 2010). A second potential navigation cue is salinity, which has been identified as a likely “signpost” in eel migration (Schabetsberger *et al.*, 2016; Cresci, 2020). Salmon have a highly sensitive olfactory system which could allow them to detect small chemical differences between water masses (Døving & Stabell, 2003), allowing them to follow salinity cues. Increased swimming speed has been seen in post-smolts experiencing a positive salinity gradient in coastal and estuarine waters (Hedger *et al.*, 2008; Martin *et al.*, 2009). Preferences for certain salinity ranges could relate to the choice of certain water masses, possibly for their associated prey fields, or perhaps for the currents signified by the water mass (e.g. the continental shelf-edge current). Thirdly, several experimental studies have shown the response of both Pacific and Atlantic salmon to magnetic cues (Quinn, 1980; Taylor, 1986; Putman *et al.*, 2014; Minkoff *et al.*, 2020), and Moore *et al.* (1990) found magnetite crystals in the lateral line of Atlantic salmon smolts and adults, suggesting a mechanism by which salmon can utilise magnetic cues in migration.

Migration modelling also requires estimates of marine swimming speeds. Post-smolt marine swimming speeds can be inferred from recaptures (10-26 km/day, Thorstad *et al.*, 2012) or estimated from acoustic telemetry, with speeds measured in Scotland and Ireland ranging from 9.7-53.8 km/day, with variation in speeds seen both between and within river populations (Main, 2021; Lilly *et al.*, 2022, 2023; Rodger *et al.*, 2025). Estimates of swimming speed are calculated using the straight line distance between detections, but post-smolts are likely to take a more convoluted route, meaning measured speeds are the minimum possible speeds. Differences in the swimming speeds measured through telemetry work also reflect the influence of local water currents, or potentially other changing conditions such as salinity, and differences in migration strategy, for example foraging vs moving as quickly as possible to the goal location.

This chapter addresses our hypothesis that interannually varying oceanographic conditions drive interannual variability in post-smolt marine migration routes (**H1**). This is split into three smaller aims: (1) to develop a post-smolt migration model applicable to the initial period of marine movement within the Scottish Shelf Model domain for the rivers displayed in Figure 2.1; (2) to examine interannual variation in migratory paths and metrics of migrations; and (3) to investigate the possible mechanisms behind this variation.

2.2 Methods

In this study, we used a Lagrangian particle tracking model (FVCOM i-state Configuration Model, detailed in Section 2.2.1 below) driven by a high-resolution ocean model hindcast (Scottish Shelf Waters Reanalysis Service, Section 2.2.1) which provided 27 years of data (1993-2019) over the Scottish Shelf Model domain (Figure 2.1). This was combined with an active swimming model which was developed to simulate the movement of salmon from Scottish, Irish, and Northern Irish rivers over the first three months at sea (Sections 2.2.2-2.2.7). Modelled migrations were

compared with observed locations of migrating post-smolts (Section 2.2.8), and we considered whether variability in modelled migrations was related to variability in environmental conditions (Section 2.2.9) or to geographical differences between rivers (Section 2.2.9). Finally, interannual variability in modelled migrations was compared with Atlantic salmon marine survival rates from rivers within our region of focus (Section 2.2.9). All model assumptions are detailed in the text and are additionally summarised in Appendix A.

Migration simulations were run on the ARCHIE-WeSt High Performance Computer (www.archie-west.ac.uk) and the analysis of results was conducted in MATLAB (Mathworks Inc., 2021).

2.2.1 Lagrangian particle tracking and the Scottish Shelf Model

The offline particle tracking software FISCAM (FVCOM i-state configuration model; Liu *et al.*, 2015; Ounsley *et al.*, 2020, https://github.com/GeoffCowles/fiscam/tree/ounsley_et_al_2019) was used to simulate the movement of Atlantic salmon post-smolts, where each particle represented a post-smolt. For a particle $\mathbf{x}_t = (x_t, y_t)^T$ at longitude x_t and latitude y_t at time t , position at the next timestep ($t + \delta t$) is given by:

$$\mathbf{x}_{t+\delta t} = \mathbf{x}_t + \left((\mathbf{u}_t + \mathbf{g}_t) \delta t + Q\sqrt{2K\delta t} \right) \mathbf{c} \quad (2.1)$$

where $\mathbf{u}_t = (u, v)^T$ is the current velocity at time t in ms^{-1} , $\mathbf{g}_t = (g_x, g_y)^T$ is the active swimming velocity of particles at time t in ms^{-1} , Q is normally distributed with mean 0 and standard deviation 1, K is the horizontal diffusion coefficient, taken to be $10 m^2 s^{-1}$, and $\mathbf{c}$ represents the conversion from metres to degrees longitude/latitude, taken here as $\mathbf{c} = (8.99322 \times 10^{-6} \cos(y_{t+\delta t}), 8.99322 \times 10^{-6})^T$. The timestep δt is discussed in Section 2.2.3. The velocities of individual particles at each timestep were integrated using the 4th-order Runge-Kutta method to update particle positions.

Currents $\mathbf{u}_t$ were derived from the Scottish Shelf Waters Reanalysis Service 3.02 (SSW-RS) reanalysis of the Scottish Shelf Model (SSM). The SSM is a hydrodynamic model covering the seas around the British Isles (Murray, 2017). It is an implementation of the Finite Volume Community Ocean Model (FVCOM; Chen *et al.*, 2003), meaning the grid is irregular and unstructured, made up of triangles which vary in shape and size. This type of model allows the resolution of the grid to vary so that coastal features can be resolved on a fine scale. Horizontal grid resolution ranges from 1 km around the coast to 20 km off the shelf. The model uses a hybrid terrain-following coordinate system, with 20 depth layers. The depth levels are evenly distributed in water of depth <120 m. In water ≥ 120 m, there are five fixed depth levels at the top of the water column, which are 3, 6, 7, 7 and 7 m thick and lie at depths of 1.5, 6, 12.5, 19.5, 26.5 m respectively, and two fixed depth levels at the bottom of the water column, both of which are 6 m thick and lie 3 and 9 m above the seabed (Barton *et al.*, 2022). The remaining 13 depth levels are evenly distributed across the remainder of the water column.

The SSSW-RS is a 27-year (1993-2019) physical reanalysis of the Scottish Shelf Model (Barton

et al., 2022). Along the open Atlantic boundary, the model was forced by the Atlantic-European North West Shelf-Ocean Physics Reanalysis (<https://doi.org/10.48670/moi-00059>). At the open Baltic boundary, the model was forced by the Baltic Sea Physics Reanalysis (<https://doi.org/10.48670/moi-00013>). Atmospheric forcing, including wind velocity, was provided by the Copernicus ERA5 global reanalysis (Hersbach *et al.*, 2020). Riverine inputs comprised of volume fluxes from both the Hydrological Predictions for the Environment over Europe dataset (Arheimer *et al.*, 2020) and the Centre for Ecology and Hydrology (CEH) Grid-to-Grid (G2G) model (Bell *et al.*, 2009). Daily sea surface temperature (SST) from the ODYSSEA satellite dataset (Autret *et al.*, 2020) was assimilated into the model. Bathymetry was taken from the AMM15 model from the European Marine Observation and Data Network (Martín Míguez *et al.*, 2019). Model temperature and salinity from the SSW-RS have been compared to in situ temperature and salinity profiles, with good agreement in the spatial and temporal patterns (Barton *et al.*, 2024).

The SSW-RS is available as hourly and daily (24-hour average) data outputs. The choice between these two formats is discussed with the choice of timestep in Section 2.2.3. Currents from the SSW-RS were interpolated at each timestep to present particle position, providing $\mathbf{u}_t$ in Equation 2.1.

2.2.2 Active swimming model

We propose an active swimming model composed of three behaviours: swimming in the direction of local currents, swimming in the direction of the local salinity gradient, and directional swimming on a constant compass bearing (magnetic cue). Together, these provided $\mathbf{g} = (g_x, g_y)^T$ in equation 2.1, with

$$\mathbf{g} = w_c \mathbf{g}_c + w_s \mathbf{g}_s + w_d \mathbf{g}_d \quad (2.2)$$

where $\mathbf{g}_c$, $\mathbf{g}_s$ and $\mathbf{g}_d$ are the current, salinity, and directional active swimming component vectors, and w_c, w_s and w_d are the respective scalar weights, where $w_c, w_s, w_d \geq 0$.

The current-following behavioural component $\mathbf{g}_c$ was given by

$$\mathbf{g}_c = s L \left(\frac{\mathbf{u}}{|\mathbf{u}|} \right) \quad (2.3)$$

where s is the swimming speed in body lengths per second, L is the body length of the fish in metres (see Section 2.2.5 below) and $\mathbf{u} = (u, v)^T$ is the current velocity.

The salinity-gradient-following component was then given by

$$\mathbf{g}_s = s L \frac{\nabla S}{|\nabla S|_{median} + |\nabla S|} \quad (2.4)$$

where ∇S is the salinity gradient, calculated as detailed below. The above format represents a saturation function where $|\nabla S|_{median}$ (the median salinity gradient magnitude) is the half-saturation point. To determine $|\nabla S|_{median}$, the salinity gradient was calculated across the whole SSW-RS domain in April-May over 5 years, giving a value of

$|\nabla S|_{median} = 0.0045 \text{ psu/km}$.

The directional component $\mathbf{g_d}$ was defined as

$$\mathbf{g_d} = s L R \frac{|\theta - \theta_{bias}|}{\pi} \mathbf{q} \quad (2.5)$$

where θ is the current direction of movement (in radians; measured anticlockwise from the positive direction of the x-axis), θ_{bias} is the preferred direction of movement, $\mathbf{q} = \begin{pmatrix} \cos \theta_{bias} \\ \sin \theta_{bias} \end{pmatrix}$ and

$$R = \begin{cases} 0 & \text{before first instance of water} > 200 \text{ m deep} \\ 1 & \text{after first instance of water} > 200 \text{ m deep.} \end{cases}$$

A depth of 200 m was selected here as it represents the boundary of the continental shelf-edge (Simpson & Sharples, 2012), and we hypothesise that a behavioural transition might occur here, in line with the change in physical and biological conditions. The preferred direction of movement θ_{bias} was chosen to be $\pi/5$ (equivalent to a bearing of 54° from north) as this is approximately the angle of the continental shelf-edge in our domain. The inclusion of R means that modelled post-smolts initially used only currents and salinity to navigate, but upon reaching deeper waters, they additionally used the directional cue. Depth therefore acted as a ‘‘signpost’’ in our model, signaling the switch from one migratory behaviour to another (Kashetsky *et al.*, 2021). We do not propose that post-smolts can directly detect the bottom bathymetry; rather they might use chemical or optical cues associated with the transition from shelf to open-ocean water.

While the maximum magnitude of each of the three components $\mathbf{g_c}$, $\mathbf{g_s}$ and $\mathbf{g_d}$ are all $s L$, their magnitudes are not necessarily equal at any given time. This reflects the use of different navigational cues throughout the migration, depending on the relative strength of each. For example, the $\mathbf{g_s}$ term will be small when there is a weak salinity gradient, meaning salinity will not be the primary method of navigation. Similarly, $\mathbf{g_d}$ is at a minimum (zero) when movement is already in the preferred direction and reaches a maximum when movement is in the opposite direction. Consequently, the swim speed s acts as an upper bound, but modelled post-smolts will almost always be moving slower than this. We enforced that $\sqrt{w_c^2 + w_s^2 + w_d^2} = 1$ in the parameter testing process (discussed in Section 2.2.7) to ensure that duplicate combinations of the weights and s were not tested.

Salinity gradient calculation

The gradient of a scalar field is the direction and magnitude of the greatest rate of increase of the field values. We calculated the surface salinity gradient ∇S at each point p using all cells within a radius ϵ of p . This ensured that the gradient was calculated on a constant scale across the domain despite the irregular grid. This method is also applicable to points lying near or on the coastline. The salinity gradient was calculated using the uppermost layer of the SSW-RS, which is the top 5 % of the water column in water less than 120 m deep, or a fixed depth layer of 0-3 m in water greater than 120 m deep. This meant that salinity was calculated over a similar,

but not identical, surface layer across the SSM domain.

The grid cells surrounding p within the radius ϵ were divided into quadrants (q_1, q_2, q_3, q_4), as in Figure 2.2. The mean value of S was calculated in each quarter $i = (1, 2, 3, 4)$ and denoted as S_{q_i} . Similarly, the mean distance (in kilometres) from the cells in each quarter i to p was calculated and denoted d_i . If any quarter does not contain any grid cells (for example if it covers land), then $S_{q_i} = 0$ and $d_i = 0$. The salinity gradient ∇S at a point p was then given by

$$\nabla S(p) = \left(\frac{S_{q_1} - S_{q_3}}{d_1 + d_3}, \frac{S_{q_2} - S_{q_4}}{d_2 + d_4} \right) \quad (2.6)$$

with units psu/km.

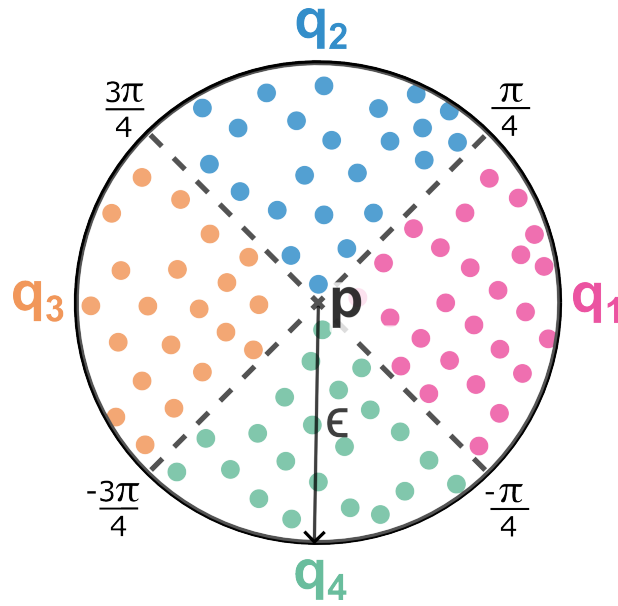


Figure 2.2: Schematic of salinity gradient calculation. Quadrants q_1, q_2, q_3, q_4 are shown, with dots representing points in the salinity field on the irregular Scottish Shelf Model (SSM) grid.

The parameter ϵ represents the area in which post-smolts can detect or extrapolate conditions, allowing them to decide which direction to swim. A smaller value of ϵ hence represents the use of small-scale patterns in salinity for navigation, while a larger value simulates the use of large-scale spatial patterns. Figure 2.3 a-c shows the salinity gradient magnitude calculated with $\epsilon = 5$ km, $\epsilon = 10$ km, and $\epsilon = 50$ km. Increasing the radius of calculation smoothed the spatial patterns in salinity. With this method, the salinity gradient was not calculated at points within the domain where the grid resolution is greater than ϵ . This is seen through the white patches in the $\epsilon = 5$ km and $\epsilon = 10$ km cases. Figure 2.3 d-f shows the salinity gradient with the saturation function of Equation 4 for $\mathbf{g}_s$ applied. This function rescaled the gradient to a more normal distribution and ensured all values lie between 0 and 1.

Unfortunately, sufficient information is not currently available to constrain ϵ on the basis of physical measurements or knowledge of post-smolt migration behaviour. However, when calculating gradients of mesozooplankton concentration in a model simulating blue whiting migration,

Dolmaire (2022) suggested that this value should be no greater than the distance travelled in one timestep so that individuals could detect conditions within a radius that they were able to cover. The final choice of ϵ is hence discussed in Section 2.2.3 alongside the choice of timestep δt .

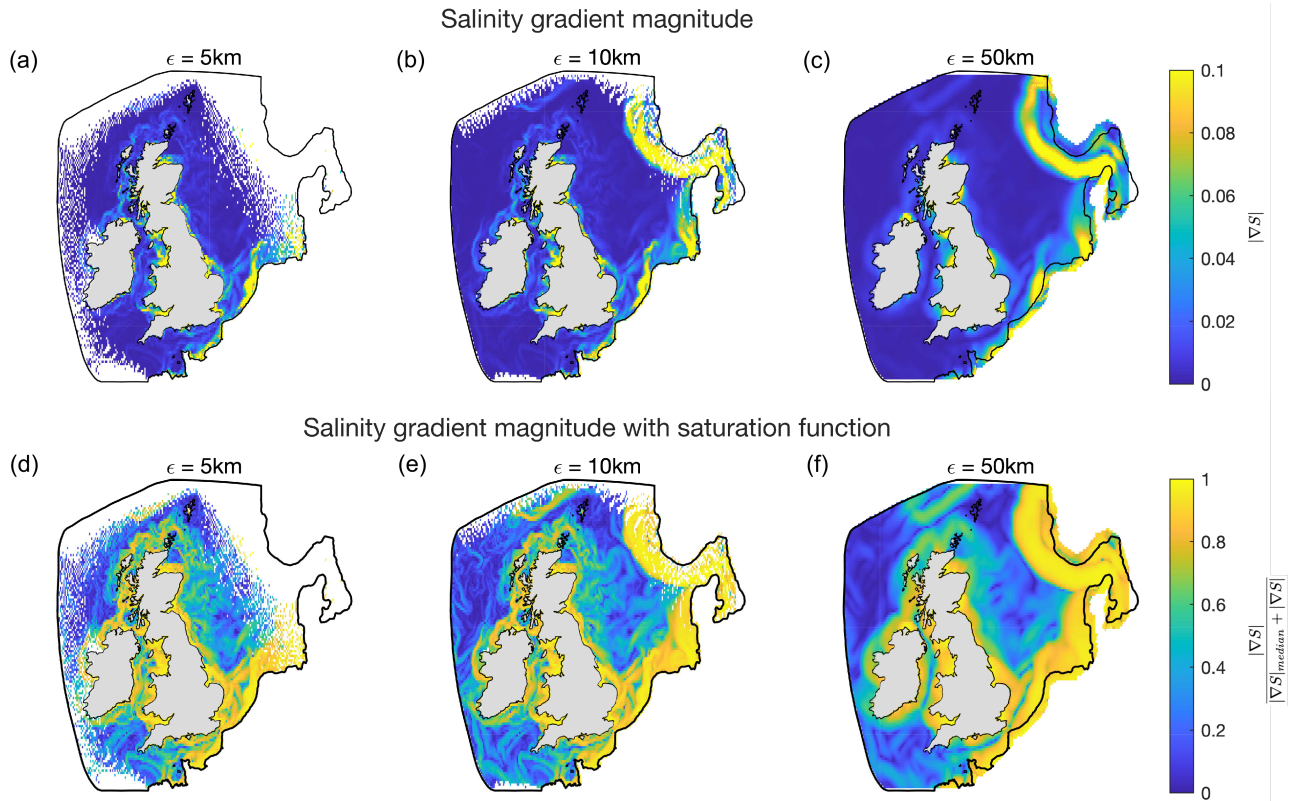


Figure 2.3: Salinity gradient magnitude calculated with: (a) $\epsilon = 5$ km , (b) $\epsilon = 10$ km, and (c) $\epsilon = 50$ km. (d)-(f) show the same salinity gradient magnitude with $\epsilon = 5$ km, $\epsilon = 10$ km, and $\epsilon = 50$ km respectively, but with the saturation function in Equation 2.4 for $\mathbf{g}_s$ applied.

2.2.3 Model timestep

The choice of timestep δt took into account several factors:

1. The desired timescale of navigational choices. This relates to the radius of salinity gradient detection ϵ (i.e. the area in which simulated post-smolts can detect conditions before deciding which direction to swim).
2. The time resolution of modelled ocean conditions used to make navigational choices (i.e. the time resolution of the SSW-RS).
3. Computational accuracy and efficiency.

Regarding 2., two options were available to force the model: the hourly or daily SSW-RS files. The former would be suitable for simulating fine-scale movement in relation to tidal currents with a small timestep, while the daily files would be suitable for simulating larger-scale navigational choices with a larger timestep, based on residual currents and representing an integration of a number of fine-scale movements. Accordingly, a smaller or larger ϵ would be suitable for these options respectively.

Passive particle tracking runs were conducted to evaluate the computational accuracy of passive movement between a smaller (1-hour) and larger (12-hour) timestep. Metrics of migrations (Section 2.2.6) were similar between the two timesteps, with differences between years much greater than differences between timestep lengths. The computational efficiency of the model is linearly related to the size of the timestep and is decreased by using the hourly rather than the daily SSW-RS files.

This left us with two distinct sets of options: a small timestep δt , with a small ϵ , forced by the hourly SSW-RS files; or a larger δt and ϵ , forced by the daily SSW-RS files. As our focus in this study is the larger-scale migration of post-smolts towards the Norwegian Sea, we chose the second set of options, using a timestep of 12 hours ($\delta t = 43200$ s) with the daily SSW-RS files. This choice allowed for increased computational efficiency, making it possible to simulate a large number of migrations over a number of years. The choice of ϵ could then be made: estimating that our simulated post-smolts would travel between 20-40 km/day (in line with tracking studies), then for a 12-hour timestep, a value of $\epsilon = 10$ km is suitable. Additionally, a radius of $\epsilon = 10$ km resolves slightly larger scale salinity patterns (Figure 2.3), which might be important for the long-distance marine migration of post-smolts.

We note that there are differences in the temporal and spatial scales between modelled behaviour here and real instantaneous swimming behaviour. These differences mean that the mechanisms modelled in this study do not necessarily represent the exact navigational behaviours employed by post-smolts at each point in time; rather the model represents an integration of the swimming behaviour and gives a sense of its consequences. While this is suitable for this work, a different approach would be required to simulate fine-scale movements. An alternate version of the model, reserved for future work, would focus on the near-coastal portion of the migration, including tidal currents, and sub-tidal-timescale behavioural decisions.

2.2.4 Particle releases

A group of 21 managed salmon rivers in Scotland, Northern Ireland, and Ireland were selected as the initial particle release locations for the model (Figure 2.1), as we expect that they have a qualitatively similar migration route (meaning they have the potential to be represented by a single migration model): we expect that post-smolts from these rivers must cross the continental shelf in a west/northwest direction and then continue northeast along the shelf-edge. This group of rivers forms a geographically bounded region, making them a suitable choice for investigating the impact of year-to-year changes in environmental conditions on migrations. Additionally, Tyldesley *et al.* (2024) found similarities in the marine survival rates of salmon from rivers in this region (using an analysis of synchrony between empirically measured return rates), suggesting they experience similar marine conditions. Other rivers were tested in the model development process (for example rivers on the east coast of Ireland) but it was found that different models would be required for rivers outside this group, and this further generalisation is left for future work.

Smolt migration timing data were available for two of the rivers displayed in Figure 2.1 (the river Bush - 10, and the Burrishoole - 15), and some additional rivers around the British Isles (Table 2.1). It is known that smolt migration occurs earlier in more southern populations than in more northern populations (Hvidsten *et al.*, 1998; Otero *et al.*, 2014) and the modelling study of Vollset *et al.* (2021) found that river location (described by longitude and latitude) is a key factor in explaining the migration timing of smolts. Therefore, we estimated the migration timing of the remaining rivers from their latitude. The mean 25th percentile dates (used as a measure for the initiation of migration) were plotted against latitude and a linear model was fitted in MATLAB ($r^2 = 0.61, p = 0.06$). Initial particle release times for the 21 rivers were then determined from this model. As seen from the 25th and 75th percentile migration timing, smolt migration from these rivers tends to occur within a short time frame, with the maximum amount of time between 25th and 75th percentile dates per river being 11 days (Table 2.1). Therefore, to represent the later migrating post-smolts and to act as a sensitivity test, we additionally released particles two weeks later than the initial dates.

River	Latitude	25th percentile date	75th percentile date
Tamar	50.4°	17th April (mean 2005-2019)	26th April
Frome	50.7°	15th April (mean 2006-2019)	N/A
Dee	53.4°	30th April (mean 1997-2019*)	5th May
Burrishoole (15)	53.9°	2nd May (mean 1993-2019)	13th May
Bush (10)	55.2°	28th April (mean 1993-2019)	9th May
North Esk	56.8°	28th April (mean 1993-2013)	9th May

Table 2.1: Mean 25th and 75th percentile Atlantic salmon (*Salmo salar*) smolt migration timing from six monitored rivers around the British Isles (Diack, 2021, <https://doi.org/10.5063/F1HQ3XD1>). River numbers are provided for the Burrishoole and the Bush, as displayed in Figure 2.1.

*data were not available 1998-2000 and 2002-2003.

1000 particles were released at each start point per year (500 per release date), corresponding to a total of 567,000 particles released over the 27 years of simulations. All particles were kept at a fixed depth of 5 m (i.e. they were subject to currents at this depth), as post-smolts are generally found at the top of the water column (Renkawitz *et al.*, 2012; Newton *et al.*, 2021). The particle release points were set 30 km away from the river mouths (as seen in Figure 2.1) as our focus in this study is on the larger-scale migration behaviour towards the Norwegian Sea and we anticipate that a different scale of modelling would be required for the initial small-scale navigation from the river mouths (Section 2.2.3). This additionally helps prevent particle collisions with the coastline.

2.2.5 Growth model

A growth model determined the fork length of simulated post-smolts, as swimming speed depends on body size. We used the growth model of Ounsley *et al.* (2020), adapted from Mork *et al.* (2012). This model was derived from the body lengths of seven post-smolts captured in the Northeast Atlantic in 2008 and 2009 (Mork *et al.*, 2012). The fork length of simulated post-smolts in metres was:

$$L = L_0 e^{\alpha d} \quad (2.7)$$

where L_0 is the initial fork length of the fish in metres, $\alpha = 0.0059$ and d is the number of days spent at sea.

The initial fork length of fish L_0 was based on observation. Scottish smolts range in fork length from 10-15 cm, with the mean lying approximately at the middle of this range (Malcolm *et al.*, 2015). However, in the river Bush in Ireland, the mean fork length of migrating smolts from 2017-2019 was 14.5 cm (Agri-Food and Biosciences Institute, unpublished data). Nearby, in the river Burrishoole in Ireland, the mean fork length from 1993-2020 (the time period of our modelling work) was 13.8 cm (Rinaldo *et al.*, 2023; de Eyto & McGinnity, 2023, additional unpublished data). Based on these values, we conservatively set the initial fork length of fish (L_0) to 13 cm ($L_0 = 0.13$ m).

2.2.6 Metrics of modelled migrations

To describe the movement patterns of the modelled migrations, three metrics were calculated:

1. Proportion of time spent in shallow water (< 200 m) vs deeper water. A depth of 200 m was selected for this metric because it lies on the boundary of the northwest European continental shelf-edge (Simpson & Sharples, 2012).
2. Speed relative to the ground (km/day).
3. Domain exit rate, calculated as the proportion of particles passing through a region at the top of the Scottish Shelf Model domain of depth 50 km, stretching from -12° to 5° longitude, within 100 days of entering the sea (i.e. exiting the SSM domain and heading towards known feeding grounds in the Norwegian Sea within an appropriate time frame).

The time of 100 days used for the domain exit rate means that smolts entering the sea at the end of April for example (Table 2.1) must reach the Norwegian Sea by early August at the latest. This aligns with observations of post-smolts in the Norwegian Sea in June, July, and August (Gilbey *et al.*, 2021). This choice of time frame might be generous, given it seems that high numbers of post-smolts have already reached the Norwegian Sea by June (Gilbey *et al.*, 2021), but trawling in this study did not extend as far south as the top of our modelling domain in July and early August, so there is no evidence to suggest that post-smolts are not still migrating northwards during this time.

2.2.7 Parameter optimisation and sensitivity

The parameters w_c , w_s and w_d , which represent the relative use of each navigational cue, could not be based on empirical values, as the exact navigational mechanisms of salmon are not yet known. Precise values of post-smolt marine swimming speeds in body lengths per second are also not known for this region. Therefore, the parameters w_c , w_s and s were tested using a uniform grid structure, and their values were optimised with respect to the domain exit rates (i.e. we developed a model which maximised the number of simulated post-smolts reaching the Norwegian Sea within an appropriate time frame). The speed relative to the ground of simulated migrations was constrained to be no more than 40 km/day, in line with estimates of post-smolt swimming speeds in this region (Lilly *et al.*, 2023). The parameter w_d was determined by the relationship $w_c^2 + w_s^2 + w_d^2 = 1$. To minimise computational time, only 20 particles were released from 6 rivers (numbers 2, 4, 6, 10, 15 and 19 in Figure 2.1), over the years 1993, 2003, 2007, 2012, and 2018 (selected as they display a range of salinity conditions in the SSW-RS domain). Values of w_c and w_s from 0 to 1 were tested at 0.1 resolution. Values of s from 3 to 7 were tested at 0.5 resolution. This equated to a total of 810 parameter combinations tested.

The selected parameters were $w_c = 0.3$, $w_s = 0.8$ and $s = 5.5$. This gives a value of $w_d = 0.5196$. These parameters were used for the migration simulations across all rivers and years. However, we note that the interannual patterns in domain exit rates were similar for all of the top 10 % parameter combinations (Figure 2.4 a), though the parameters varied (Figure 2.4 b-c). This suggests that the model results are not highly sensitive to the choice of parameters w_c , w_s and s . We also note that the model produced reasonable domain exit rates for each of the five test years (Figure 2.4 a), a consistency one would expect in a real evolved behaviour.

The optimisation process also allowed us to evaluate whether all three components of the behavioural model $\mathbf{g}$ were serving an important purpose. When either the salinity gradient following weight, w_s , or the directional swimming weight, w_d , were set to zero (Figure 2.5 b-c, domain exit rates were low across years (<0.5)). This suggests that these components are key in this model for simulating post-smolt migrations from this group of rivers. Contrastingly, when the current following weight, w_c , was set to zero, domain exit rates were, in some cases, not much lower than the optimal solution (Figure 2.5 a). However, the variability within years was increased in these cases. The optimal solution, with nonzero w_c , was therefore still deemed beneficial.

A small change in the value of θ_{bias} had only a minor negative impact on the domain exit rates

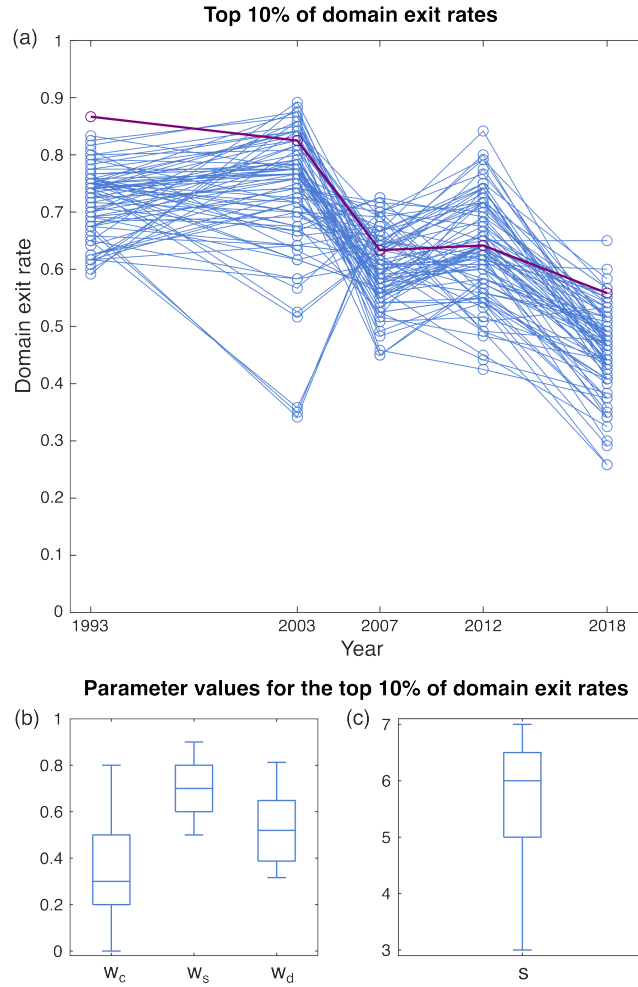


Figure 2.4: (a) the top 10 % of domain exit rates for the parameter optimisation runs. The top 10 % was determined from the means across each of the five years. The optimal solution (greatest mean across the five years) is shown in purple. (b) Boxplots showing the spread of values of parameters w_c , w_s , and consequently w_d in the top 10 % of runs. (c) Boxplot showing the values of s in the top 10 % of runs.

(Figure 2.6). An increase in ϵ resulted in a slight increase in domain exit rates, while a decrease in ϵ resulted in a significant decline in exit rates. This suggests that, while following a salinity gradient is beneficial for migration, it must be on the right spatial scale. A larger value of ϵ allows simulated post-smolts to sense conditions over a larger area before deciding on their swimming direction, which might allow a more optimal route to be selected. However, a radius greater than $\epsilon = 10$ km might be unrealistic (Section 2.2.2) and Figure 2.6 suggests that a larger radius of detection is unnecessary anyway, so our choice of $\epsilon = 10$ km is validated. A small change in the threshold depth at which R in Equation 2.5 is set to 1 (i.e. the depth at which the directional component is added) had a negative impact on the domain exit rates, suggesting that a behavioural transition is indeed beneficial upon reaching 200 m (or approximately the continental shelf-edge).

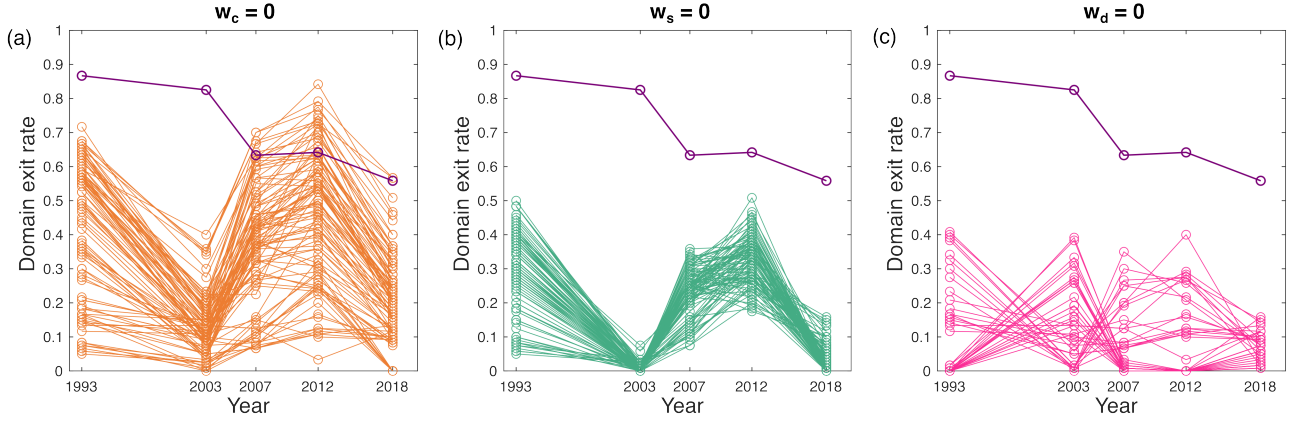


Figure 2.5: Domain exit rates are displayed for all cases where: (a) $w_c = 0$; (b) $w_s = 0$; (c) $w_d = 0$. The purple line again depicts the optimal solution, in which all weights were non-zero ($w_c = 0.3, w_s = 0.8, w_d = 0.52$).

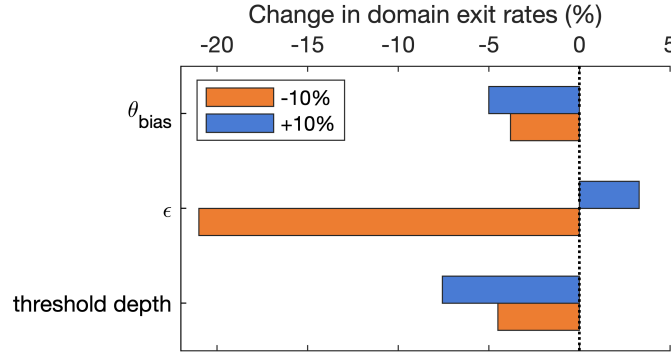


Figure 2.6: Changes in domain exit rates when varying the parameters θ_{bias} , ϵ , and the threshold depth at which R is set to 1 (Equation 2.5) by $\pm 10\%$.

2.2.8 Comparing modelled migrations with locations of post-smolts

Observations of salmon migrations (in terms of both position and timing) are very rare on the scale of our study, despite an abundance of acoustic tracking data in coastal and estuarine regions (Barry *et al.*, 2020; Newton *et al.*, 2021; Lilly *et al.*, 2022, 2023; Rodger *et al.*, 2025). Here, we compared our model outputs with the locations of Atlantic salmon post-smolts sampled near the continental shelf-edge during the SALSEA-Merge project (<http://salmonatsea.com/the-salsea-merge-project/>; Utne *et al.*, 2020). Sampling was conducted in 2008 and 2009, but we only used the 2008 data here, due to limited observations within our model domain in 2009. To check both the spatial and temporal overlap of our model output with these observations, we calculated progression along a general migration track for our modelled post-smolts and for the observations. We chose this general migration track to follow the continental shelf-edge due to multiple observations of post-smolts at the shelf-edge (Shelton *et al.*, 1997; Holm *et al.*, 2000; Utne *et al.*, 2020; Gilbey *et al.*, 2021).

2.2.9 Analysis of migration metrics

Environmental conditions from the SSW-RS were averaged over a region covering the continental shelf west of Ireland and Scotland (i.e. the area relevant to the selected start points for this modelling, Figure 2.1) and a similar region covering the shelf-edge. These regions were kept separate as they are influenced by different physical processes on different time scales. Conditions were averaged over April to June each year. This period was selected to cover the majority of the modelled migrations, from particle release dates (Section 2.2.4) to domain exit. While domain exit rates are calculated after 100 days, we expected that many modelled post-smolts will reach the domain exit region earlier than this (with a mean time to exit of 44 days observed in the optimal parameters run in Section 2.2.7), so April to June will cover the key migration period for most simulated post-smolts.

In the on-shelf region, mean surface salinity and mean surface eastward and northward currents were calculated, as we anticipate that these conditions will impact migration from these rivers across the shelf out to the continental shelf-edge. In the shelf-edge region, we calculated mean surface salinity, mean surface current velocity at a bearing of 54° (representing along-shelf flow), and the surface current velocity perpendicular to this (representing across-shelf flow; on-shelf positive). A more complex velocity calculation for along- and across-shelf flow in which the coordinate axes precisely followed the terrain gave very similar results. To prevent bias of any of these means due to the greater number of nodes/elements per unit area in some regions of the domain, particularly around the coastlines, the mean of each variable was first taken over 0.5° bins and then the mean of the means was taken.

We also considered variability within the migration period by taking two-week averages from April to June each year of these conditions in both regions. Two-week averages are selected to filter out spring-neap tidal variation and other tidal signals aliased by the 24-hour SSW-RS averages. While the use of tidal currents may be important during the initial, near-shore, migration of post-smolts (e.g. holding position in flow tides and then migrating during ebb tides, Main, 2021; Lilly *et al.*, 2022), we expect that residual currents are more important for the remainder of the marine migration (as modelled in this study).

Finally, we considered two indices which describe large-scale climate variability in the North Atlantic and hence might relate to variability in local oceanographic conditions along the post-smolt migration route. We considered the North Atlantic Oscillation (NAO) index (obtained from www.ncei.noaa.gov/access/monitoring/nao/) and the subpolar gyre (SPG) index: several versions of this index are available, but we used that of Hátún & Chafik (2018), which is calculated using principal component analysis of sea surface height; this is seen to be effective in describing water mass variability in the northeastern Atlantic (Koul *et al.*, 2020). As a reanalysis, the SSW-RS encompasses changes to water properties described by changes in the SPG and NAO indices. However, we still find these climate indices of interest on their own as they might be useful indicators of post-smolt migrations, particularly for years preceding the start of the SSW-RS (1993). The annual mean SPG and NAO indices over our study period are shown in Appendix A. We also considered the mean NAO index over only April-June each year (coinciding with the

time period of averaging of the SSW-RS conditions). This time series was included as it provides a more time-specific measure of surface wind forcing (which influences surface currents) in this region. This version of the NAO index follows a similar pattern as the annual mean NAO index, but with greater peaks and troughs.

To consider the potential relationships between environmental conditions (salinity, currents, NAO and SPG indices) and migrations, all correlations between the metrics for these conditions and the metrics of modelled migrations were calculated. Initially, each combination of metrics was plotted against each other (not shown) to check for any obviously non-linear relationships; none were found. Then, Pearson correlation coefficients (r) were calculated for each combination of metrics, giving a measure of the linear dependence of each of these relationships. Additionally, p-values were calculated for each combination, testing the null hypothesis that there is no relationship between each metric and each environmental condition. Some of the environmental variables display autocorrelation, so the modified Chelton method, where the degrees of freedom are altered based on the level of autocorrelation, was used to calculate stricter p-values (Pyper & Peterman, 1998).

To consider differences in migration metrics between rivers, two metrics were calculated for each river mouth start point:

1. The minimum straight line distance from each start point to the continental shelf-edge (defined by the 200m isobath).
2. The total minimum migration distance, a combination of the above distance and the remaining distance along the continental shelf-edge track line (Section 2.2.8) to the domain exit.

The relationships between each of these metrics of migration distance and the mean migration metrics of each river were tested by calculating r and p values as above.

Modelled domain exit rates per year were compared with a time series of combined normalised marine return rates of one-sea-winter (1SW) Atlantic salmon from five rivers on the west coasts of Ireland, the United Kingdom, and France (Tyldesley *et al.*, 2024). The return rates act as a proxy for marine survival rates, and the rivers include the Bush, Burrishoole, and Corrib (numbers 10, 15, and 17 respectively in Figure 2.1). Pearson correlation coefficients and stricter p-values accounting for autocorrelation in the time series were calculated as detailed in Section 2.2.9. Additionally, these correlation coefficients were calculated between modelled domain exit rates and detrended return rates ($r_{detrend}, p_{detrend}$), where the time series were detrended by subtracting the mean value from each data point.

2.3 Results

2.3.1 Modelled migrations

Most modelled migrations followed a common route along the continental shelf-edge. However, some modelled post-smolts were found outside this common route in the Irish Sea and the Celtic Sea (Figure 2.7). Any particles passing through the defined domain exit region were removed from the simulations. The locations of domain exit were concentrated in a small region (Figure 2.7) which aligns with the continental shelf-edge, suggesting simulated post-smolts stay in the shelf-edge current.

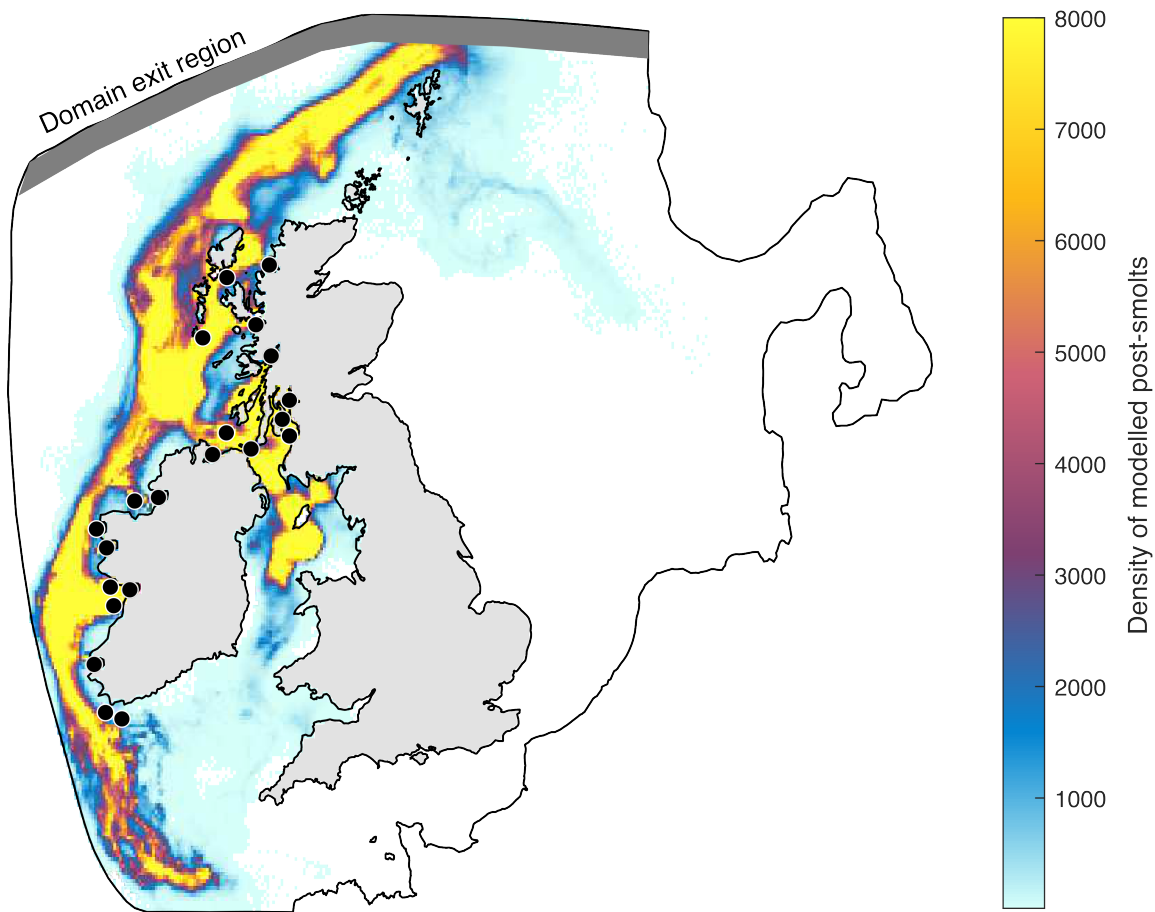


Figure 2.7: Density of modelled Atlantic salmon post-smolts (*Salmo salar*) from all releases of all years, measured as the total number of incidences of particles per 30 km² bin. Modelling start points (river mouths) are shown as black circles. The domain exit region, used for calculating domain exit rates, is also displayed.

Spatial concentrations of simulated post-smolts for each year of simulations are additionally provided in Appendix A. Some differences in distributions were seen between years. For example, there was a concentration of particles south of Ireland (in the Celtic Sea) in some years but not others (e.g. 2002 but not 2008). In some years there was also a concentration of particles in the

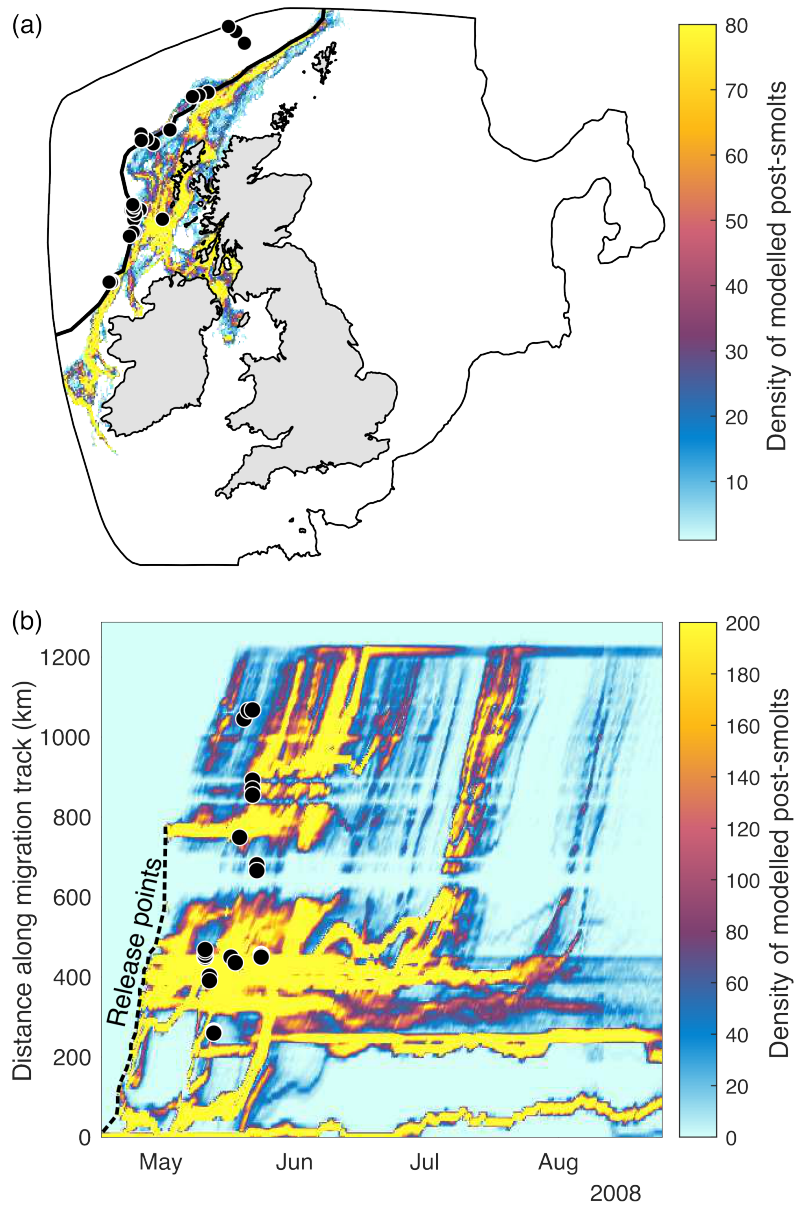


Figure 2.8: (a) simulated Atlantic salmon post-smolt (*Salmo salar*) density (total number of particles per 30 km² bin) from 2008 within ± 1 week of all observations from the SALSEA-Merge project (<http://salmonatsea.com/the-salsea-merge-project/>; Utne *et al.*, 2020), which are marked as black dots. The general migration track following the continental shelf edge is shown as a black line. (b) Distance along this general migration track with time for simulated post-smolts and observations, again marked as black dots. The black dashed line displays particle release locations and timing.

northern North Sea (e.g. 2017 but not 2016).

The modelled distribution of post-smolts was mainly consistent, spatially and temporally, with observations of post-smolts from the SALSEA-Merge project in 2008 (Figure 2.8). There was greater overlap, both spatially (Figure 2.8 a and b) and temporally (Figure 2.8 b) with the lower latitude observations, which lie close to the continental shelf-edge.

2.3.2 Variability in environmental conditions and migrations

Both on the shelf and at the shelf edge, conditions from April-June varied between years (Figure 2.9). Surface salinity on the shelf was lower than at the shelf edge, but interannual variability was seen in salinity across both regions. Surface currents also varied significantly between years both on the shelf and at the shelf edge.

Among two-week periods in April-June, salinity was variable in the shelf region, while it was fairly consistent within years at the shelf-edge (Figure 2.9 a and d). Currents were highly variable between the two-week periods both on the shelf and at the shelf-edge (Figure 2.9 c, d, e and f).

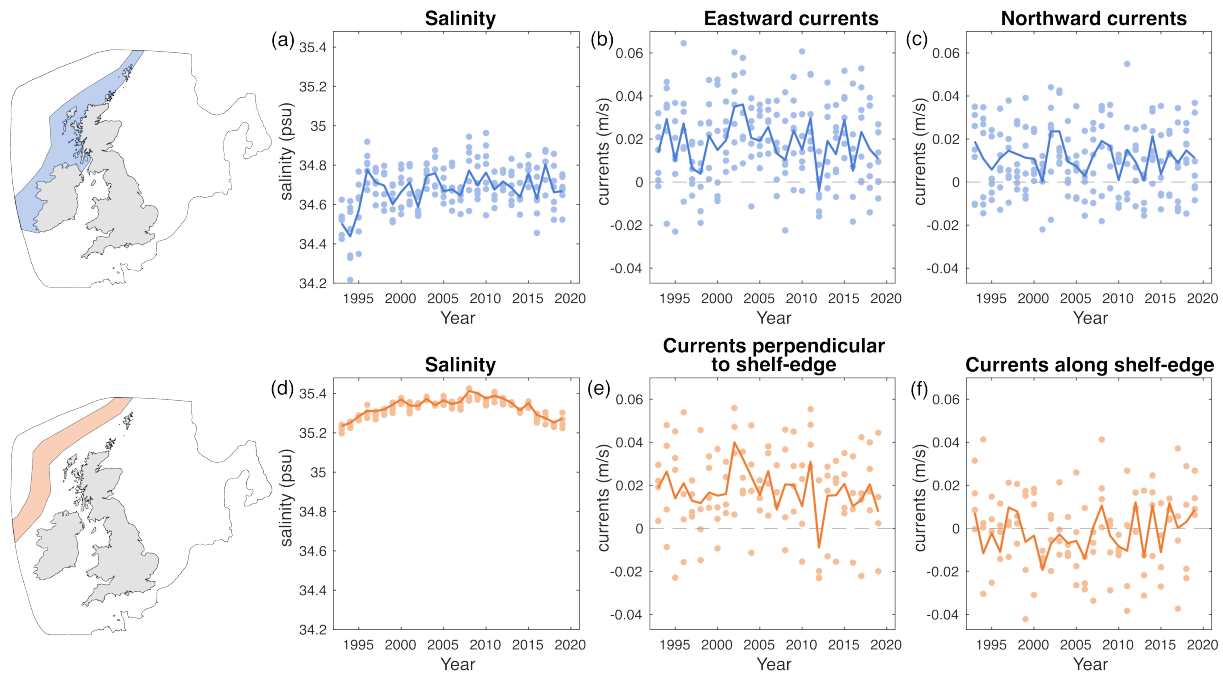


Figure 2.9: Scottish Shelf Waters Reanalysis Service (SSW-RS) conditions averaged over April-June each year for the shelf region (blue) and the shelf-edge region (orange): (a) shelf salinity; (b) shelf eastward currents; (c) shelf northward currents; (d) shelf-edge salinity; (e) currents along the shelf-edge; (f) currents perpendicular to the shelf-edge (on-shelf positive). Lines show conditions averaged over 1st April - 30th June each year. Dots show conditions averaged over 2-week periods from 1st April - 24th June.

Metrics of modelled migrations varied both between years and between rivers (Figure 2.10). The proportion of time spent in water of depth less than 200m was very high (>0.9) across all rivers in some years (e.g. 2002-2004), while in other years it was more variable between rivers. In addition, some rivers had high values (>0.8) of this metric across most years (e.g. rivers 6-8 and 20-21: Leven, Glenmore, Ayr, Owenreagh, Coomhola). The mean metric per year across all rivers ranged from a minimum of 0.81 in 2016 to a maximum of 0.98 in 2003 and 2017.

Speeds of modelled migrations also varied between years and rivers (Figure 2.10 c and d). Some rivers had noticeably high or low speeds across most years: rivers 6-8 (Leven, Glenmore, Ayr) displayed fast speeds (>25 km/day) across all years, coinciding with a high proportion of time spent

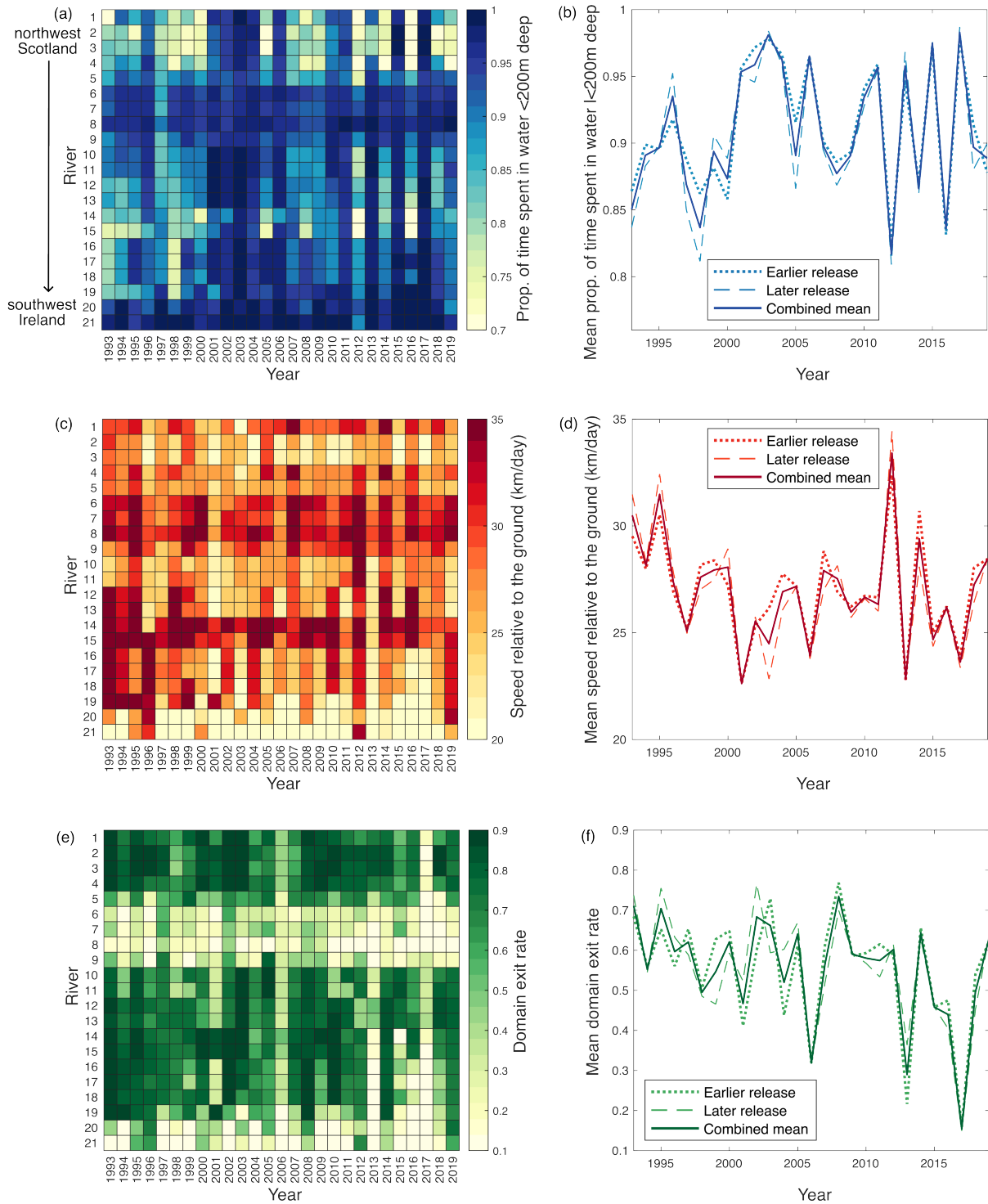


Figure 2.10: (a), (c), (e): heatmaps displaying metrics of modelled Atlantic salmon (*Salmo salar*) migrations per river per year (including both releases). (b), (d), (f): metrics of modelled migrations (mean taken across rivers) for the earlier and later (2 weeks later) particle releases, and the combined mean (both releases).

in shallow water (Figure 2.10 a). Contrastingly, rivers 20 and 21 (Owenreagh and Coomhola) showed lower speeds (~ 20 km/day) across years, while also spending a high proportion of time in shallow water. Migration speeds were highly variable across years: the mean speeds ranged from a minimum of 22.6 km/day in 2001 to a maximum of 33.4 km/day in 2012.

Domain exit rates showed significant variation between rivers and between years (Figure 2.10 e and f). Across rivers, particularly low rates (~ 0.25) were seen across the period for rivers 6-8 and 20-21, the same group of rivers which spent high proportions of time in shallow water. Other rivers maintained high exit rates (> 0.7) in most years (e.g. rivers 1-4: Bharp, Mhuil, Ullapool, and Arnisdale). The mean domain exit rate (mean across rivers per year) ranged from a minimum of 0.15 in 2017 to a maximum of 0.73 in 2008. There was a weak declining trend in the domain exit rates over the study period (mean change of -0.007 per year, $r^2 = 0.166$, $p = 0.03$).

There were only minor differences in the migration metrics between the earlier and later releases (Figure 2.10 b, d, f), with much greater variability between years than between releases.

2.3.3 Mechanisms behind variability in migrations

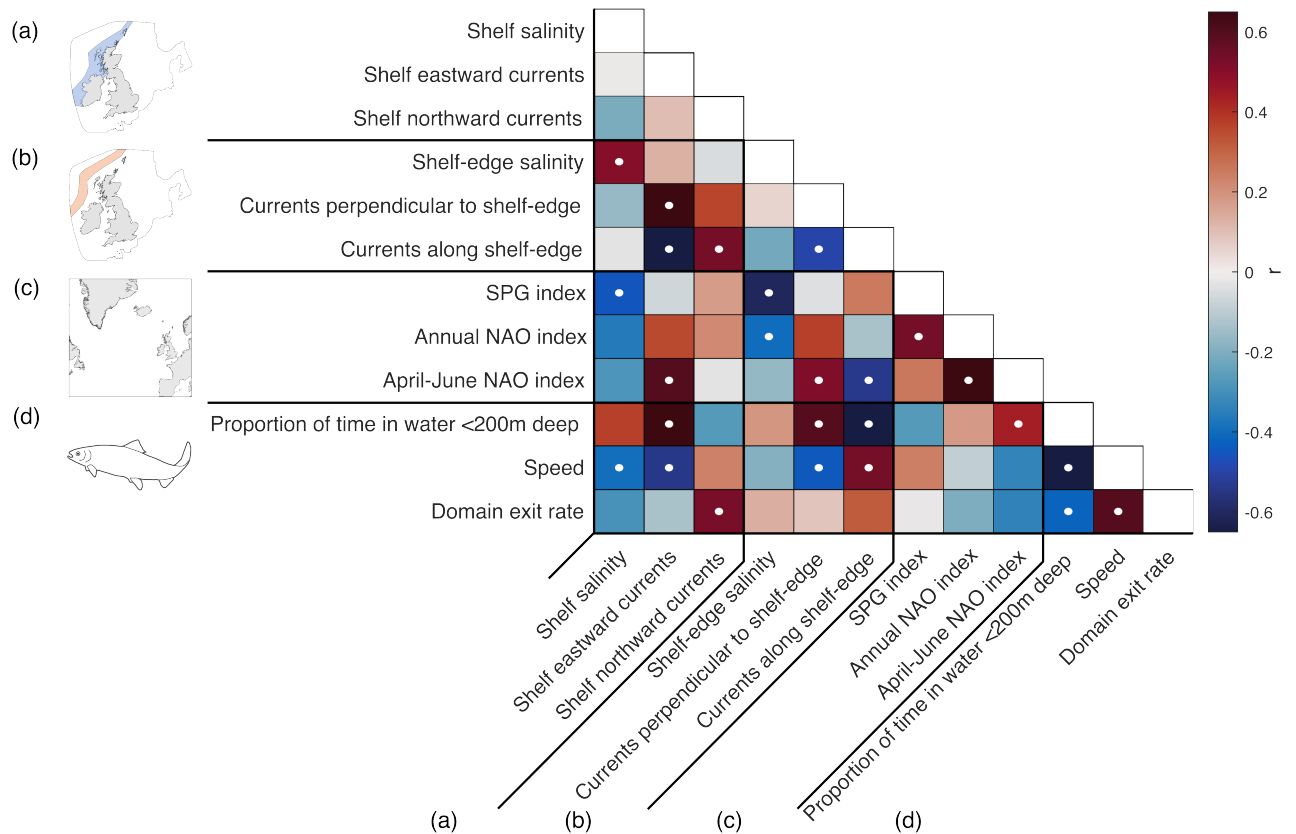


Figure 2.11: Correlation matrix between: (a) on-shelf salinity and currents, (b) shelf-edge salinity and currents, (c) large-scale climate indices (subpolar gyre SPG and North Atlantic Oscillation NAO), (d) modelled Atlantic salmon (*Salmo salar*) migration metrics. Pearson correlation coefficients (r) between each combination are shown via the colour scale. Significant correlations ($p^* < 0.05$) are denoted by white dots.

On the shelf, both surface salinity and currents influenced modelled migrations. On-shelf salinity and eastward currents were both significantly negatively correlated with the speed of migrations, while eastward currents were also positively correlated with the proportion of time spent in water <200 m deep (Figure 2.11 a and d). Northward currents on the shelf were positively correlated with domain exit rates.

At the shelf-edge, surface salinity had no clear impact on modelled migrations (Figure 2.11 b and d). Surface currents perpendicular to the shelf-edge were positively correlated with the proportion of time spent in water <200 m deep, while currents along the shelf-edge were negatively correlated with this metric. Similarly, currents perpendicular to the shelf-edge were negatively correlated with the speed of migrations, while currents flowing along the shelf-edge were positively correlated with speed.

The April-June mean NAO index was positively correlated with the proportion of time spent in water <200 m deep (Figure 2.11 c and d). While the SPG index was not directly correlated with the migration metrics, it was significantly correlated with shelf and shelf-edge salinity. The April-June NAO index was additionally correlated with shelf and shelf-edge currents, which are themselves correlated with the speed of modelled migrations and the time spent in water <200 m deep.

The minimum distance from each river start point to the continental shelf-edge and the total minimum migration distance from each river were both correlated with the proportion of time spent in shallow water and the domain exit rate (Table 2.2). Neither of these distances were correlated with the speed of migrations.

	Proportion of time in water <200 m deep	Speed relative to the ground	Domain exit rate
Minimum distance to continental shelf-edge	$r^2 = 0.381, p = 0.003$	No correlation	$r^2 = 0.677, p < 0.0001$
Total minimum migration distance	$r^2 = 0.561, p < 0.0001$	No correlation	$r^2 = 0.271, p = 0.02$

Table 2.2: Linear relationships between the mean migration metrics per river and the minimum distance from each river to the continental shelf-edge, or the total minimum migration distance.

2.3.4 Comparison between marine return rates and modelled migrations

There was weak evidence (at the 90% confidence interval, $p < 0.1$) of a correlation between 1SW marine return rates and the modelled domain exit rates (Figure 2.12). This correlation did not hold when the time series were detrended ($p_{detrend} > 0.1$).

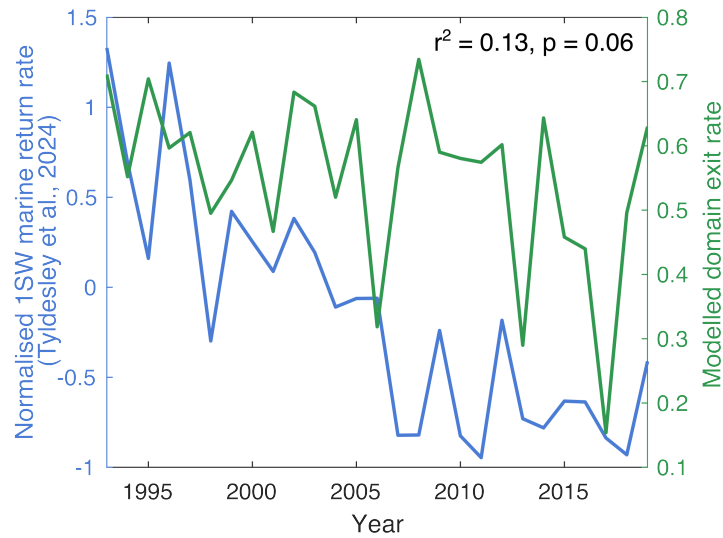


Figure 2.12: Time series of grouped one-sea-winter (1SW) normalised return rates from western populations (blue line; Tyldesley *et al.*, 2024, normalisation was by z-scores across whole time series, 1980-2019) and modelled domain exit rates (green). Correlation coefficients between the time series are shown.

2.4 Discussion

2.4.1 Migration model

We developed a post-smolt migration model combining three mechanisms: following local currents, following the local salinity gradient, and directional swimming. The behavioural model developed in this study may not exactly represent the real instantaneous swimming behaviour of post-smolts as the spatial and temporal scales in the model are greater than those used for real instantaneous navigation. However, it gives a representation of migrations which shows good agreement with limited observational data (Figure 2.8). This representation allows us to consider interannual variability in migrations and the mechanisms driving this.

All three of the behavioural components considered were found to be beneficial in terms of domain exit rates (Figure 2.4), meaning they resulted in a model where simulated post-smolts exited our domain in high numbers within a time that was in line with trawling studies in the Norwegian Sea (Gilbey *et al.*, 2021). We also found that reasonably high domain exit rates could be obtained when omitting the current-following behaviour (Figure 2.5 a). This suggests that currents might be less important as an active swimming cue than the salinity gradient following and directional swimming behaviours. This agrees with the modelling studies of Newton *et al.* (2021), who found that post-smolt swimming direction was not explained by the current direction, and Ounsley *et al.* (2020), who found that post-smolt migrations from around Scotland could not be simulated with only a current-following behaviour. This result might not hold universally, however, given that other studies have indeed found evidence of post-smolts using currents to guide their migration (e.g. Lilly *et al.*, 2022). Additionally, even if ocean currents are not used

as an active swimming cue, they will still passively influence post-smolt migrations.

The spatial and temporal overlap of our modelled distributions of post-smolts with observations of post-smolts from the SALSEA-Merge project (Figure 2.8) suggest that our movement model can describe post-smolt migrations in this region to a reasonable accuracy. However, the observations from the SALSEA-Merge project are not comprehensive and, crucially, they do not provide information on where post-smolts were not found. Additionally, comparisons between our modelled migrations and the observations must be interpreted cautiously as we do not know the rivers of origin of the observed post-smolts and there are likely to be differences in migration routes and timings between stocks (though some post-smolts captured in this region have been genetically assigned to British/Irish origin; Gilbey *et al.*, 2021). There are also likely to be significant differences in migration patterns between years, but we could only compare with observations from one year (2008) of our 27-year study period.

Most modelled migrations followed a route along the continental shelf-edge (Figure 2.7), which is consistent with multiple observations of post-smolts in the shelf-edge current (Shelton *et al.*, 1997; Holm *et al.*, 2000; Utne *et al.*, 2020; Gilbey *et al.*, 2021). However, given the highly variable conditions which force modelled movement, plus the stochastic element of movement, we did not expect to see all modelled migrations taking exactly the same route. Instead, we found variation in paths both within and between years (Figure 2.7 and Appendix A). Some simulated post-smolts from rivers 6-9 travelled south into the Irish Sea (Figure 2.7), which explains the low domain exit rates seen for these rivers (Figure 2.10). Similarly, some post-smolts from rivers 20 and 21 (Owenreagh and Coomhola) travelled south into the Celtic Sea in some years (e.g. 2002). This agrees with the findings of Mork *et al.* (2012), who simulated post-smolt migrations in this region in 2002 and 2008 and found a concentration of post-smolts south of Ireland in 2002, but not in 2008.

The low domain exit rates and southwards direction of travel observed here for rivers 6-9 and 20-21 might suggest that post-smolts from these rivers have to utilise a different behaviour or navigational cue in their initial marine migration, in which case a different model would be required to simulate their migrations. Further work could investigate the application of different behavioural models to these rivers, for example using a different threshold for the inclusion of the directional component, or a different bearing for the directional component.

2.4.2 Variable migrations

The differences in migration trajectories between years shown in the Appendix A relate to differences in the metrics of migrations. For example, in 2015 there was a greater concentration of simulated post-smolts distributed across the shelf than in 2016, relating to a larger proportion of time spent in shallow water in 2015 (0.98) than in 2016 (0.84). This metric was high (>0.8) across all years, indicating that the majority of each modelled migration was spent on the shelf and that the overall speed of migrations was faster once off the shelf (this result is at least in part caused by the addition of the directional component at a depth of 200 m). At present, there is unfortunately no empirical data with which to compare the modelled proportion of time spent

on the shelf. Physical conditions differ between the continental shelf and the shelf-edge (Figure 2.9) and biological conditions, such as prey and predator fields, are also likely to differ between the on and off-shelf regions (Simpson & Sharples, 2012). This suggests that year-to-year changes in the proportion of time spent in shallow water could result in changes in the physical and biological conditions experienced by post-smolts during their early marine migration, influencing growth and survival. If prey conditions are richer on the shelf, then spending a large proportion of time on the shelf could be beneficial to post-smolts, or vice-versa.

Mean domain exit rates ranged from 0.15 and 0.73 between years (Figure 2.10). This variation shows that modelled migrations are highly influenced by interannual changes in environmental conditions. While the domain exit rates might not directly correlate to the “success” or survival of real post-smolts, these rates might still suggest years in which migration might be easier (higher domain exit rate) or harder (lower domain exit rate). If the interannual variability in the domain exit rates of our modelled migrations is greater than the variability in real post-smolt migration success during this time, this may suggest that post-smolts can adapt their migratory behaviour between years to deal with changes in conditions, as concluded by Burke *et al.* (2016a) for modelled juvenile Pacific salmon migrations.

It is hard to draw comparisons between our model results and the marine survival rates of Atlantic salmon for two main reasons: firstly as we did not include any mortality in our modelling, and secondly as we only modelled migrations over the first 100 days at sea, while most Atlantic salmon will spend 1-4 years at sea (Aas *et al.*, 2010). However, there was some evidence of a weak relationship between marine return rates and modelled domain exit rates (Figure 2.12), which have both declined over the study period. This might suggest that the declining success (or increasing difficulty) of post-smolts reaching their summer feeding grounds might be one factor driving declines in marine survival. However, detrended marine return rates were not significantly correlated with modelled domain exit rates, so interannual fluctuations in modelled migrations are not synchronous with fluctuations in marine survival rates.

Speeds of up to 33.4 km/day were seen in our modelled migrations. These are in line with rapid post-smolt migration speeds measured recently in the Irish Sea of up to 39.9 km/day (Lilly *et al.*, 2023), and speeds of up to 53.8 km/day measured to the west of Scotland (Rodger *et al.*, 2025).

In addition to the interannual variation in modelled migrations, we also saw differences between rivers (Figure 2.10). This is in line with the telemetric study results of Rodger *et al.* (2025), who observed differences in migration paths and speeds between rivers. We found that between-river differences in domain exit rates were related both to their minimum distance from the continental shelf-edge and to their total minimum migration distance (Table 2.2). This is in line with the finding of Lilly *et al.* (2023), who saw that the minimum migration success of post-smolts in the Irish Sea (based on receiver detections of acoustically tagged fish) was correlated with their minimum distance of travel (from river of origin to the marine arrays). Here, the minimum distance from each river to the shelf-edge explained 68 % of the between-river variation in domain exit rates, while the total minimum migration distance explained only 21 % (Table 2.2). This might suggest there are greater navigational challenges in the first section of the marine migration

(i.e. from the coastline out to the continental shelf-edge) than the rest of the journey (following the continental shelf-edge towards the Norwegian Sea).

2.4.3 Environmental variability and its relation to variability in migrations

Both within and between years, surface salinity was highly variable on the shelf (Figure 2.9 a). Wind-driven changes influence the propagation of freshwater from the coastline across the shelf west of Ireland and Scotland and the transport of higher-salinity Atlantic water onto the shelf, causing such variability in salinity (Jones *et al.*, 2018; Barton *et al.*, 2024). At the shelf-edge, we found that salinity was much less variable, and the magnitude of variability was greater between, rather than within, years (Figure 2.9 d).

The shelf-edge current was highly variable between years (Figure 2.9 e and f). We found that stronger currents perpendicular to the shelf-edge (on-shelf positive) caused an increased amount of time to be spent in shallow water (i.e. it was harder for the simulated post-smolts to reach or remain at the shelf-edge or in deeper water), while stronger currents along the shelf-edge reduced the amount of time spent in shallow water (Figure 2.11). Therefore, years with stronger, or more directed, currents along the shelf-edge might allow for a faster or easier migration. These relationships are in line with the findings of Moriarty *et al.* (2016) that variability in surface currents is related to variability in modelled post-smolt migrations.

We expected that the within-year variability in the shelf-edge current (Figure 2.9 e and f) might also have a significant impact on migrating post-smolts: the differences between two-week periods could mean that post-smolts leaving their rivers earlier or later experience different currents at the shelf-edge, which could lead to different outcomes to their initial marine migration. However, we found that the metrics of modelled migrations were similar across our two release dates (Figure 2.10), which suggests that the date of commencing migration is less important than the differences in conditions between years.

While we did not find a significant difference in modelled migration metrics between the two release dates (Figure 2.10), we anticipate that a change in migration timing has impacts stretching beyond those conveyed by our results. The timing of prey availability is an important factor in the survival and recruitment of fish populations (Cushing, 1990) and in anadromous salmonids it is vital that the timing of migration coincides with the timing of sufficient prey availability (Satterthwaite *et al.*, 2014; Wilson *et al.*, 2021). Therefore, while a two-week difference in migration timing had only a minor impact on the outcome of modelled migrations, this change might have a greater effect on the real growth or survival rates of post-smolts.

Surface salinity on the shelf was negatively correlated with the speed of migrations (Figure 2.11 a and d). This suggests that years with lower on-shelf salinity might have a larger, or more directed, salinity gradient. Therefore, if post-smolts indeed use salinity as a cue to guide their migration, they might be able to migrate more quickly or easily in lower salinity years.

The SPG index was negatively correlated with salinity on the shelf and at the shelf-edge. These relationships are expected: it is known that variability in the shelf-edge current is related to

changes in the strength of the subpolar gyre (Marsh *et al.*, 2017; Clark *et al.*, 2022). Given that salinity (on-shelf and shelf-edge) and shelf-edge currents were seen to influence modelled migrations (Figure 2.11 a/b and d), we expect that the strength of the subpolar gyre will have an indirect effect on migrations. Similarly, the April-June NAO index was correlated with shelf and shelf-edge currents, suggesting it will influence migrations. This agrees with the finding of Mork *et al.* (2012) that modelled migrations differed between a positive NAO year (2002) and a negative NAO year (2008). The correlations found between environmental conditions and metrics of modelled migrations (Figure 2.11) provide evidence to support our hypothesis that interannual variability in oceanographic conditions drives interannual variability in modelled migrations (**H1**). Based on the significant correlations, a summary of the beneficial oceanographic conditions for simulated post-smolt migrations is provided in Figure 2.13.

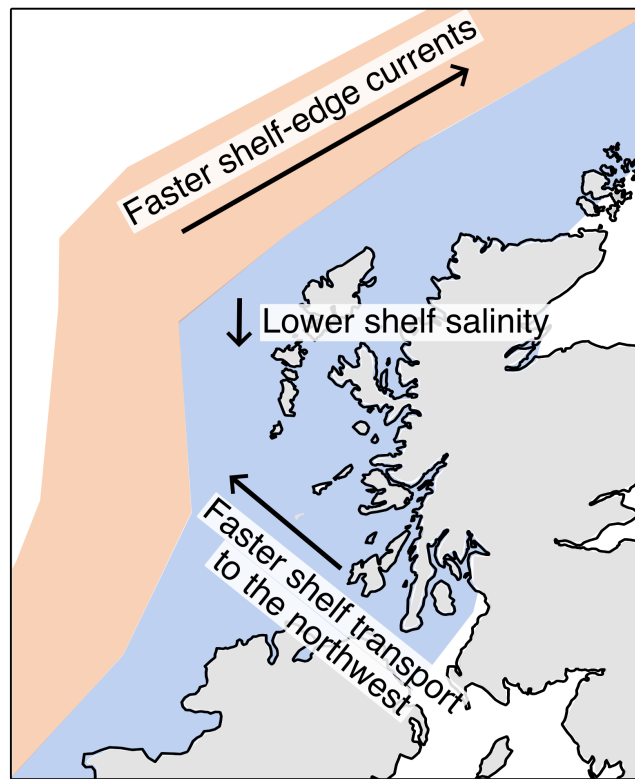


Figure 2.13: A summary of the beneficial oceanographic conditions for simulated Atlantic salmon (*Salmo salar*) post-smolt migrations, based on the correlations displayed in Figure 2.11. Faster shelf-edge currents and faster on-shelf northwest currents are both associated with a negative North Atlantic Oscillation (NAO) index. Lower on-shelf salinity is associated with a stronger subpolar gyre (SPG) index.

We have seen that changes in local salinity and surface currents, and changes described by the SPG and NAO indices, can physically influence post-smolt migrations, regarding the path taken or the time taken to migrate, but these changes likely have further impacts on post-smolts. Shifts in water masses related to a stronger subpolar gyre have been related to an increase in the abundance of *Calanus finmarchicus* and other copepods in the northeast Atlantic (Hátún *et al.*, 2009), key species in the energy transfer from phytoplankton to forage fish, of which the larvae

are a prey item of post-smolts (Utne *et al.*, 2021b). Similarly, negative phases of the NAO have been related to increased *Calanus finmarchicus* abundance in the northeast Atlantic (Greene & Pershing, 2000; Drinkwater *et al.*, 2003). Changes in zooplankton energy such as the above have been related to salmon return rates within our study region (Tyldesley *et al.*, 2024). Given we found that the beneficial oceanographic conditions for post-smolt migrations in this study (Figure 2.13) were associated with a negative NAO index and a strong SPG index (Figure 2.11), these relationships suggest that good prey conditions for post-smolts might occur concurrently with good physical migration conditions.

Our finding that a negative NAO phase relates to beneficial physical ocean conditions for migrations is in line with the negative correlation found between the NAO index and salmon marine survival from the rivers Burrishoole and Corrib (river locations displayed in Figure 2.1, Peyronnet *et al.*, 2008). Contrastingly, Jonsson & Jonsson (2004) found a positive relationship between the NAO index and salmon growth during the first year at sea for a Norwegian river. This highlights the potential differences in the effects of variable environmental conditions across different regions and emphasises the need to focus on underlying mechanisms driving changes in growth and survival.

At present, there is a lack of empirical data on post-smolt migrations. This means that aspects of our work remain uncertain, and we hope that future advances and new data sources (e.g. in telemetric methods or trawling studies) will help clarify our results. The precise migration paths of post-smolts cannot be predicted by our model, nor can we say that our model represents the exact navigational cues used by post-smolts (especially as our modelling is on a larger spatial scale than instantaneous navigation). While we have evaluated the direction of response of the migration metrics to various changes in environmental conditions, the scale of variability in migration metrics among rivers and years is still uncertain, particularly as our model did not include mortality. Additionally, despite the optimisation process applied to develop our behavioural model, it is still difficult to say exactly which environmental cues are used to “signpost” post-smolt migration. Future surface trawling or marine telemetry studies for post-smolts should consider the oceanographic conditions both at the known locations of post-smolts and in nearby locations where post-smolts were not observed. This might provide a better idea of the potential choice of environment by post-smolts, as well as providing further basis to the behavioural decisions made in future modelling work.

Despite these uncertainties, our work has revealed that particular oceanographic conditions are beneficial for post-smolt migrations and that changes in these conditions might explain some year-to-year variability in migrations. We also found that differences in migration metrics between rivers were well explained by their distance to the continental shelf-edge, which agreed with the findings of a recent telemetry study in the same area (Lilly *et al.*, 2023). Our results are of value in marine spatial planning, for example evaluating the potential overlap between migrating post-smolts and offshore energy developments, fisheries, and aquaculture sites. Further development of this migration model will offer better integration of the variable opportunities and risks associated with feeding, growth and predation along and between migration corridors. These results can

be used to improve the quality of salmon-focused ecosystem assessments (Bull *et al.*, 2022) and develop predictions for future marine survival chances.

2.5 Conclusion

This study modelled interannual variation in Atlantic salmon post-smolt migration pathways from Scottish, Northern Irish and Irish rivers over 27 years. We developed an active swimming model in which post-smolts utilised ocean currents, salinity, and magnetic cues to guide their migration. The model does not predict the exact paths taken by migrating salmon, but instead it allows us to consider the mechanistic impact of various physical environmental conditions on migrations. We found that migrations varied significantly between years, with metrics of migrations correlated with time series of local surface currents and salinity. Beneficial oceanographic conditions for migrations were found to be: low salinity on the shelf, fast northwest currents on the shelf, and fast shelf-edge currents. These conditions are associated with a negative NAO index and a strong SPG index. The physical differences in migrations between years (in the proportion of time spent in shallow water, the speed of migrations, and the domain exit rate) suggest the likelihood of differences in the biological conditions experienced by fish, for example in the prey fields they might encounter along their migration. Variation in migrations between rivers suggests that post-smolts migrating from different rivers are impacted differently by environmental conditions. Future modelling work could extend this model to be applicable to a larger set of rivers and compare regional differences while still considering the full 27-year period as we have done here. These results could test whether similarities in the outcomes of modelled migrations between groups of rivers relate to groupings in marine return rates or phylogenetic groupings.

Data availability

The particle tracking software FISCAM is available at https://github.com/GeoffCowles/fiscam/tree/ounsley_et_al_2019. The SSW-RS is available at <https://doi.org/10.7489/12423-1>. Smolt migration timing data is available at <https://doi.org/10.5063/F1HQ3XD1>. Body lengths of juvenile salmon from the Burrishoole river are available at <https://data.gov.ie/dataset/fish-lengths-of-juvenile-atlantic-salmon-from-the-burrishoole-catchment-co-mayo-ireland-1997-2019>.

Chapter 3

Movement modelling of migrating Atlantic salmon post-smolts reveals the value of a portfolio of behavioural strategies

3.1 Introduction

Migration occurs in many different forms, over a vast range of spatial and temporal scales (Dingle & Drake, 2007; Chapman *et al.*, 2014). It is a risky strategy, with potential costs including increased mortality and increased energetic expenditure (Alerstam *et al.*, 2003; Béguyer-Pon *et al.*, 2012). Still, migration has evolved where species or populations gain benefits that could not be obtained from a resident life-history, such as an increase in reproductive success, access to better feeding resources, or avoiding predation (Dingle, 1996; Alerstam *et al.*, 2003; Chapman *et al.*, 2011; Bandara *et al.*, 2021). Migration behaviour is heterogeneous within species and populations (Chapman *et al.*, 2011), with behaviour likely driven by minimising costs (such as energy, time, or predation risk) or maximising benefits (such as feeding opportunities) of migration (Alerstam & Lindström, 1990; Lank *et al.*, 2003). For many species, migration is becoming increasingly risky due to anthropogenic activity, with decreases in habitat quantity or quality, increases in migration barriers, and ongoing global climate change (Wilcove & Wikelski, 2008).

High mortality rates of Atlantic salmon (*Salmo salar*) during the early marine migration (post-smolt life stage) are thought to drive range-wide trends of low marine survival rates (Thorstad *et al.*, 2012), which in turn have driven large declines in populations in recent decades (Friedland *et al.*, 2009; Chaput, 2012; Pardo *et al.*, 2021). Despite this, the drivers of mortality of salmon during the marine migration are yet to be fully understood (Thorstad *et al.*, 2021; Bull *et al.*, 2022).

Salmon are termed post-smolts between entering the sea and the end of their first winter at sea

(Allan & Ritter, 1977). Acoustic telemetry has revealed some of the pathways of migrating post-smolts in rivers, estuaries, and coastal areas in certain locations around the British Isles (e.g. Newton *et al.*, 2021; Lilly *et al.*, 2022, 2023; Rodger *et al.*, 2025). Once post-smolts have exited coastal waters, data is more sparse and consists of occasional locations of trawled fish. These have revealed concentrations of post-smolts at the continental shelf-edge and the Norwegian Sea (Shelton *et al.*, 1997; Holm *et al.*, 2000; Gilbey *et al.*, 2021). In other regions, including the North Sea, little is known about the migratory routes of post-smolts (ICES, 2023e). Even in locations where data are plentiful, neither trawling nor telemetric methods have the ability, at present, to reveal the full path of a salmon post-smolt. Similarly, these techniques cannot reveal the behaviours underlying migration. Modelling is therefore a useful exercise to “fill the gaps” in these sparse datasets, as well as testing hypotheses on migratory mechanisms, or helping to inform future empirical research. Previous post-smolt migration models have revealed differences in migration routes between rivers (Moriarty *et al.*, 2016; Utne & Mousing, 2025) and between years, correlated with interannual differences in ocean currents, salinity or temperature (Mork *et al.*, 2012; Byron *et al.*, 2014; Moriarty *et al.*, 2016; Borland *et al.*, 2025). Each of these studies focused on different locations and/or time periods and used different models for post-smolt swimming behaviour, suggesting that no singular migration behaviour is applicable across all salmon populations (Byron & Burke, 2014). Even within a single study in a smaller spatial region (Scotland) for one year, Ounsley *et al.* (2020) found that a combination of different swimming behaviours was required to successfully simulate migrations from a number of rivers.

As discussed in Chapter 1, it is possible that some of the differences in resulting modelled behaviours between these studies resulted from methodological differences. The model selection criteria varied between the studies, as did the hydrodynamic ocean models. However, salmon are locally adapted to their specific environment (Taylor, 1991), so differences in migratory behaviour are likely. Empirical evidence also supports the hypothesis that migration behaviours vary between populations (Lacroix, 2008, 2013). Furthermore, differences in migration behaviour between salmon populations are unsurprising when considering the genetic structure of Atlantic salmon. The species is made up of many genetically distinct populations (King *et al.*, 2001; Bourret *et al.*, 2013), maintained by limited reproduction between populations resulting from the homing of salmon to their natal rivers to spawn (Verspoor *et al.*, 2007). Populations are locally adapted, meaning they have increased fitness within their home environment (Taylor, 1991; Fraser *et al.*, 2011). This is illustrated by the common garden experiment of Plantalech Manel-la *et al.* (2011), in which hatchery-reared fish originating from two distinct rivers were released into a Norwegian fjord, and their movements were followed using acoustic telemetry. The smolts with parents from a river with a long migration to the sea migrated earlier, faster, and more successfully compared to the smolts originating from a river with a short migration to the sea. These results suggest that the migratory behaviour of the two populations has evolved to suit their unique migration routes. However, more generally, it is unclear how much of the variability in salmonid migration traits is genetically-driven as opposed to environmentally-driven (Reed *et al.*, 2025), and genetic diversity is also observed within rivers and even between individuals (Verspoor *et al.*, 2007; Cauwelier *et al.*, 2018).

Genetic and phenotypic diversity between and within salmon populations can dampen species- or stock-level variability in return rates (Schindler *et al.*, 2010; Carlson & Satterthwaite, 2011; Griffiths *et al.*, 2014). This is an example of the portfolio effect, a concept originally borrowed from finance (Markowitz, 1959; Sharpe, 1963), which has important applications in ecology. By spreading risk across multiple “assets” (such as populations with differing life-history strategies), portfolios can protect populations or species against environmental fluctuations, thereby increasing resilience (Den Boer, 1968; Greene *et al.*, 2010). In salmon, the biological mechanisms driving the observed portfolio effects are often unclear, though Griffiths *et al.* (2014) found a negative correlation between the portfolio performance of salmon fisheries and anthropogenic modification of watersheds. Understanding the drivers behind these observed portfolio effects in salmon will allow focused conservation efforts aimed at maintaining diversity.

Chapter 2 revealed that interannual variability in local oceanographic conditions drove variability in modelled migration success. Here, we hypothesise that diversity in the swimming behaviours of salmon post-smolts may dampen this variability, contributing to a portfolio effect. In this study, we use the parameterisation of a post-smolt movement model for 38 rivers around the British Isles (Figure 3.1) as a method to study the similarities and differences in plausible swimming behaviours between river populations and to consider the value of a range, or portfolio, of behaviours being utilised within each river. This method addresses our hypothesis that different post-smolt swimming behaviours are utilised between and within populations (**H2**). Note that the numbering of the Irish, Northern Irish and Scottish rivers differs here from Chapter 2 (Figure 2.1); this was necessary as more rivers are considered in this chapter. The river numbers in Figure 3.1 are retained for the remainder of this thesis.

3.2 Methods

3.2.1 Model structure

A post-smolt migration model was developed for a group of Irish, Northern Irish and Scottish rivers (including rivers 29-38 in Figure 3.1) in Chapter 2. Here, it was generalised for rivers surrounding the British Isles. A summary of the model is provided below, with further analysis and justification of the behavioural components, the salinity gradient calculation, the timestep, and the timings of particle releases provided in Chapter 2.

The model consisted of a Lagrangian particle tracking model (FVCOM i-state configuration model; Liu *et al.*, 2015; Ounsley *et al.*, 2020) coupled with an active swimming model. The active swimming velocity $\mathbf{g} = (g_x, g_y)^T$ in m s^{-1} was given by

$$\mathbf{g} = w_c \mathbf{g}_c + w_s \mathbf{g}_s + w_d \mathbf{g}_d, \quad (3.1)$$

where $\mathbf{g}_c$ is a current-following behaviour, $\mathbf{g}_s$ represents following an increasing salinity gradient, $\mathbf{g}_d$ is a directional component (simulating the use of magnetic cues), and w_c, w_s and w_d are the respective nonnegative weights of each component with $\sqrt{w_c^2 + w_s^2 + w_d^2} \equiv 1$. The three

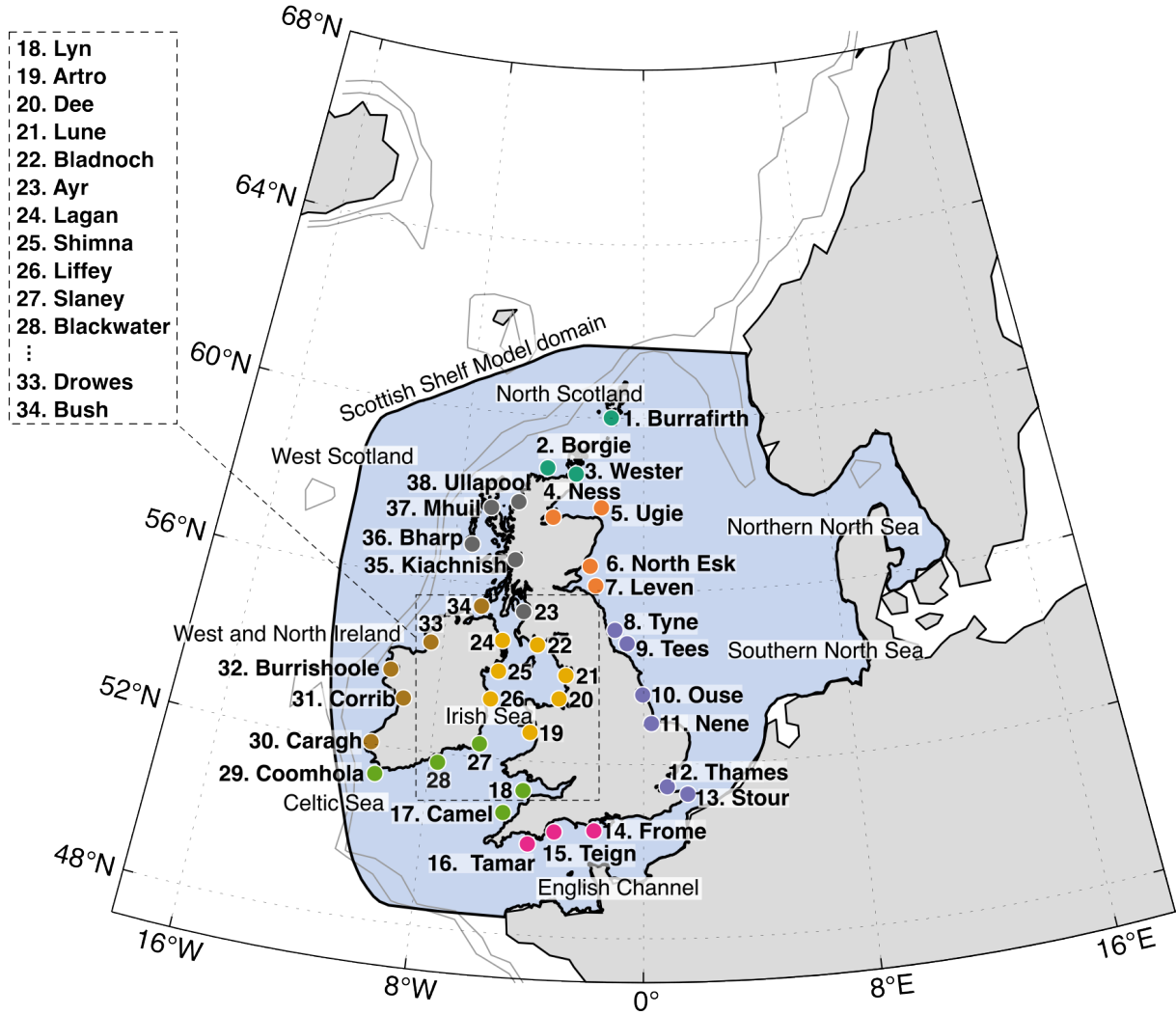


Figure 3.1: The 38 salmon rivers included in this study, coloured and labelled according to their geographical location, and the Scottish Shelf Model domain (blue).

behavioural components were given by

$$\mathbf{g}_c = s L \left(\frac{\mathbf{u}}{|\mathbf{u}|} \right), \quad (3.2)$$

$$\mathbf{g}_s = s L \frac{\nabla S}{|\nabla S|_{median} + |\nabla S|}, \quad (3.3)$$

$$\mathbf{g}_d = s L R \frac{|\theta - \theta_{bias}|}{\pi} \mathbf{q}. \quad (3.4)$$

The parameter s relates to the maximum swimming speed of post-smolts (BL s^{-1}), L is body length (m), $\mathbf{u} = (u, v)^T$ is surface current velocity (m s^{-1}), ∇S is the surface salinity gradient (psu km^{-1}) calculated over a 10 km radius, $|\nabla S|_{median}$ is the median salinity gradient magnitude across the model domain ($0.0045 \text{ psu km}^{-1}$), R is a binary variable representing the “switching on” of the directional behaviour, θ is the present direction of movement, θ_{bias} is the preferred

direction of movement, and $\mathbf{q} = \begin{pmatrix} \cos \theta_{bias} \\ \sin \theta_{bias} \end{pmatrix}$. Body length of simulated post-smolts was given by the growth function $L = L_0 e^{0.0059 \cdot d}$ where d is the number of days spent at sea (Mork *et al.*, 2012; Ounsley *et al.*, 2020). The parameter R was defined as

$$R = \begin{cases} 0 & \text{before first occurrence of a threshold value of salinity, bathymetry, or time} \\ 1 & \text{after first occurrence.} \end{cases} \quad (3.5)$$

The parameters w_c, w_s, w_d, s , the threshold for R , and θ_{bias} were tested and tuned for each of the study rivers. By doing this, we considered similarities and differences in the potential swimming behaviour of post-smolts from these rivers.

The movement model was driven by the Scottish Shelf Waters Reanalysis Service 3.02 (SSW-RS), a 27-year (1993-2019) physical reanalysis of the Scottish Shelf Model (Barton *et al.*, 2022), covering the domain shown in Figure 3.1. Daily or hourly outputs of the SSW-RS are available; here, we used daily outputs with a 12-hour timestep. Currents from the SSW-RS were interpolated to particle positions at each timestep, providing $\mathbf{u}$ above. Particle release locations were 38 rivers around the British Isles, with each point set 30 km away from the coastline to prevent collisions (locations shown in Figure 3.1). Migration timing (i.e. particle release dates) followed the same latitudinal gradient as in Chapter 2, and simulations ran for 100 days.

3.2.2 Model parameterisation

Summary metrics

While some empirical data describing the locations of post-smolts in the marine environment is available (Section 3.2.4), these data only cover small areas of the study region and are not relevant to all of the 38 rivers, so the model could not be parameterised based on these observations. Instead, we chose plausible simulations based on the domain exit rate, calculated as the proportion of particles reaching a defined “domain exit region” (at the northern boundary of the SSM domain, from -12° to 5° longitude and 75 km thickness) within 100 days of entering the sea, with this time frame based on observations of post-smolts in the Norwegian Sea from June-August (Gilbey *et al.*, 2021). Maximising the domain exit rates of the model ensured that the maximum number of simulated post-smolts migrated “successfully” to the Norwegian Sea within an appropriate time period. However, a high exit rate may correspond to an unrealistic energy expenditure. Therefore, a lower bound on the energy use of simulated post-smolts (from swimming and growth only) was calculated and compared to an upper bound of energy acquisition. Empirical data on the abundance and distribution of the prey of post-smolts, such as forage fish larvae, in this region are limited (in terms of availability, correct life-stage, and spatial scale, see Chapter 5 and Tyldesley *et al.*, 2024), so it was not plausible to obtain or simulate a prey field to use within a full bioenergetics model (e.g. as done in the Norwegian Sea by Utne & Mousing, 2025). Instead, the lower bound energy use of post-smolts was calculated post-simulation as a summary metric and used to reject individual modelled post-smolts where the upper bound on

energy acquisition was exceeded. This differs from a typical bioenergetic modelling approach, where energy limitations would constrain movement in each timestep, but both methods ensure that all accepted high exit rate runs are also feasible energetically.

The lower bound of energy use was calculated as the sum of the respiratory energy and the minimum assimilated energy required for growth. Other metabolic losses (e.g. egestion, excretion, specific dynamic action) occur in addition to the lower bound energy budget but are not considered here. The lower bound energy at each timestep was given by

$$E_t = R_t + A_t, \quad (3.6)$$

where R_t is the energy (J) used for respiration at timestep t , from Smith *et al.* (2009), and A_t is the assimilated energy (J) required for growth, given by a rearrangement of the equations of Smith *et al.* (2009). Respiratory energy R_t was a function of fish body weight, sea temperature, and swimming speed. Growth energy A_t was driven by the same variables, as well as fish length. The weight of the post-smolts was not included in our movement model output, so the minimum weight (g) was calculated at each timestep using the modelled body length and assuming that a minimum condition factor of 0.65 was required for survival (Utne & Mousing, 2025). Using the minimum weight was appropriate as the energy estimate E was a lower bound on the total energy expenditure.

The maximum daily consumption rate (in g d^{-1} ; wet weight) was calculated and converted to an energy equivalent E_{cmax} by multiplying by a maximum prey energy density of 5000 J g^{-1} as per Smith *et al.* (2009). Then, the total E_t (summed over all active timesteps, ending after 100 days or when a simulated post-smolt reached the domain exit region) was compared against the upper bound on energy consumption E_{cmax} for each individual simulated post-smolt. If the energy constraint was violated, then the domain exit rate was set to zero; this had the effect of marking model runs with unfeasible energy use as ‘unsuccessful’, meaning they were not considered further.

Parameter testing

Parameter combinations were sampled from the distributions in Table 3.1. Five years (1993, 2003, 2007, 2012 and 2018) were used for the parameterisation process, as it was too computationally expensive to include the full 27-year SSW-RS period. These years were selected to represent a range of ocean conditions (in terms of surface salinity and currents). Twenty particles were released per year and river for 1053 parameter combinations. The number of parameter combinations was limited by computational cost. However, a side experiment where the number of parameter combinations for three rivers was increased by a factor of 5 yielded very similar “optimal” parameters. All simulations were run on the ARCHIE-WeSt High Performance Computer (www.archie-west.ac.uk) and analysis of the simulations was undertaken in MATLAB (Mathworks Inc., 2021).

After applying the energy constraint, the simulations with the top 25 exit rates were retained

Parameter	Distribution	Justification for distribution
w_c	Continuous: U(0,1)	Swimming behaviour can include any proportion of each navigational cue.
w_s	Continuous: U(0,1)	As above.
w_d	Continuous: U(0,1)	As above.
s	Continuous: U(4,6)	Empirical estimates find a wide range of swimming speeds (e.g. 0.3-4 BL/s from Rodger <i>et al.</i> , 2025, assuming a body length of 0.15 m)*, while a previous parameter optimisation obtained $s = 5.5$ (Borland <i>et al.</i> , 2025).
θ_{bias}	Discrete: -45°, 0°, 45°	NW, N and NE bearings; as used in the post-smolt movement model of Ounsley <i>et al.</i> (2020).
Threshold for $R = 1$	Discrete, three categories Depth: 100, 150, or 200 m Salinity: 34.5, 35, 35.5 psu Time: 0, 10, 20 days	A behavioural transition might occur at various environmental thresholds. Depth is unlikely to be directly sensed by post-smolts, but chemical signatures of changing water masses might act as a proxy.

Table 3.1: Prior distributions of the movement model parameters.

*Note that these are minimum straight-line speeds between telemetry detections, and they are expressed in speed relative to the ground, rather than speed relative to the post-smolt (i.e. Eulerian rather than Lagrangian), so are not directly comparable with s .

for each river. Simulations were then run for this set of parameters for each river over the full 27-year period (1993-2019), and this set of model runs was used for the remainder of the analysis.

3.2.3 Portfolio analysis

A version of the Sharpe index, a metric that describes the risk-adjusted performance of a portfolio (Moore *et al.*, 2010; Griffiths *et al.*, 2014), was used to quantify the value of different-sized portfolios of swimming behaviours for each river. Each portfolio p was a set of n exit rate time series ($n = 1 : 25$, time series 1993-2019). For each river, the top 25 exit rates were arranged into a 27×25 (years $\times$ parameter combinations) matrix K , where each row represented a time series, and each column represented a parameter set. For a portfolio of size $n = 1$, the first row of K was considered; for $n = 2$, the first and second rows were considered. The Sharpe index of each portfolio was given by

$$\Omega_n = \frac{\mu_n}{\sigma_n}, \quad (3.7)$$

where μ_n is the mean return of the portfolio and σ_n is the standard deviation. The mean return is given by

$$\mu_n = \sum_{i=1}^n X_i \bar{K}_i, \quad (3.8)$$

where $\bar{K}_i$ is the mean of row i and X_i is the proportional contribution of time series i to the whole portfolio K

$$X_i = \frac{\sum_{j=1}^{27} K_{i,j}}{\sum_{i=1}^n \sum_{j=1}^{27} K_{i,j}}. \quad (3.9)$$

Then,

$$\sigma_n^2 = \sum_{i=1}^n \sum_{j=1}^n X_i X_j cov_{i,j} \quad (3.10)$$

where $cov_{i,j}$ is the covariance of rows i and j . For $i = j$, this represents the variance of i . There are, therefore, two main sources of ‘risk’ in the portfolios: high variance (within each time series) and high covariance (between time series). The optimal portfolio will maximise the mean exit rate (μ_n) and minimise the interannual variance in exit rate (σ_n^2).

The value of n (portfolio size) for the highest-performing portfolio per river (highest Ω_n) was considered to be the optimal portfolio size for that river. Where several portfolios gave the same optimum Ω_n , the largest was retained as the ‘optimum’, such that all relevant parameter sets were considered.

3.2.4 Validation and interpretation

The minimum migration distance from each river to the domain exit region was compared with its optimal portfolio performance. Pearson correlation coefficients (r , p) were calculated to evaluate whether there was evidence of a relationship between portfolio return or standard deviation and minimum migration distance.

The optimal portfolio for each river was selected to plot modelled migrations and for further analysis of the results. To generate a particle density plot, the occurrences of simulated post-smolts in small 20 km² bins were counted and then weighted such that each river had the equivalent number of particles as the largest portfolio size.

Studies using acoustic telemetric methods have examined the nearshore post-smolt migration around the west coast of Scotland, within the Irish Sea, and within the Moray Firth in northeast Scotland (Rodger *et al.*, 2025; Adams *et al.*, 2025). Additionally, the work of Newton *et al.* (2026) used epipelagic trawls to identify post-smolts within the North Sea east of Scotland and within the Moray Firth. To test and validate the model, monthly simulated post-smolt densities were compared with the known locations of post-smolts from these studies.

To consider the portfolio effect in a wider sense, we calculated the coefficient of variation of the domain exit rates (CV; standard deviation divided by mean) on three different scales, similar to Schindler *et al.* (2010). CV is equivalent to $\frac{1}{\Omega_n}$ (i.e. the reciprocal of the Sharpe index); this measure was used here because certain simulated migrations had domain exit rates with $\sigma_n = 0$, generating an infinite Sharpe index, so a mean value of Ω_n could not be taken across rivers. The smallest scale of variation over which CV was calculated was between individual swimming behaviours. Next, river-level variation was considered, i.e. the variation across aggregate exit rates for the ‘optimal’ portfolio for each river. Then, stock-level variation was calculated as the variation across the aggregate of all exit rate time series, with each river weighted evenly. Each scale of CV was calculated for the domain exit rates generated by: the selected optimal portfolio for each river; the single top performing swimming behaviour per river ($n = 1$); and the entire set of swimming behaviours per river ($n = 25$). This comparison could inform whether the existence of optimal portfolios for each river notably improved CV at the stock-level.

3.3 Results

Initial full-parameter-space model runs were conducted over the five test years, then the 25 parameter sets giving the highest domain exit rates were selected for each river and run for the full 27-year period. Optimal portfolios were selected per river according to the optimal Sharpe ratios (representing the best tradeoff between high mean exit rates and low interannual variability). The selected model consisted of portfolios of multiple modelled swimming behaviours for each of the 38 rivers.

3.3.1 Modelled post-smolt migrations 1993-2019

The concentration of modelled post-smolts for the selected parameter sets for all rivers is shown in Figure 3.2. For many of the rivers on the west side of the British Isles, a common route following the continental shelf-edge is observed (as in Chapter 2). There was not a clearly defined route throughout the whole North Sea, but there were higher densities of modelled post-smolts east of the Scottish coast and near Shetland. Migration paths from the three English Channel rivers were split between the east (through the North Sea) and the west (west of Ireland or through

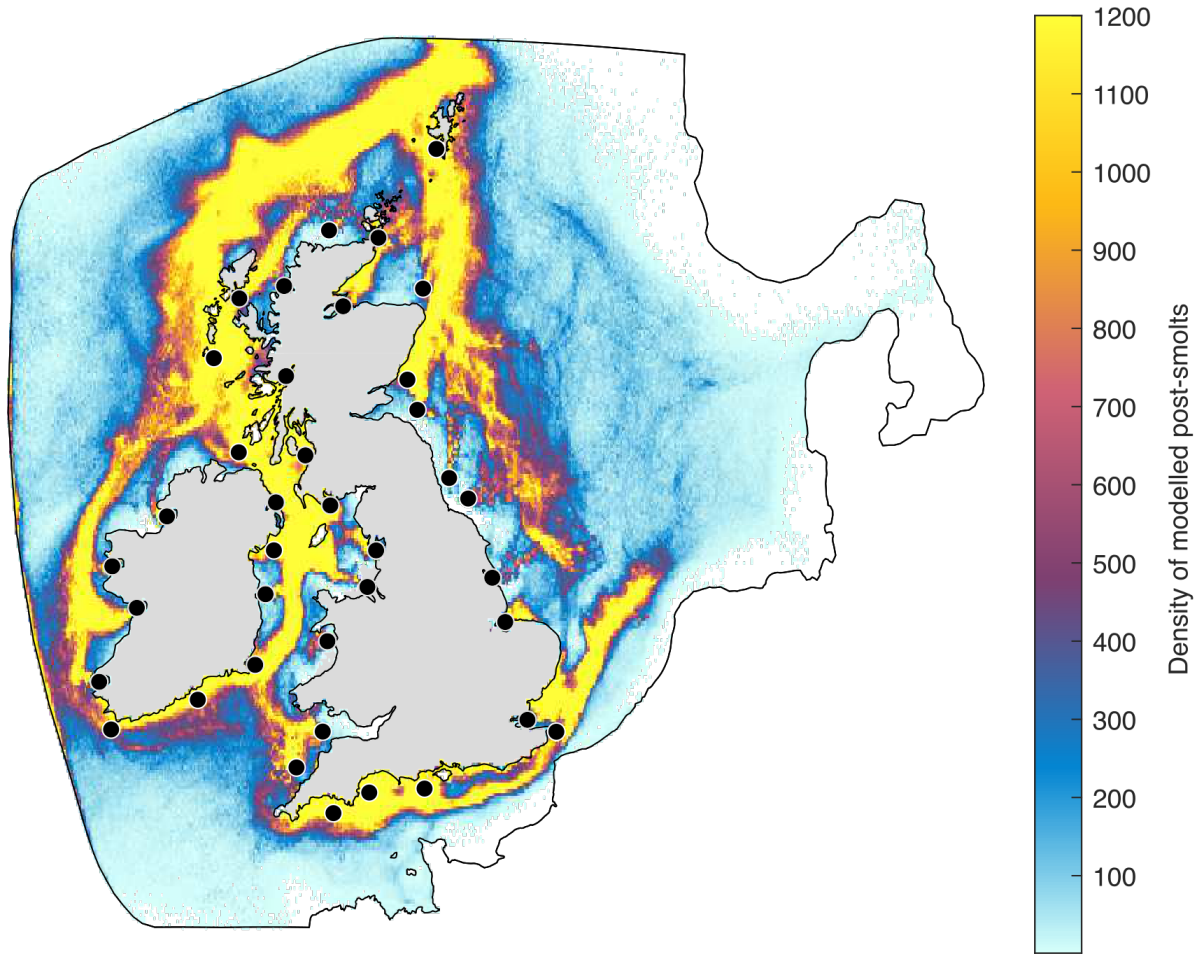


Figure 3.2: Density of modelled Atlantic salmon post-smolts (total number of occurrences per 20 km² bin) from all rivers, 1993-2019. Modelled migrations were weighted so that each river had the equivalent number of particles as the river with the largest portfolio size. Black dots denote river mouth start points.

the Irish Sea).

Monthly concentrations of modelled post-smolts showed good spatial and temporal agreement with telemetry data around Ireland and the west coast of Scotland (April to June, Figure 3.3 a-c). Both the model and the telemetry detections found post-smolts to be mainly constrained to the coastline (or perhaps further south than the telemetry receivers) in April. In May, both modelled and observed post-smolts were found at receivers in transitional and coastal waters, while in June, there were few modelled or observed post-smolts.

However, in the Moray Firth (northeast Scotland) in May (Figure 3.3 b), the modelled post-smolts took a direct, northward route, while the observed post-smolts from the telemetry and trawl studies more commonly took an eastward route (Adams *et al.*, 2025; Newton *et al.*, 2026). Similarly, the model suggested a fairly direct northward migration path in the North Sea east of Scotland in May, whereas the nonzero epipelagic trawls were distributed over a slightly wider area (Figure 3.3 d).

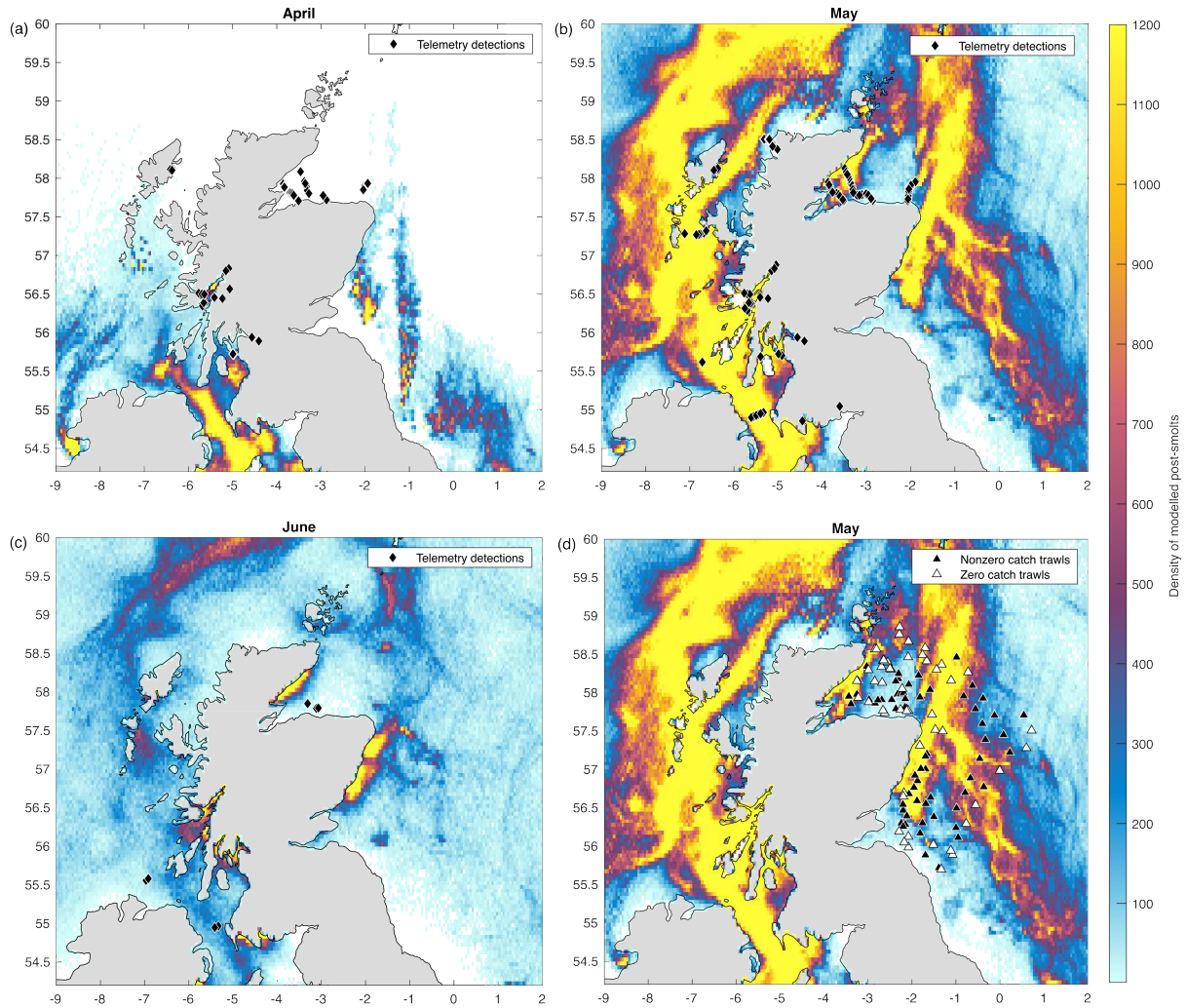


Figure 3.3: Monthly densities of modelled Atlantic salmon post-smolts, compared with: (a)-(c) telemetry detections between April and June (Rodger *et al.*, 2025; Adams *et al.*, 2025); and (d) epipelagic trawl data in May (Newton *et al.*, 2026).

3.3.2 Optimal portfolios of swimming behaviours

The ranges of the weights w_c, w_s, w_d and the swim speed s selected in the optimal portfolios were large for many rivers (Figure 3.4). In Figure 3.5, rivers were grouped according to their locations in a ternary plot of w_c^2, w_s^2 , and w_d^2 . Rivers with parameter sets lying solely in one third of the ternary plot were categorised, and hence a regional summary of behaviours is displayed, though it is still apparent that the majority of river models included a wide range of parameter sets. Only models for rivers 14 and 15 in the English Channel selected currents as the main navigation cue, and there were rivers throughout the domain for which salinity was selected as the primary navigation behaviour (Figure 3.5 a-b). Only more northern rivers (in the Scottish Outer Hebrides, the east coast of Scotland, and the northeast coast of England) mainly used directional cues, and many rivers throughout the domain selected a wide range of navigational cues (Figure 3.5 c-d).

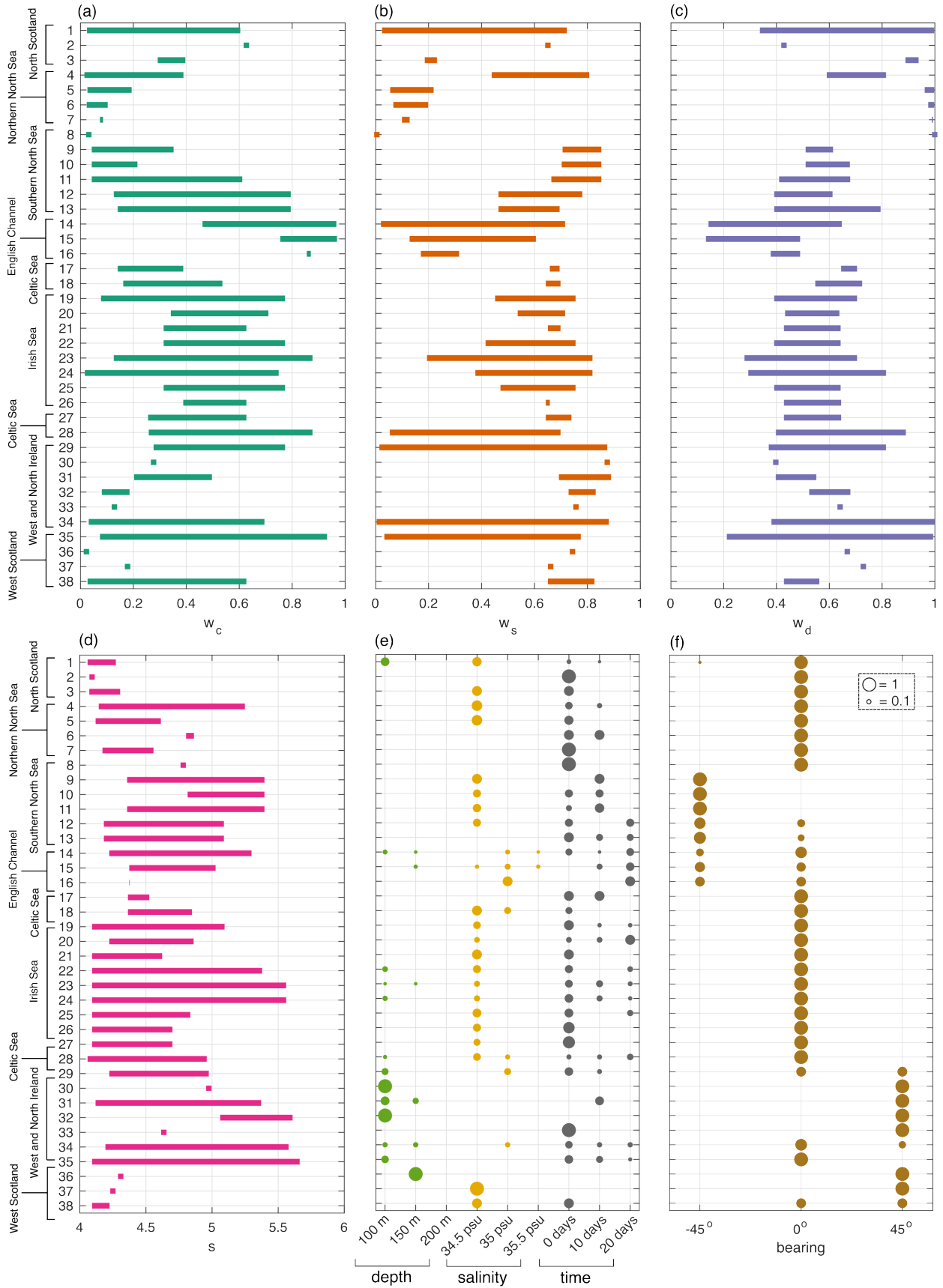


Figure 3.4: Intervals of the parameters in the selected optimal portfolio of each river. Intervals are displayed for the continuous parameters: (a) w_c ; (b) w_s ; (c) w_d ; and (d) s . Probabilities are displayed for the discrete parameters: (e) the threshold for $R=1$; and (f) θ_{bias} . Probabilities are indicated by circle size, with a probability of 1 corresponding to all solutions within the optimal portfolio taking the same value.

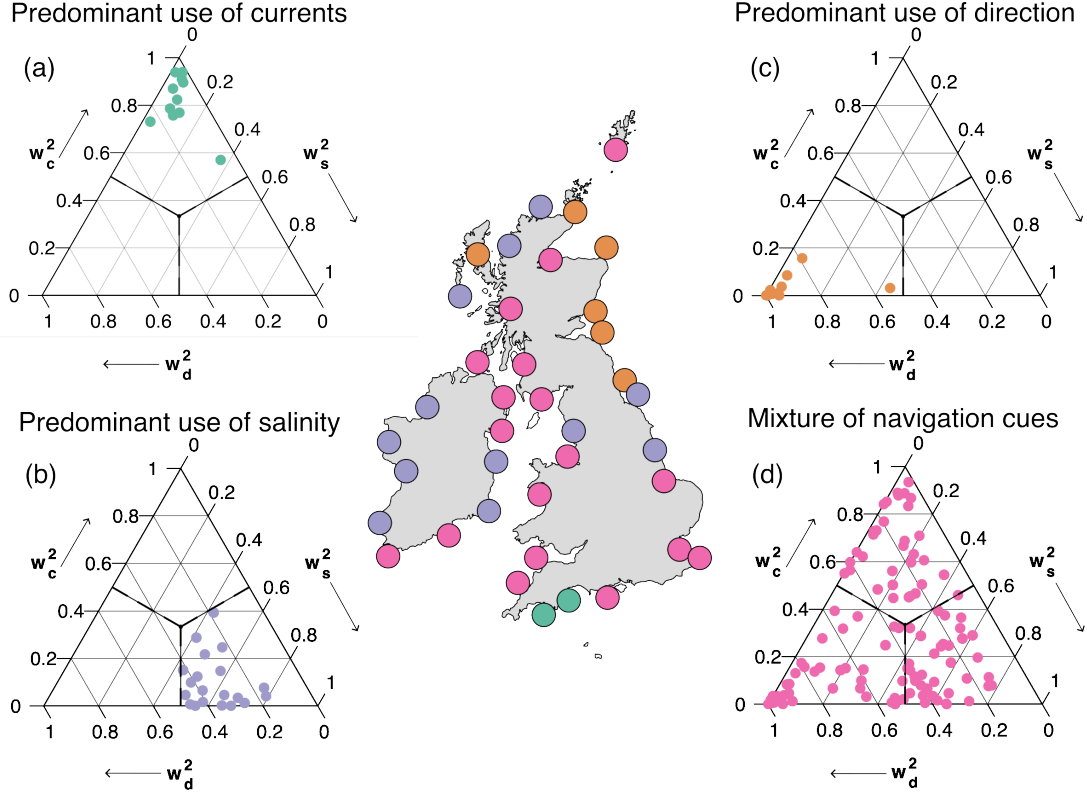


Figure 3.5: Rivers grouped according to the relative weights of the three navigation cues w_c^2 , w_s^2 , and w_d^2 : (a) rivers with parameter sets solely in the upper third of the ternary plot (i.e. predominant use of currents to navigate); (b) those only in the lower right third (i.e. predominant use of salinity); (c) those only in the lower left third (i.e. predominant use of direction); and (d) those spanning wide ranges of navigational cues.

The various thresholds (bathymetry, salinity, and time) tested for the inclusion of the directional component ($R = 1$) each appeared in the optimal parameter set for at least some rivers (Figure 3.4). The depth thresholds were the least common of the three types, and the 200 m threshold never appeared in the optimal parameters. Of the salinity thresholds, the lowest value of 34.5 psu was the most common, while the highest threshold of 35.5 psu was only selected for two rivers (14 and 15 in the English Channel). The time thresholds were generally the most applicable across all rivers, with the earlier thresholds (0 and 10 days) being more commonly selected than the later option. The selected bearings are clearly defined geographically, summarised in Figure 3.6.

The optimal portfolio size varied between rivers, with some rivers attaining the best performance with a single behaviour and others with up to 24 behaviours (Figure 3.7). For some rivers (e.g. river 21 in the Irish Sea), the Sharpe ratio was similar for a wide range of portfolio sizes (Appendix B, Figure B.1), suggesting that combinations of migratory behaviours were feasible. For others, there was a clear winning portfolio (e.g. rivers 36-38). The size of the optimal portfolio was strongly driven by the standard deviation term σ_n . The top 25 mean exit rate runs had already been selected, so the mean return μ_n declined monotonically, with a shallow

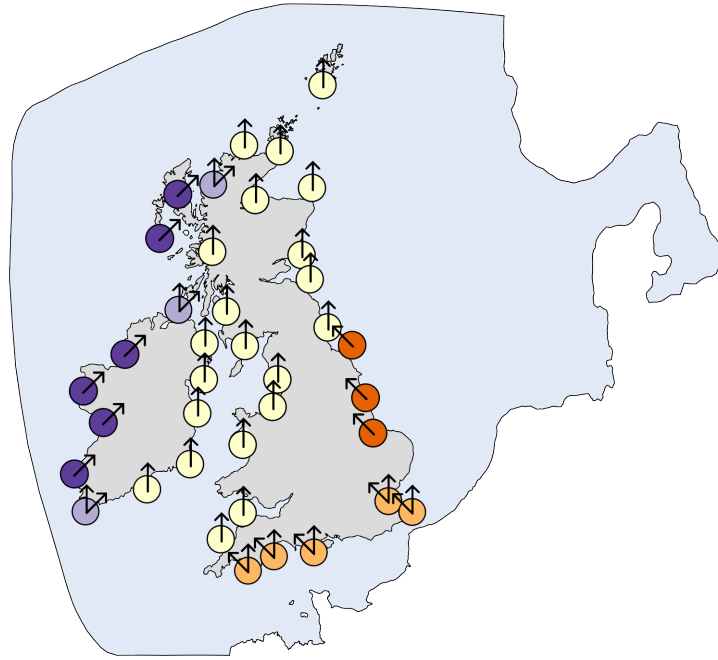


Figure 3.6: The selected bearings within the optimal portfolio for each river (-45° , 0° , 45° , or a combination; shown by colour and arrow direction).

gradient, as portfolio size n increased. Contrastingly, σ_n showed different patterns (increases and decreases) for different rivers. The Sharpe ratio was maximised at large portfolio sizes for rivers where σ_n decreased with portfolio size, driven by low covariance between exit rate time series. An example is provided in Appendix B (Figure B.2), for a river with a lower optimal number of strategies (river 27, $n = 4$) and one with a higher optimal number of strategies (river 28, $n = 23$). These results are reflected in the domain exit rates of portfolios of differing sizes for these rivers (Appendix B, Figure B.3), where it is clear that a large portfolio size ($n = 23$) increases interannual variability of the portfolio exit rate for river 27, and decreases variability for river 28.

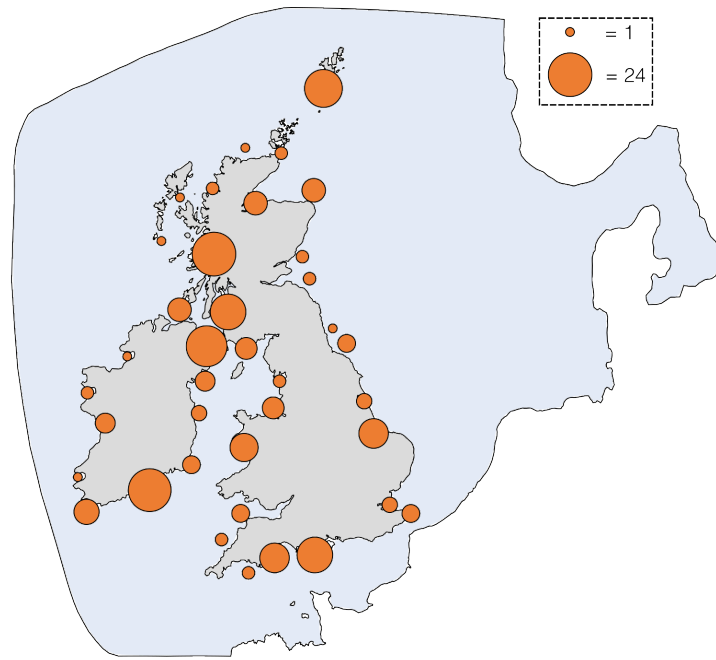


Figure 3.7: The optimal number of swimming behaviours (i.e. parameter sets) for each river, determined by the maximum Sharpe ratio.

3.3.3 Portfolio effects in migration metrics

Interannual patterns in domain exit rates varied between rivers (Figure 3.8). Particularly low exit rates were seen for rivers 12-16 (southern North Sea and English Channel).

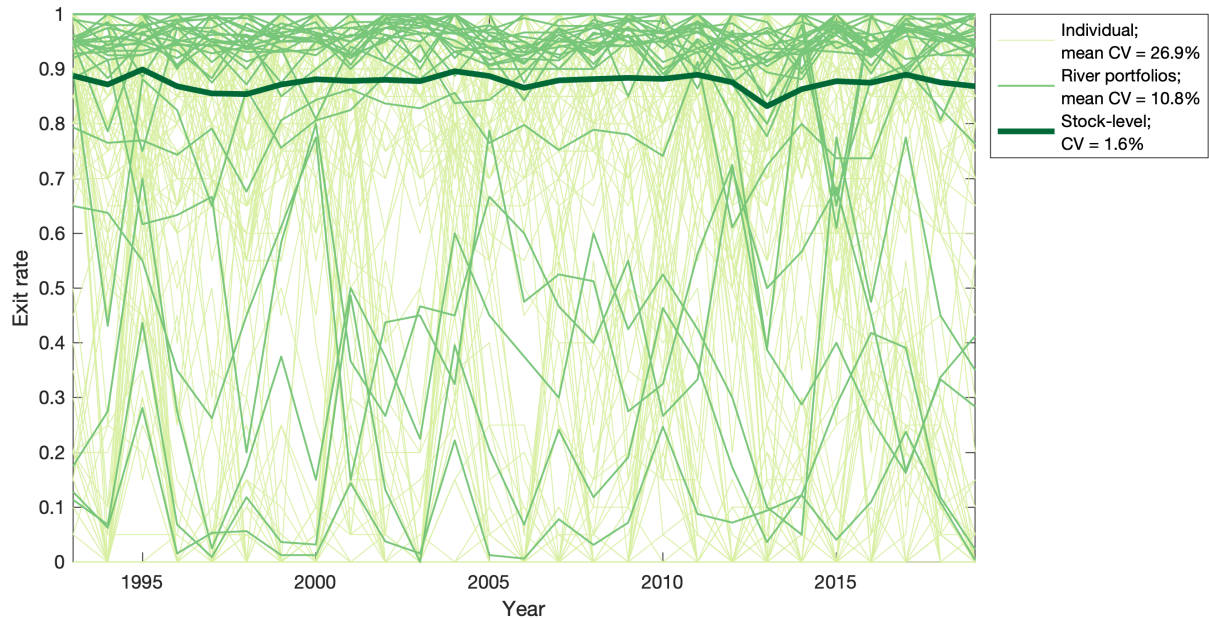


Figure 3.8: Domain exit rate time series for: individual parameter sets (only those selected in the optimal portfolios); aggregated river portfolios; aggregated for all rivers (stock-level). Coefficients of variation (CV) are displayed for each level.

The coefficient of variation (CV) in exit rates decreased with increasing scales of observation, from individual behaviour level, to river-level, to stock-level (Figure 3.9). This was true when the optimal portfolio of swimming behaviour models was selected per river, but also when a single behaviour was selected $n = 1$, or the entire set of behaviours was selected $n = 25$. However, the optimal portfolio scenario, as was used to select the models presented in this study, produced the lowest stock-level CV, in addition to the lowest river-level CV.

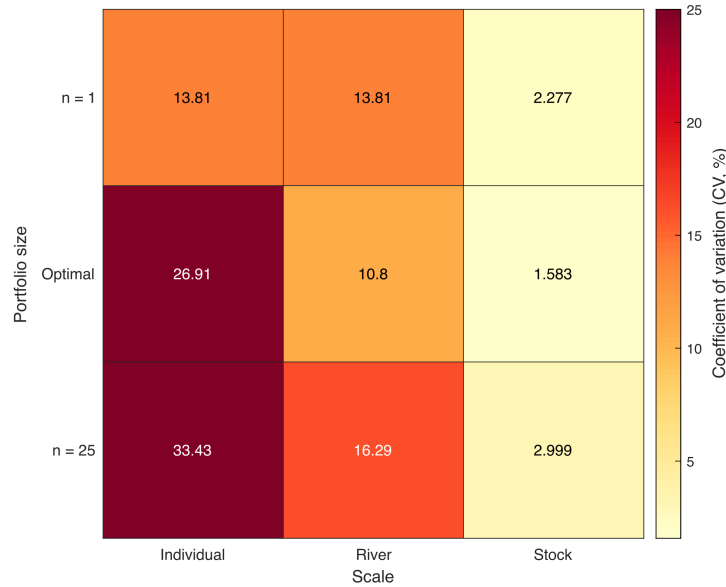


Figure 3.9: The coefficient of variation (CV) on individual-, river- and stock-levels for: $n = 1$, i.e. the single best swimming behaviour per river; the selected optimal portfolio per river; and $n = 25$, i.e. the set of all modelled swimming behaviours per river.

3.4 Discussion

3.4.1 The post-smolt migration model

A model was developed to simulate post-smolt migrations over the first 1-3 months at sea from 38 rivers around the British Isles. Portfolios of modelled swimming behaviours were selected by maximising mean domain exit rates and minimising interannual variance. Simulated post-smolts from rivers on the west side of the British Isles mainly followed the continental shelf-edge (Figure 3.2), in line with previous empirical and modelling studies (Shelton *et al.*, 1997; Holm *et al.*, 2000; Mork *et al.*, 2012; Gilbey *et al.*, 2021; Borland *et al.*, 2025). Near the coastline, modelled post-smolt densities were compared with telemetric detections and post-smolt epipelagic trawls (Rodger *et al.*, 2025; Adams *et al.*, 2025; Newton *et al.*, 2026). At acoustic telemetric receivers around the west coast of Scotland and the Irish Sea, high densities of modelled post-smolts coincided with detections of tagged post-smolts. This suggests that the model developed here accurately depicted the broad spatial and temporal patterns in migration from Scottish, Irish, Northern Irish, and northwest English rivers described by Rodger *et al.* (2025).

In the Moray Firth, modelled post-smolts did not coincide with a relatively small number of

telemetric detections in April, as the modelled migrations began at the start of May for these rivers. However, the majority of post-smolts in the Moray Firth were first detected in May (Adams *et al.*, 2025), when the highest densities of modelled post-smolts were observed in this region, suggesting there was a reasonable temporal coincidence of the model and this data. The highest densities of modelled post-smolts were found along the northern edge of the Moray Firth, whereas Adams *et al.* (2025) and Newton *et al.* (2026) found higher densities of post-smolts along the southern edge. However, there was some variation between individuals in the telemetric data, and Adams *et al.* (2025) found that later-migrating post-smolts took a more northward route in the Moray Firth, more similar to the modelled spatial densities of post-smolts.

In the North Sea east of Scotland, high modelled densities of post-smolts co-occurred with both nonzero and zero catch trawls from Newton *et al.* (2026). This presents a challenge of working with this data: the zero and nonzero trawls are geographically very close, and there are no clearly defined regions where smolts were found or not found. It is also noted that the sampling of Newton *et al.* (2026) was undertaken over four years, but different areas were sampled between years, meaning that interannual variation in migration paths could have influenced the results. Additionally, all sampling by Newton *et al.* (2026) was undertaken in early May, so it could not be confirmed if post-smolts still inhabited the region in later months (simulated post-smolts remained in the North Sea in June, but at lower densities, Figure 3.3 c). Nevertheless, the most eastern nonzero trawls in May had relatively high catch per unit effort values (Newton *et al.*, 2026), whereas the model predicted the highest densities of modelled post-smolts closer to the coastline. This suggests that post-smolts are more widely distributed in the North Sea than our model suggests.

Based on the comparisons with the available empirical data, it appears that this method of selecting model parameterisations (i.e. swimming behaviours) of post-smolts based on optimising the domain exit rates and minimising the interannual variance is effective for rivers around the west coast of Scotland and the Irish Sea. This may be because post-smolts from these rivers do indeed select an ‘optimised’ migration route towards the Norwegian Sea. Contrastingly, the empirical data in the North Sea and the Moray Firth suggest that post-smolts do not take an optimised, short migration route in this region (the same result was found in the inner Moray Firth by Newton *et al.* (2021); similarly Main (2021) found that post-smolts migrating from the River Dee in Aberdeen took a southeast migration path initially after entering the sea). Therefore, our method of maximising domain exit rates is less effective for rivers in eastern Scotland, where post-smolts do not take direct migration paths. We therefore consider the resulting simulated migrations from rivers 4-7 (which lie within the area covered by the studies of Adams *et al.* (2025) and Newton *et al.* (2026)) to have greater uncertainty, compared to the other rivers. However, we note that omitting these rivers does not significantly alter the remainder of the results presented here: in Figures 3.8 and 3.9, the coefficients of variation remained very similar when omitting rivers 4-7 (Appendix B, Figure B.4).

In this model, simulated post-smolts navigated using only physical water properties (currents, salinity) and directional cues. Prey availability was not included as a driver of movement because

data on the distribution and abundance of prey items for post-smolts is lacking in this region (Tyldesley *et al.*, 2024). Similarly, predator encounters were not included due to a lack of data. We suggest that prey availability or predator encounters may be the drivers behind the ‘suboptimal’ migration paths from Scottish east coast rivers. This hypothesis could be tested in the future if sufficiently fine-scale data on prey availability for post-smolts were available. The model could be adapted to include an element of movement dedicated to foraging (e.g. Utne & Mousing, 2025; Daniels *et al.*, 2026); if it were then able to reproduce the observed distributions of post-smolts better, it could be concluded that prey availability has a significant impact on the choice of migration paths by post-smolts. Based on this hypothesis, Chapter 5 considers marine prey energy availability along modelled migration paths.

3.4.2 The portfolio effect: modelled swimming behaviours and resulting domain exit rates

Portfolios containing multiple swimming behaviours were found to be optimal for 32 of the 38 rivers, with the largest portfolio consisting of 24 behaviours (for river 35 in west Scotland). This suggests that the existence of a range of swimming behaviours helps to dampen interannual variation in domain exit rates, which is likely to be driven by changes in local currents and salinity (Chapter 2). Only rivers 2, 8, 30, 33, 36 and 37 (located in north Scotland, northeast England, southwest Ireland, and northwest Scotland) obtained a maximum Sharpe ratio for a single migration behaviour. This is because the top-performing behaviour for these rivers had zero, or very low, standard deviation. However, a moderately high (>9) Sharpe index was still obtained for these rivers when a larger number of strategies ($n = 25$) were considered. Therefore, a portfolio of behaviours is either optimal or well-performing for all rivers considered here. The selected portfolio sizes were dependent on the interannual covariance between the domain exit rates within each portfolio. Where there was low covariance between portfolio components, the standard deviation of the portfolio was minimised with a large portfolio size. Under the assumption that Sharpe scores reflect ecologically optimised systems that balance return and risk, these results suggest that the existence of behaviours that cause different interannual fluctuations in migration outcomes within a population is beneficial.

The assumption that salmon populations have evolved to have a range of migratory behaviours that balance mean and variance in migratory success (i.e. they can be represented by maximum Sharpe scores) is comparable to the concept of ‘bet-hedging’ in ecology. The fitness of a population over generations is a multiplicative function of reproductive success, so the bet-hedging theory suggests that the geometric mean of between-generation fitness should be maximised (Simons, 2011; Yasui, 2022). The geometric mean declines as variance increases, hence the optimal bet-hedging strategy might compromise on the arithmetic mean fitness of individual generations to maximise the geometric mean fitness (Starrfelt & Kokko, 2012). This is parallel to the assumption in this study that an increased portfolio size (i.e. wider range of migration behaviours) with slightly lower mean domain exit rates is beneficial if it decreases variance (i.e. maximises the Sharpe score).

Bet-hedging is expected to have evolved in populations experiencing variable and unpredictable environmental conditions (Nevoux *et al.*, 2010). Empirical evidence of this phenomenon is challenging to obtain, particularly because the benefit may only be apparent over long timescales (Simons, 2011), but studies suggest the existence of bet-hedging in life-history traits and behaviours of birds, fish and amphibians (Nevoux *et al.*, 2010; Morrongiello *et al.*, 2012; Erich *et al.*, 2015). Notably, Reilly & Reilly (2009) developed a migration model for juvenile passerines under interannually varying wind conditions, finding that a bet-hedging strategy combining multiple flying directions for each cohort could enhance geometric-mean fitness. With variable oceanographic conditions driving interannual variability in modelled migration success of salmon (Chapter 2), it is plausible that salmon might have evolved a bet-hedging strategy in migration behaviours to increase population-level fitness over generations, as represented by our method using Sharpe scores (i.e. balancing mean and variance in domain exit rates).

The parameter sets within the optimal portfolios often represented wide ranges of different swimming behaviours. For example, the portfolio for river 29 (at the southwest tip of Ireland) had values of w_s ranging between $[0.01, 0.87]$. The lower end of this range represents practically no use of salinity as a navigational cue, while the upper end represents an almost exclusive use of salinity. Other rivers had similarly large ranges of w_c , w_s and w_d , as well as the swim speed s . Many rivers also had multiple thresholds (for the switch in swimming behaviour) included in the optimal portfolio. Overall, a very wide range of behaviours were used successfully. For most rivers, choosing a single one of these behaviours reduced the portfolio performance, even though $n = 1$ represented the highest domain exit rate behaviour, emphasising the importance of diversity in migration.

The wide range of modelled swimming behaviours within rivers also meant that many rivers displayed similarities in the selected parameter sets. There were overlapping ranges of the weights w_c , w_s and w_d and the swim speed s for most of the rivers, suggesting that these behaviours might not be river-specific. This result is perhaps comparable with the finding of Cauwelier *et al.* (2018), where greater genetic similarity was found between salmon populations in neighbouring rivers in northeast Scotland than between populations within upper and lower reaches of the same rivers. The parameter that diverged from this observation was θ_{bias} , the bearing of directional movement, for which there were clear geographic patterns (Figure 3.6). This is in line with the results of Ounsley *et al.* (2020), who simulated post-smolt migrations from Scottish rivers and found that different bearings (northwest, north, or northeast) were required for different rivers. Together, these results suggest that the innate compass following ability of salmon (e.g. Moore *et al.*, 1990; Minkoff *et al.*, 2020) might require local adaptation. Additionally, we found that the directional swimming component was nonzero in every river’s optimal portfolio, emphasising the importance of this behaviour.

Interannual fluctuations in domain exit rates differed between rivers, which may be because different environmental conditions influence rivers around this region, or because they respond differently to similar fluctuations. Due to this, aggregating the exit rates on larger scales reduced variance (as is always the case where temporal trends in assets are not all positively correlated,

Doak *et al.*, 1998). We found the coefficient of variation (CV) of stock-wide aggregated exit rates to be an order of magnitude smaller than the mean CV of individual parameter runs. This was true when the optimal portfolio was selected for each river, but also when the single best strategy was selected per river ($n = 1$), or when all strategies were selected for all rivers ($n = 25$). However, we found that the stock-level CV was lowest (1.58%) when the optimal portfolios were selected for each river. Note that this result held when rivers 4-7 were removed due to the lower confidence in their results (Appendix B, Figure B.4).

These results encourage conservation action aimed at minimising larger-scale variance. Our results suggest that stock-wide fluctuations in the migration success of post-smolts could be minimised by promoting naturally optimised behavioural diversity within rivers (i.e. the optimal portfolios, rather than $n = 1$ or $n = 25$). Furthermore, promoting populations which have low covariance with others can boost the portfolio effect, and hence salmon resilience (Carlson & Satterthwaite, 2011; Satterthwaite & Carlson, 2015). Unfortunately, no portfolio can negate "systematic" risk where all assets are influenced equally (Sharpe, 1964), as might be caused, for example, by a large-scale ocean-climate shift (Griffiths *et al.*, 2014). However, even small differences in the strength of the response of populations to changes could buffer the larger-scale response.

Several factors were not modelled in this study, including mortality (due to predation or other factors) or variability in feeding. Prey availability and predator encounters are expected to differ with variability in migration paths driven by variation between migration behaviours (Humston *et al.*, 2004; Furey *et al.*, 2015) and between years (Friedland *et al.*, 2012). A metric of migratory success in which domain exit rates were also influenced by mortality and feeding would therefore be expected to be more variable than domain exit rates alone, which represent an upper bound on the total migration success rate. Additionally, migrations in this study were only simulated over the first section of the marine migration: at least 1300 km of travel may remain, assuming that the initial post-smolt migration extends to 70° (e.g. Gilbey *et al.*, 2021). As such, the modelled migrations here represent $< 50\%$ of the total outward migration distance. Across the region considered here, an increased migration distance resulted in an increased standard deviation σ_n (Appendix B, Figure B.5). If this relationship held across the remainder of the post-smolt marine migration, then interannual variability in migration metrics would be increased for all rivers. Therefore, if additional factors were included in the model (feeding, predation, additional distance), the selection of optimal portfolios may have been altered: it is plausible that additional migration behaviours might have been selected to add additional resilience (provided combinations of behaviours with low covariance in domain exit rates existed).

The results of this study point towards the importance of conserving genetic and phenotypic diversity within and between populations. Unfortunately, many anthropogenic factors can threaten population diversity. While hatchery stocking can help restore or maintain populations (Lennox *et al.*, 2021), it can also reduce fitness and population diversity (Ryman & Laikre, 1991; Youngson & Verspoor, 1998; May *et al.*, 2024). Similarly, genetic introgression of escaped farmed salmon can compromise local adaptation and reduce population fitness (McGinnity *et al.*, 1997; Glover

et al., 2017; Lennox *et al.*, 2021). Farmed salmon display different behaviours than wild fish (Jonsson, 1997; Islam *et al.*, 2020; Nilsen *et al.*, 2022b), suggesting that interbreeding could have direct consequences on the behavioural diversity that was shown to be important in this study. Any other factors which constrain the natural behavioural and life-history choices of salmon may lead to a narrow range of migratory traits being selected, and hence a further loss of diversity (e.g. Sturrock *et al.*, 2020).

3.5 Conclusion

In this study, a set of models simulating the marine migrations of Atlantic salmon post-smolts over the first 1-3 months at sea was successfully developed for 38 rivers in the British Isles. Multiple swimming behaviours were selected within each population, and swimming behaviours varied between river populations, though there were overlapping ranges in some of the parameters between rivers, providing evidence to support **H2**. The existence of portfolios of swimming behaviours was found to be beneficial in dampening year-to-year variance in modelled migratory "success" of post-smolts. This was true when variance was considered for individual rivers and for all rivers combined (stock-wide variance). Our results suggest that promoting diverse salmon populations will boost the resilience of the species as a whole. With extreme environmental fluctuations projected to increase in frequency with climate change (IPCC, 2021), a strong portfolio effect across Atlantic salmon populations is also likely to reduce vulnerability to sudden changes.

Chapter 4

Quantifying the exposure of migrating Atlantic salmon to pelagic fisheries in the northeast Atlantic to reveal potential bycatch hotspots

4.1 Introduction

Declines in Atlantic salmon *Salmo salar* (hereafter salmon) populations have been observed in many areas across the North Atlantic over the last fifty years (Parrish *et al.*, 1998; Limburg & Waldman, 2009; Lehnert *et al.*, 2019; Olmos *et al.*, 2019). Reduced marine survival is thought to be a major contributory factor to the observed population declines in recent decades (Chaput, 2012; Thorstad *et al.*, 2012; Pardo *et al.*, 2021), even while increased controls on salmon fisheries exploitation have substantially reduced fishing pressure (Jacobsen, 2012; ICES, 2024a). As such, a better understanding of the drivers underlying the observed changes in marine survival is vital to inform management strategies to protect salmon populations (Bull *et al.*, 2022). This study focuses on the exposure of migrating juvenile salmon to pelagic fisheries during their first few months at sea to consider the space-time domains where they may be at risk of bycatch.

Salmon is an anadromous fish species that begins its life cycle in rivers, hatching from eggs in spring and then remaining in freshwater for 1-8 years, before migrating towards the sea in spring or early summer (Hansen & Quinn, 1998; Klemetsen *et al.*, 2003). They then spend 1-4 years at sea before returning as adults to reproduce in rivers (Aas *et al.*, 2010). After first entering the sea as juveniles, and until the end of the first winter at sea, salmon are known as ‘post-smolts’ (Allan & Ritter, 1977), and variable mortality rates of this life-stage are believed to drive overall trends in the species’ marine survival (Thorstad *et al.*, 2012). The migration paths of post-smolts during their first months at sea are not yet fully known, but post-smolts from southern European rivers enter the sea from April to June and migrate towards the Norwegian Sea (Otero *et al.*,

2014; Gilbey *et al.*, 2021). Scientific surface trawling has identified relatively high numbers of post-smolts at the continental shelf-edge west of the British Isles (Holm *et al.*, 2000; Gilbey *et al.*, 2021). Contrastingly, there is very little data on the migration routes of post-smolts in the North Sea (ICES, 2023e). Along their marine migration, post-smolts generally remain within the top five metres of the water column, with occasional deeper dives recorded down to a depth of 37 metres (Davidsen, 2008; Plantalech Manel-La, 2009; Renkawitz *et al.*, 2012; Guðjónsson *et al.*, 2015). Post-smolts occupy the same environments as many commercially important pelagic finfish species, such as herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and sardine (*Sardina pilchardus*) (ICES, 2023g, 2024b).

Concern has been expressed about the potential bycatch of salmon in pelagic fisheries that target finfish in the northeast Atlantic (Gillson *et al.*, 2022; ICES, 2023e,c; Elliott, 2023; ICES, 2023a). Several million tonnes of pelagic fish are landed annually in this region (ICES, 2024c), often in areas and periods with a potential risk of bycatch of salmon. Salmon are classified as ‘near threatened’ globally, and ‘vulnerable’ in Europe, by the International Union for the Conservation of Nature (IUCN) Red List Assessment (Darwall, 2023; Sayer, 2024) and are listed as an Endangered, Threatened, and Protected (ETP) species under national and international legislation (OSPAR, 2008; Nieto, 2015; Elliott, 2023). Despite their ETP status, salmon were only included on the list of species considered by the International Council for the Exploration of the Sea (ICES) Working Group on Bycatch of Protected Species (WGBYC) for the first time in 2025 (ICES, 2025a). This means that the mobilisation of data on salmon bycatch is in its infancy, and more research is required to better understand the bycatch risks of pelagic fisheries on this ETP species.

Insufficient monitoring has limited the availability of salmon bycatch data, with the majority of bycatch observer effort allocated to demersal fisheries (ICES, 2023e). When monitoring is undertaken, logistical challenges may arise due to the difficulty of detecting small post-smolts in large trawl and purse seine catches (ICES, 2004). However, despite these difficulties, there have been numerous records of salmon bycatch in pelagic fisheries (ICES, 2004, 2013a; Olafsson, 2016; ICES, 2021c; Elliott, 2023). Several gear types are liable to salmon bycatch, for example the Netherlands Institute for Fisheries Research (RIVO) reported bycatch of salmon in gillnets, trammel nets, otter trawls, and pelagic trawls between 2000 and 2003 (ICES, 2004). The likelihood of salmon bycatch with different gear types is not currently known, nor is it clear if there are interactions between gear selectivity and increasing post-smolt body size along migration corridors. Monitoring of mackerel and herring landings in the Icelandic pelagic trawl fisheries between 2010-2013 found 0.0055 salmon to be bycaught per tonne of mackerel and herring, with approximately 13% of these being post-smolts (i.e. 0.00075 post-smolts per tonne; Gudbergsson *et al.*, 2014). This value will be dependent on the spatial-temporal distribution of salmon as well as the fishing effort and gear type. ICES (2004) reported a much higher value of 57 post-smolts per tonne of mackerel in the Norwegian Sea, though there were differences in the gear type and operating depth of that study in comparison with the commercial fishery.

Bycatch of Chinook salmon (*Oncorhynchus tshawytscha*) and Chum salmon (*O. keta*) in north

Pacific trawl fisheries is well documented and sampled using at-sea observers, cameras and electronic monitoring, allowing for estimation of the impacts of bycatch on populations (Witherell *et al.*, 2002; Ianelli & Stram, 2015; Sabal, 2023). For other fishes, marine mammals, and seabirds, detailed information on fishery bycatch is not always available, in which case analysis of bycatch risk might be undertaken by comparing satellite-tracked movements with fishing effort from expected at-risk fisheries (Queiroz, 2019; Clay, 2019), or by developing species distribution models and comparing these with fishing activity (Stock, 2019; Hines, 2020; Hatch, 2023; Frantz, 2024). For salmon, this process is further complicated by our present incomplete knowledge of post-smolt migration paths (Gilbey *et al.*, 2021). Acoustic telemetry studies (e.g. Lilly *et al.*, 2023; Artero, 2023) are unable to reveal the full migration paths of post-smolts due to limitations on the placements of acoustic receivers, while modelling studies (e.g. Mork *et al.*, 2012; Borland *et al.*, 2025) have not been undertaken for all post-smolt migration regions (ICES, 2023e). Stable isotope analysis can also provide larger-scale insight into migration pathways, but the coarser resolution of this approach means it has not yet inferred the precise paths of migrating post-smolts (Hanson *et al.*, 2022). Environmental DNA (eDNA) analysis is increasingly being used to analyse bycatch risk (Albonetti, 2023; Maiello, 2024; Urban, 2024), and recent technological advances in eDNA analysis have allowed estimates of species abundance, as well as composition, to be made (Guri, 2024). However, this approach has not yet been implemented for salmon bycatch, and access to eDNA data requires a legislative shift to enable such data to be collected onboard fishing vessels.

Risk, applicable but not exclusive to bycatch, can be modelled as a function of exposure and sensitivity to pressures (Samhuri & Levin, 2012). Exposure to pelagic fisheries is defined by the spatial and temporal extent and intensity of pelagic fishing occurring within salmon migration corridors (ICES, 2023e), where a higher intensity of fishing infers a higher exposure. Sensitivity would then be defined by the mortality (i.e. bycatch) rates of salmon per unit of fishing, but this information is not currently known. It is not therefore possible to determine what quantity of landings represents a significant bycatch risk to post-smolts, but it is assumed that a higher exposure to pelagic fisheries causes a greater probability of bycatch risk.

This study aimed to narrow down the space-time domains in the northeast Atlantic in which bycatch of salmon post-smolts is most likely to occur. To address our hypothesis that Atlantic salmon post-smolts are at risk of bycatch in pelagic finfish fisheries (**H4**), the first objective of this study was to quantify exposure to pelagic fisheries through a newly mobilised high-resolution dataset on pelagic landings of six commercially important finfish species identified by ICES as potentially problematic in terms of salmon bycatch risk (mackerel *Scomber scombrus*, herring *Clupea harengus*, horse mackerel *Trachurus trachurus*, sardine *Sardina pilchardus*, capelin *Mallotus villosus*, and chub mackerel *Scomber colias*) within post-smolt migration regions. The locations and time periods of higher exposure represent regions where salmon may be at risk of bycatch, providing specific focus for future studies which can expand this analysis. Although fishing effort data (e.g., hours fished) would provide a better measure of exposure to pelagic fisheries than landings, these data are hard to obtain (Greenstreet *et al.*, 2009) and were not

available at the high spatial and temporal resolution required for analysis in this study. In the absence of effort data, landings can be used as a proxy of fishing intensity (Greenstreet *et al.*, 2009; Batista, 2015; Fisheries & Authority, 2018). Landings and effort are not equivalent but they may be positively correlated (Greenstreet, 2007), with the exact relationship between them varying among fish species and biomass, spatial regions, vessels, gear types, and time of year (Arnason, 1996; Batista, 2015; ICES, 2024c). For this study, the newly mobilised, high-resolution data on pelagic landings in the northeast Atlantic represented the best available measure of fishing intensity that could be used to quantify exposure to pelagic fisheries. Given the potential threat of bycatch to vulnerable salmon populations (ICES, 2023e,c,a) and the limited previous analyses of salmon bycatch likelihood due to scant data (ICES, 2004, 2005), undertaking such an analysis using landings data represents a practical step forward in the challenge of understanding the factors affecting salmon survival at sea.

The second objective of this study was to evaluate correlations between the marine return rates of salmon and pelagic landings along migration pathways. These correlations were evaluated to indicate potential population-level effects, or synchronous fluctuations, with pelagic fisheries, though they must be interpreted carefully as they do not necessarily represent causative relationships. Positive correlations between salmon return rates and pelagic landings could be indicative of synchronous population responses to changes in marine environmental conditions. In contrast, negative correlations between salmon return rates and pelagic landings might arise from bycatch-induced mortality.

4.2 Methods

4.2.1 Study area and post-smolt migration regions

For post-smolts originating from European rivers (Figure 4.1), monthly regions of occupation were defined. Spatial aggregation of migration routes was necessary as the precise migration paths of post-smolts are not known. Survey data on the capture of post-smolts at sea between April and August from 1995-2012 (Gilbey *et al.*, 2021) were binned into ICES statistical rectangles (0.5° latitude by 1° longitude resolution) and used to define general regions covering the likely post-smolt migration corridor. The whole migration corridor was divided into regions relevant to salmon populations entering the sea in the southwest, west, and east regions of the model domain, as well as a ‘common’ region where all populations aggregate (Figure 4.2), with the divisions between these informed by the genetic assignment of trawled post-smolts at sea to regions/countries of Gilbey *et al.* (2021). The latitudes of post-smolts observed in the surveys ranged from 52.2° to 76.3°. However, given that salmon rivers further south than this observed capture latitude also migrate through the study domain (Gilbey *et al.*, 2021), the regions were extended south to 41° latitude, the location of the river Ulla in Spain (the southernmost known river where smolt emigration timing data was available, Otero *et al.*, 2014). The continental shelf-edge was used as the western boundary where there were limited post-smolt observations available. This boundary surrounds the main areas of high occupancy of simulated smolts by

Mork *et al.* (2012). The North Sea was included (east region) despite there being only one surveyed post-smolt location there, as there are several salmon rivers in this region, and other studies document the migration of post-smolts within the North Sea (Turrell, 1997; Main, 2021).

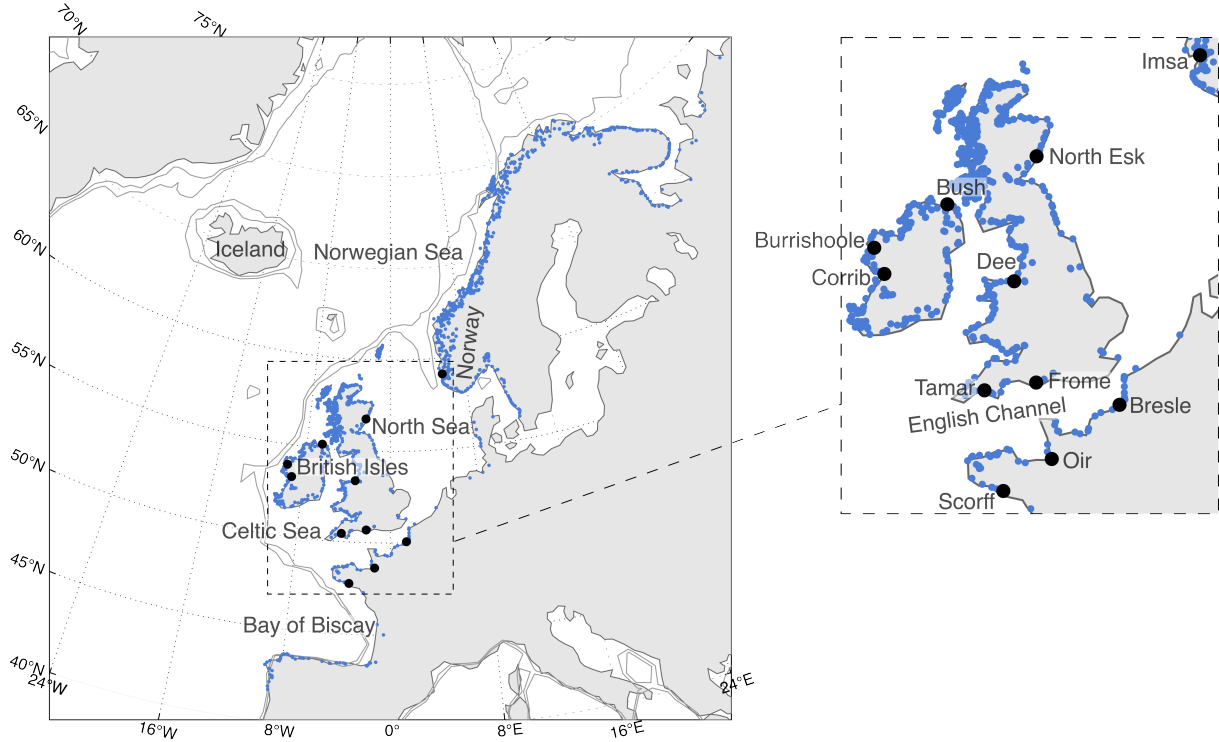


Figure 4.1: Salmon rivers in the northeast Atlantic (blue) and monitored rivers with time series of marine return rates available for analysis (black). Isobaths at 200m and 400m indicate the location of the continental shelf-edge.

Using the observed capture locations of post-smolts per month, these general regions (Figure 4.2 a) were split latitudinally by month from April to August (Figure 4.2 b-f), the period when post-smolts are known to migrate northwards. While there are no observations further south than 57° latitude in April, smolts from rivers between 41° – 57° latitude migrate in April (Otero *et al.*, 2014). Due to the nature of the post-smolt migration, not all the regions are occupied each month (for example, the ‘common region’ is not yet occupied in April, because post-smolts are not expected to reach this latitude that early in the year).

It should be noted that the locations of captured post-smolts used here are not comprehensive because surveys were not conducted over our entire study region and locations where no post-smolts were found were not recorded in the dataset, i.e. presence-only data. The locations where higher densities of post-smolts were observed (Figure 4.2) do not necessarily represent the actual locations with higher densities of post-smolts; they may represent areas which were more well-sampled. While these data (along with the known emigration timing from several rivers) allow us to determine the general regions which are likely to be occupied by post-smolts each month, we cannot infer the exact locations and concentrations of post-smolts. As such, we did not consider exposure within the individual ICES rectangles of these observations. Instead, we

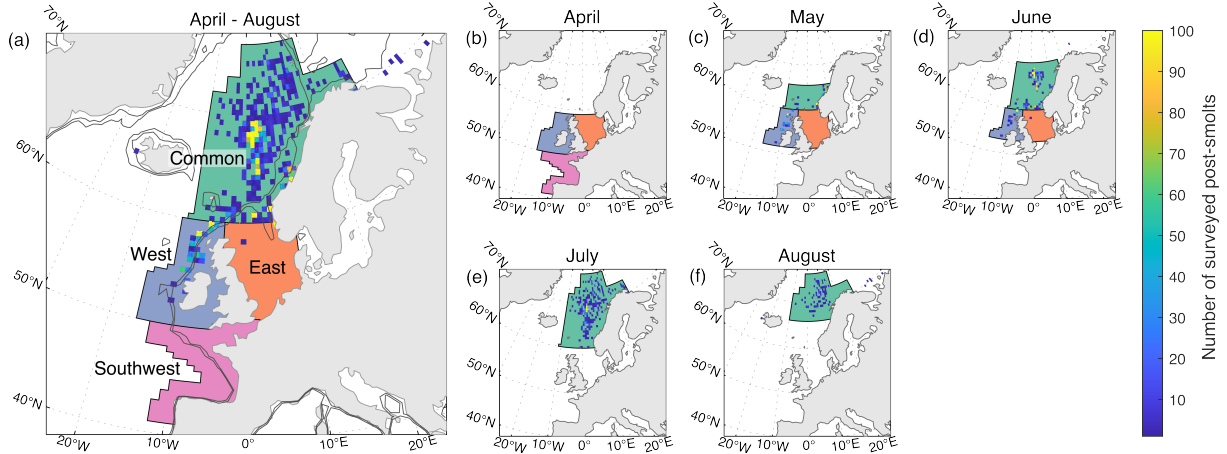


Figure 4.2: ICES rectangle scale (0.5° latitude $\times$ 1° longitude) locations and concentrations of surveyed post-smolts (Gilbey *et al.*, 2021) for: (a) April to August; (b) April; (c) May; (d) June; (e) July; and (f) August. Defined post-smolt migration regions are displayed (southwest, west, east, common). Isobaths at 200 m and 400 m in (a) indicate the location of the continental shelf-edge.

assume that post-smolts are evenly distributed within the defined post-smolt migration regions per month. Then, the quantity of pelagic landings within each of these regions is taken as a measure of bycatch exposure.

4.2.2 Pelagic fisheries data

Landings data in tonnes per ICES statistical rectangle for six pelagic finfish species (mackerel, herring, horse mackerel, sardine, capelin, and chub mackerel) were obtained by the ICES Working Group on North Atlantic Salmon (WGNAS, ICES, 2025b) after a data call associated with an ICES/North Atlantic Salmon Conservation Organisation (NASCO) Workshop on Salmon Mortality at Sea (ICES, 2023c). Blue whiting (*Micromesistius poutassou*) was also included in the list of species identified by the ICES WGNAS, however it was not included in the present analysis as the operational fishing depth of the blue whiting fisheries (300-600 m, ICES, 2023g) exceed the reported swimming depth of post-smolts (0 to 50m). The six fisheries of focus here operate, at least partly, at depths of 0-50 m (ICES, 2023g), suggesting a similar vertical range as post-smolts (further information on these fisheries is provided in Appendix C, Figure C.1). The following nations responded to the data call, providing landings data with a geographic resolution of 0.5° latitude and 1° longitude (i.e. ICES statistical rectangles) for the years 2000-2022: Denmark, France, Great Britain, Iceland, Ireland, Lithuania, Netherlands, Norway, Poland, Spain, and Sweden.

Spatial maps of monthly landings per ICES rectangle within the post-smolt migration regions (Figure 4.2) from April to August were developed for total landings of all of the six species combined and for each individual species. Within each of the post-smolt regions, individual and total species landings were summed per month (April-August) and year (2000-2022) to create time series indexing pelagic fishing activity relevant to post-smolts. Pelagic landings

time series were also trialled over a smaller subset of the west post-smolt region encompassing the continental shelf-edge, a location with multiple observations of post-smolts. However, the resulting time series showed similar temporal trends as the time series for the wider west region, so this result was omitted.

The pelagic landings dataset did not include landings taken by Russia or the Faroe Islands, nations that contribute a significant proportion (26% by tonnage in 2023) of herring and mackerel landings in the northeast Atlantic (ICES, 2024c). A method was developed to estimate the temporal and geographic distribution of landings from these nations. Fishing effort, obtained from Global Fishing Watch (<https://globalfishingwatch.org/>), from Russia and the Faroe Islands was multiplied by a catch per unit effort (CPUE) factor calculated from Icelandic landings and effort (Appendix C). Several assumptions had to be made in this analysis (e.g. it was assumed that Global Fishing Watch data reflects all fishing effort from these nations, all trawls were pelagic, and there was a constant CPUE across nations per month), causing uncertainty in the resulting estimated landings. The Global Fishing Watch effort was not disaggregated by species, so blue whiting fishing activity could not be removed. Additionally, the landings could only be estimated across nine years of the 22-year period considered in this study, so we chose not to combine these estimated landings with landings from the other nations presented in this analysis.

4.2.3 Comparing pelagic landings time series with salmon one-sea-winter (1SW) return rates

The second objective of this study was to evaluate correlations between the marine return rates of salmon and pelagic landings. Marine return rates of salmon can be used as a proxy for marine survival (Chaput, 2012), though we note that they are also dependent on maturation rates. Here, we used one-sea-winter (1SW) return rates (i.e. the fish returning after one winter at sea), because this study focused on vulnerability to bycatch during the early marine (post-smolt) phase and post-smolt survival rates are likely to be a stronger signal in 1SW return rates, compared to the return rates of fish spending multiple winters at sea (MSW). We note that 1SW return rates are influenced by the varying proportion of fish maturing after one winter at sea, in addition to marine survival. Annual 1SW return rates were available from 11 monitored rivers within our study domain (Figure 4.1 ICES, 2023e). There are differences in the methods used to estimate return rates among rivers (ICES, 2023e) which could influence the time series; we therefore chose to use normalised return rates from each river to remove some of the small quantitative differences caused by dissimilarities in estimation methods, while retaining the trends in return rates.

We acknowledge that there are other challenges associated with using marine return rates here, such as the fact that they are only available for a limited number of rivers within our study region; other challenges and limitations of this approach are discussed later in this chapter. This analysis is included even though we do not expect it to provide strong results, as it is a typical approach taken in many other papers identifying drivers of salmon mortality, making our analysis comparable with previous studies (e.g. Jonsson *et al.*, 2003; Peyronnet *et al.*, 2007, 2008;

Hvidsten *et al.*, 2009; Armstrong *et al.*, 2018; Tyldesley *et al.*, 2024).

Monitored rivers were grouped according to the geographical divisions in Figure 4.2. In each region, the mean of the normalised annual 1SW return rates for the relevant rivers was used as an index of return rates within that region (Figure 4.3). Return rates for the North Esk were only available for 2000-2002 and 2005-2009, so the East grouped return rates consist solely of the Imsa return rates for the remaining years. Our grouped return rates differed from those used by Tyldesley *et al.* (2024) because this study grouped monitored rivers based on geographical divisions rather than a clustering analysis.

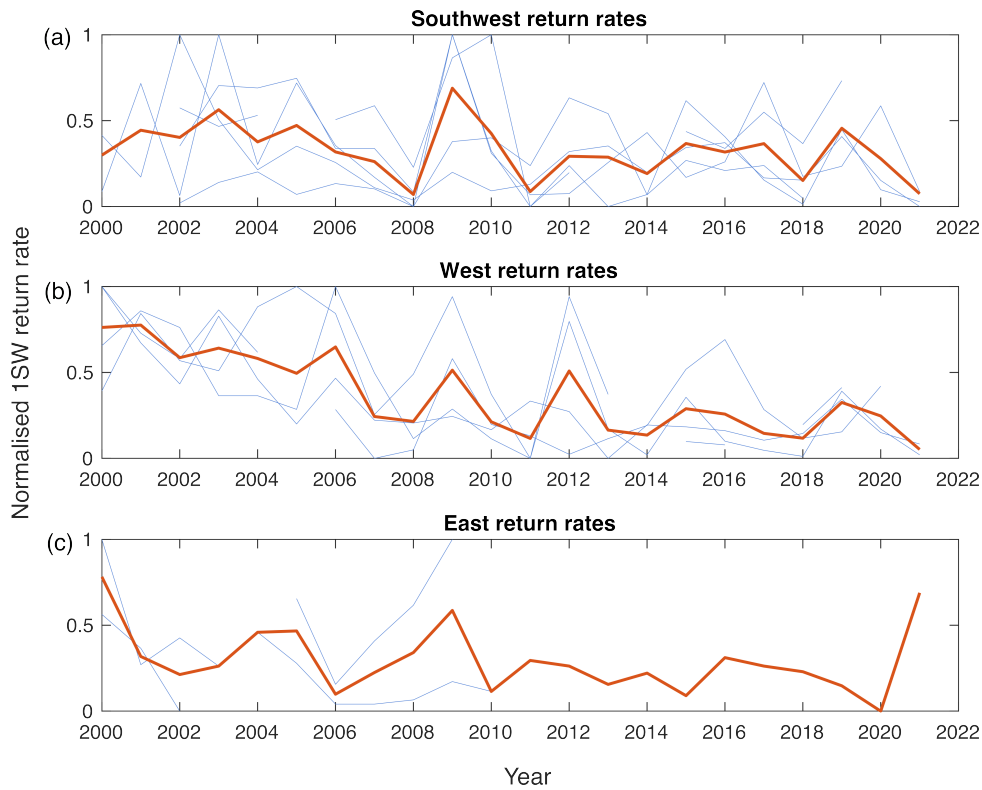


Figure 4.3: Normalised marine return rates for one-sea-winter (1SW) salmon for individual populations (thin blue lines) and combined means per region (thick orange lines) from 2000-2021 for: (a) the southwest region (including the Scorff, Oir, Bresle, Tamar, and Frome); (b) west region (Corrib, Burrishoole, Bush, and Dee); and (c) east region (North Esk and Imsa).

Each grouped annual marine return rate time series (southwest, west, and east) was correlated with landings from each pelagic fishery in the relevant post-smolt regions. The year associated with the return rates (Figure 4.3) is the year in which smolts enter the sea, so no lag is required when calculating correlations with landings during the post-smolt migration period. Only those combinations of landings and return rates where the salmon population would migrate through the landings region were considered (for example, we did not consider correlations between east landings and west return rates). A finer-scale analysis, where annual return rates were correlated with landings in individual ICES rectangles, was also trialled, but there were not enough years of landings data available within each rectangle to identify relationships.

Pearson correlation coefficients (r) were calculated for each annual marine return rate and monthly post-smolt region landings time series combination. As the annual marine return rates and landings time series exhibit autocorrelation, the modified Chelton method (Pyper & Peterman, 1998), where the degrees of freedom are adjusted based on the level of autocorrelation, was used to determine p-values. Correlation coefficients (r, p) were also calculated between detrended annual marine return rates and landings time series to consider whether interannual fluctuations in landings and returns were also correlated. Return rates were detrended by determining the linear trend via a least-squares regression and then subtracting this from the time series.

Rather than determining the significance of correlations based on a single arbitrary confidence level, the approach proposed by Muff *et al.* (2022) was applied to categorise correlations by the strength of evidence, whereby $p \leq 0.001$ is considered to be very strong evidence, $0.001 < p \leq 0.01$ to be strong evidence, $0.01 < p \leq 0.05$ as moderate evidence, $0.05 < p \leq 0.1$ as weak evidence, and $p > 0.1$ as little or no evidence.

When conducting multiple statistical tests, there is an increased chance of a type I error (false positive) occurring in one of the tests. Methods such as the Bonferroni correction are sometimes employed in this case to ‘correct’ p-values and reduce the likelihood of a type I error. However, these methods increase the likelihood of a type II error, meaning ‘real’ relationships can be lost (particularly if the relationships are weaker). Though we conduct multiple correlative tests in this chapter, we opt to follow the recommendation of Armstrong (2014), who suggested that this correction should only be applied if it is vital that a type I error is avoided (even at the expense of a potential type II error), or if numerous tests are undertaken without any preplanned hypotheses. Neither of these conditions apply here: we expect that any relationships between fisheries exposure rates and return rates would be weak anyway, so avoiding a type II error is likely to be more pressing; and we are investigating correlative relationships between fisheries exposure in specific migration regions and return rates to investigate our hypothesis that post-smolts are at risk of mortality due to bycatch in pelagic fisheries (**H4**).

4.3 Results

4.3.1 Pelagic landings within monthly post-smolt migration regions

For each month from April to August, there were substantial pelagic fishery landings within the post-smolt migration regions (Figure 4.4). The landings also exhibited variation across months, years and regions (Figure 4.5). In the southwest region, landings predominantly consisted of mackerel, horse mackerel, and sardine (Figure 4.5 and Appendix C Figures C.10, C.12, C.13). There were fewer landings in the west region, mainly mackerel and horse mackerel in April-May and herring in June. While landings in the west region were relatively low throughout all months, there was also a decrease from April to June. Contrastingly, landings in the east region (which were mainly herring) increased from April to June, becoming much greater than in other regions. In the common region, landings were predominantly herring and mackerel, with an increase in landings observed between May and June. There were very few landings of chub mackerel and

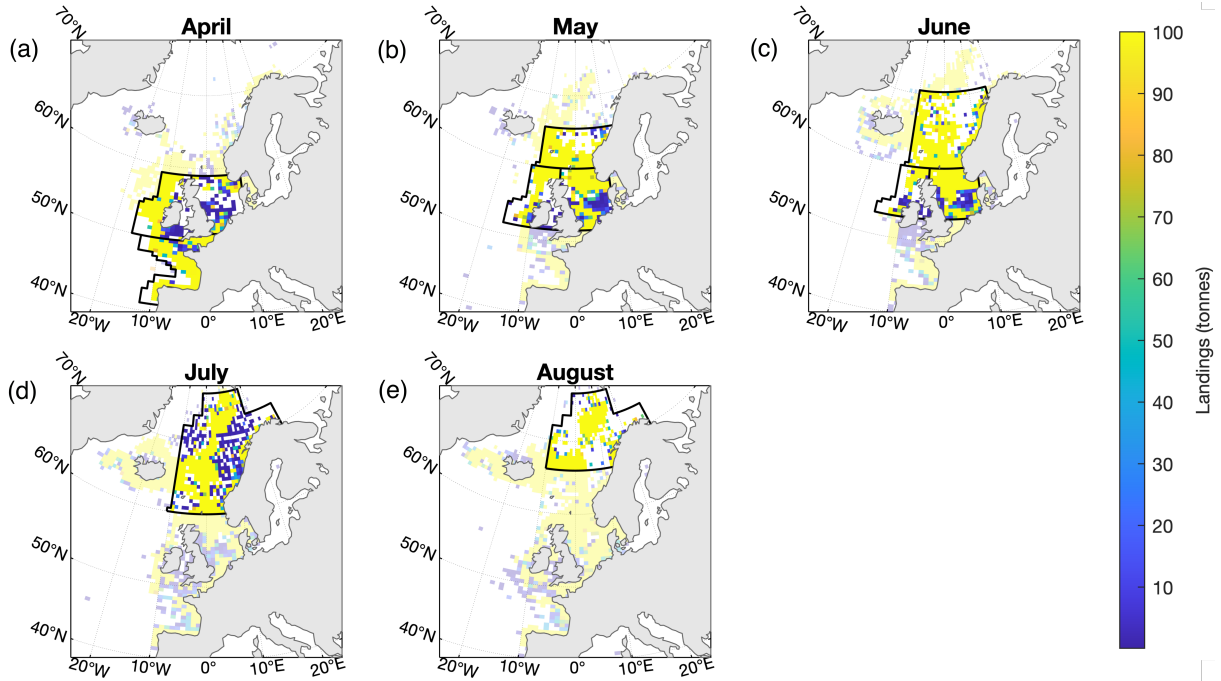


Figure 4.4: Total landings of all species (mackerel, herring, horse mackerel, capelin, chub mackerel, sardine) by ICES rectangle within the post-smolt regions (outlined in black) per month across 2000-2022.

capelin within the post-smolt regions.

Fishing effort for Russia and the Faroe Islands was found to be generally concentrated in the Norwegian Sea, i.e. the common region (Appendix C Figures C.1, C.2). Despite uncertainty in their values, estimated landings by these nations were greater than the landings from other nations in the Norwegian Sea and displayed different interannual patterns (Figure C.9).

The mean landings per region and month from the other nations are summarised in Figure 4.6. Capelin and chub mackerel were omitted as there are very few landings of these species across regions and periods.

4.3.2 Comparing time series of pelagic landings and salmon 1SW return rates

Correlations between 1SW return rates and monthly landings time series with at least moderate evidence ($p < 0.05$) are shown in Figure 4.7. It should be noted that there were many more non-significant correlations than significant correlations. No correlations between pelagic landings in the common region and 1SW return rates were considered due to considerable missing data relevant to this region. The incomplete landings data in the common post-smolt region also prevented a correlative analysis between return rates and ‘along-migration’ landings (where, for example, southwest populations might be exposed to southwest landings in April, west landings in May and common region landings in June-August).

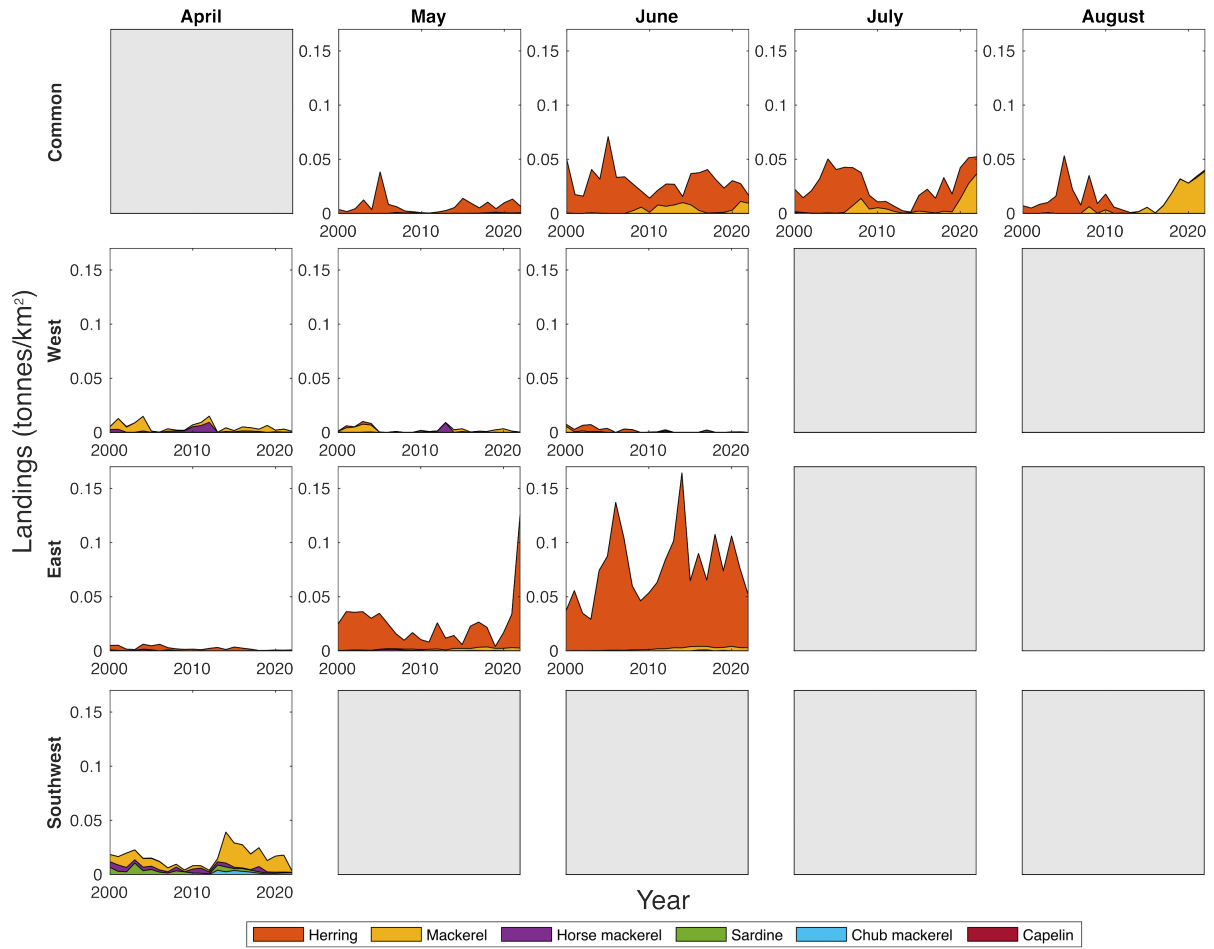


Figure 4.5: Time series from 2000-2022 of all landings (in tonnes per square kilometre) per region and per month, coloured by the proportional contribution of each species.

4.4 Discussion

This study quantified the exposure of migrating salmon post-smolts to pelagic fisheries over broad spatial regions occupied during the first few months of the marine migration. A large degree of spatial-temporal overlap was found between the post-smolt migratory regions and pelagic fishing activity in the northeast Atlantic, indicating that post-smolts are exposed to pelagic fisheries throughout their initial marine migration. Therefore, the findings presented here support the postulations of previous studies that post-smolt migration corridors overlap with pelagic fisheries targeting commercially important finfish species (ICES, 2004, 2005, 2023c). There were a large number of pelagic landings taken within each of the post-smolt migration regions each month from April to August, suggesting a potential risk of bycatch of post-smolts from all populations throughout their entire migration up to and through the Norwegian Sea and hence supporting our hypothesis that post-smolts are at risk of bycatch in these fisheries during their first 3-5 months at sea (**H4**).

	Mackerel	Herring	Horse mackerel	Sardine	All species (summed)
April SW	0.0097	5×10^{-5}	0.0025	0.0028	0.0158
April W	0.0034	2×10^{-5}	0.0017	2×10^{-5}	0.0051
April E	2×10^{-4}	0.0020	2×10^{-4}	3×10^{-5}	0.0024
May W	0.0017	2×10^{-4}	7×10^{-4}	0	0.0026
May E	0.0013	0.0240	5×10^{-4}	3×10^{-5}	0.0258
May C	2×10^{-4}	0.0068	1×10^{-4}	0	0.0071
June W	5×10^{-4}	0.0013	2×10^{-4}	0	0.0020
June E	0.0017	0.0700	2×10^{-4}	5×10^{-6}	0.0719
June C	0.0034	0.0265	2×10^{-5}	0	0.0299
July C	0.0055	0.0206	1×10^{-5}	0	0.0261
August C	0.0076	0.0084	0	0	0.0160
Total (summed)	0.0352	0.1599	0.0064	0.0029	

Figure 4.6: The mean landings (tonnes/km²) per fishery and month within the regions occupied by post-smolts (SW = southwest, W = west, E = east, C = common) between 2000 and 2022. Boxes are shaded according to lower values of mean landings (blue = less than 0.002 tonnes/km²), moderate values (yellow = between 0.002 and 0.02 tonnes/km²), and higher values (orange = greater than 0.02 tonnes/km²). The black box displays the cells where the landings are known to be a lower bound due to missing data from some nations (Appendix C).

4.4.1 Pelagic fisheries exposure analysis

There was increased exposure to pelagic fisheries for post-smolts from eastern populations emigrating later in the year (e.g. mid-May to June), while contrastingly there was a decreased exposure for later emigrating post-smolts in the west. However, exposure was much lower overall in the west region than in the east region. Across the north Atlantic, smolts have been initiating their seaward migration 2.5 days earlier per decade in response to global climate change (Otero *et al.*, 2014). The results presented here suggest that this climate-driven shift to an earlier migration might slightly lower the risk of bycatch for some populations (those in the west) but

	April	May	June
All species landings	NSC	NSC	NSC
Mackerel	Correlations between west landings and west returns ($r=0.46$, $p=0.04$). Correlations between east landings and east returns ($r=0.59$, $p=0.004^*$) and east landings and detrended east returns ($r=0.44$, $p=0.04$).	NSC	Correlation between west landings and west returns ($r=0.50$, $p=0.02$).
Herring	NSC	Correlation between west landings and west returns ($r=0.54$, $p=0.01$).	Correlation between west landings and west returns ($r=0.51$, $p=0.03$).
Horse mackerel	Correlation between southwest landings and detrended southwest returns ($r=-0.43$, $p=0.045$)	NSC	NSC
Sardine	Correlation between west landings and southwest returns ($r=-0.49$, $p=0.02$). Correlations between west landings and detrended southwest returns ($r=-0.53$, $p=0.01$) and detrended west returns ($r=-0.51$, $p=0.02$).	NSC	NSC
Capelin	NSC	NSC	NSC
Chub mackerel	NSC	NSC	NSC

Figure 4.7: Correlations (with at least moderate evidence, $p < 0.05$) between pelagic landings in the post-smolt regions and grouped 1SW return rates. Correlations between common region landings and return rates were not considered due to missing data relevant to this region (Appendix C). Negative correlations are denoted by purple shaded text and positive correlations by orange shaded text. NSC = no significant correlation. Strong evidence is denoted by *.

increase the risk for others (eastern populations) if the pelagic fishery remains stable in space and time. However, it should be noted that pelagic fishing activity varies according to the target species distribution and abundance, which are known to fluctuate with climatic conditions (ICES, 2024c).

In the common post-smolt region, landings appeared to be lower than in the eastern region. However, landings in the Norwegian Sea would be higher if landings from the Russian and

Faroese fleets were included in this study. Despite it not being feasible to directly combine the estimated landings with the landings from the other nations in this analysis, we found that the magnitude and interannual patterns of the estimated landings differed from the total landings from the other nations in the common region (Appendix C). This indicates that the time series of landings in the common region (Figure 4.5) is a lower bound on the total landings from all nations. This does not affect the conclusions for the rest of the study domain, as Russian and Faroese fishing effort was concentrated in the Norwegian Sea.

Along the whole migration corridor, post-smolts have the greatest total exposure to the mackerel and herring fisheries. Mackerel fisheries operate predominantly in the west, while the herring fisheries operate more in the east, and herring landings were higher in total. Post-smolts have a lower total exposure to the horse mackerel and sardine fisheries as they only operate on the southern part of the migration corridor. There were very few landings of capelin and chub mackerel in the post-smolt migration regions, so we expect that these fisheries pose a negligible risk to post-smolts in this region from April to August. However, a northwards expansion has been observed in the distribution of chub mackerel (ICES, 2021b), and if this trend continues, then the chub mackerel fishery might have greater overlap with post-smolts in the future. Climate-driven northwards expansions in the spatial distribution of herring and mackerel have also been observed (Rose, 2005; Pacariz, 2016), which could indicate a future change in the exposure of post-smolts to these fisheries.

Interannual fluctuations in landings suggested differences in the exposure levels of post-smolts among years. The broad post-smolt migration regions were kept constant among years (2000-2022) due to a lack of specific annual data, but previous modelling studies have suggested that post-smolt migration routes are likely to vary with interannual changes in environmental conditions (Mork *et al.*, 2012; Moriarty *et al.*, 2016; Borland *et al.*, 2025). Considering shifting migration paths alongside pelagic landings was beyond the scope of this study, but future work could calculate exposure using specific annual modelled post-smolt migration routes; considering this may increase interannual variability in estimated exposure. Migration paths of post-smolts also vary among populations (Gilbey *et al.*, 2021; Rodger *et al.*, 2025), suggesting some populations will have greater exposure than others to pelagic fishing activity.

A typical post-smolt will enter the sea at a body length of 10-20 cm (Thorstad *et al.*, 2011) and might grow to approximately 30 cm by late August (Mork *et al.*, 2012). This change in size may alter the likelihood of bycatch: there is some evidence to suggest that larger fish are more likely to be caught (Dubost, 2014; Bisch, 2024), however this will depend on the fishery and gear type used. It may be hypothesised that the risk of bycatch is higher when post-smolts are a similar size to the fishery target species, but at present there is no evidence to confirm this. The size composition of landings is not generally available, but minimum landing sizes in the fisheries considered here vary from 15 cm for horse mackerel to 30 cm for mackerel (ICES, 2019), a range that overlaps with post-smolt body length over the first months of migration. Identifying whether salmon bycatch risk is influenced by post-smolt size-based capture selectivity in pelagic fishing gears along their migration routes would be a valuable focus for future research.

4.4.2 Correlative relationships between pelagic pelagic and 1SW returns

Our second objective in this study was to identify correlations between salmon marine return rates and pelagic landings. Where they existed, correlations between mackerel or herring landings and salmon return rates were positive, which might suggest synchronicity in the response of salmon post-smolts, mackerel and herring to large-scale variability in marine environmental conditions (e.g. driving similar changes in habitat availability and/or trophic dynamics that affect the abundances of these species). However, the mackerel and herring stock sizes (relating to landings) will have been influenced by marine conditions for several years prior to marine entry of the post-smolts, so the conditions experienced will never be identical. Furthermore, the existence of a positive relationship does not imply that there is no bycatch of post-smolts in these fisheries, but simply that any effect of bycatch is not large-scale and consistent enough to be revealed through this correlative analysis.

Horse mackerel landings in the southwest post-smolt region were negatively correlated with detrended southwest return rates. This suggests that interannual fluctuations in horse mackerel landings occur synchronously with interannual fluctuations in return rates. This provides evidence towards the hypothesis of post-smolt bycatch in this fishery. A negative relationship was also found between return rates and sardine landings in the west region in April. However, there were relatively few sardine landings in this region and period (compared to the sardine fishery in the southwest region, or the other fisheries in the west region) and in many years there were zero landings. This suggests the possibility that this observed relationship may be spurious, rather than evidence towards the hypothesis of post-smolt bycatch.

Most combinations of landings and return rate time series did not yield significant correlations, but there are several reasons why relationships might not be revealed through a correlative analysis (even if there is indeed a mechanistic link between pelagic fishing and salmon marine survival). Firstly, the return rates were only for a small subset of salmon rivers (11 of 1456 rivers shown in Figure 1) and may not be representative of all populations (in particular, they are not representative of populations in southern France and Spain, and return time series coverage is limited for populations in the North Sea). Secondly, we considered pelagic landings over the first three to five months at sea, but 1SW return rates are influenced by many biotic and abiotic factors, including feeding and predation, across up to 18 months at sea. Thirdly, 1SW return rates are not directly equivalent to marine survival rates and are also influenced by maturation rates, which vary between years and populations (ICES, 2024a; Tréhin, 2024; Elliott *et al.*, 2026). For these reasons, any non-correlations between return rates and pelagic landings are not interpreted as evidence that post-smolts are not influenced by these fisheries. Secondary effects of the pelagic fishing activity examined in this study include reductions in post-smolt prey items such as blue whiting or herring larvae (Haughland *et al.*, 2006; Utne *et al.*, 2021b). Changes in interspecific competition could potentially arise, though the diet overlap between post-smolts and herring or mackerel is relatively low (Utne *et al.*, 2021a). Due to a lack of data on secondary effects from pelagic fishing, we did not analyse such risks.

4.4.3 Conservation measures

Post-smolts had the highest total exposure to the mackerel and herring fisheries, indicating that these fisheries are likely to pose a bycatch risk for salmon during their early marine migration. However, as this analysis only calculated the exposure of post-smolts to the fisheries, not sensitivity (due to a lack of data), it is also possible that fisheries with a lower total exposure could also pose a notable bycatch risk to salmon. Therefore, based on the exposure levels quantified in this study, we recommend that the highest priority fisheries for future post-smolt bycatch research should be: (1) the herring fishery operating in the North Sea between April and June and the Norwegian Sea between June and August; and (2) the mackerel fishery in the Bay of Biscay and the shelf-edge west of the British Isles in April and the Norwegian Sea between June and August. Then, the following fisheries should be considered at a slightly lower priority: (3) the horse mackerel fishery in the Bay of Biscay and the shelf-edge west of the British Isles in April; and (4) the sardine fishery in the Bay of Biscay in April. We note that the negative relationship between horse mackerel landings in the Bay of Biscay in April and return rates provides additional motivation for this fishery to be considered. Our suggested fisheries for future research prioritisation are in line with the estimated risks posed by different fisheries proposed by (ICES, 2023c).

Considering these prioritised pelagic fisheries, the next step is to evaluate sensitivity levels, i.e. the bycatch rates of salmon per tonne of landings, which could then be combined with the exposure values defined here to complete a full bycatch risk analysis. Given the logistical challenges of detecting bycaught post-smolts using onboard fisheries observer programmes, we suggest that eDNA analysis of landings and/or landings port observations are the most feasible methods for this analysis (Yin *et al.*, 2024). This work could also be extended to the entire marine life stage of salmon, and future work could use a multivariate statistical analysis to bring together evaluated bycatch risk with other factors that likely influence salmon survival, such as environmental conditions and prey availability (Beaugrand & Reid, 2003, 2012; Mills *et al.*, 2013; Sobocinski *et al.*, 2021). Understanding each of the drivers of salmon mortality is an ongoing challenge (Bull *et al.*, 2022; Gillson *et al.*, 2022), but this work helps further understanding of the conditions experienced by salmon at sea, informing the ongoing discussion about why salmon populations continue to decline despite concerted efforts to protect them in their natal rivers (ICES, 2024a).

4.5 Conclusion

This study revealed that pelagic fishing activity for six commercially important finfish species (mackerel, herring, horse mackerel, sardine, capelin, and chub mackerel) occurs annually in the areas occupied by salmon post-smolts during their early marine migration. We found that the total exposure of post-smolts was highest for the mackerel and herring fisheries, and medium exposure levels were found for the horse mackerel and sardine fisheries in April. It is suggested that these fisheries are the focus of future work investigating salmon bycatch, but with the caveat

that two key nations (Russia and the Faroes) were missing from our analysis. Additionally, a negative correlation between detrended salmon return rates and horse mackerel landings was found, providing further evidence that this fishery should be examined for bycaught salmon.

Despite using the best available data, only equivocal evidence was found regarding which pelagic fisheries in the northeast Atlantic pose the greatest bycatch risk to salmon post-smolts. The next step forward to improve bycatch risk estimates would be to combine the exposure results presented here with metrics of sensitivity to bycatch. To do so requires robust estimates of the bycatch rates of salmon per unit of landings, which could be obtained with eDNA analysis and/or landing port observations. Landings of the pelagic finfish considered in this study which are for human consumption are normally individually inspected. We suggest that identification and reporting of bycaught salmon within these landings (if made mandatory) could provide an extremely valuable data source for further bycatch risk analysis. Future work expanding this exposure analysis into a full risk analysis will create a useful indicator of post-smolt bycatch risk, forming another piece of the puzzle of explaining the drivers of salmon mortality at sea.

Chapter 5

Zooplankton energy available to forage fish

5.1 Introduction

Higher growth rates of salmon during their first months at sea have been linked with higher overall marine survival rates (Friedland *et al.*, 2000), emphasising the importance of growth during this period. The first months of fast growth after entering the sea allow post-smolts to obtain sufficient length to escape the “risk-size window” where they are highly vulnerable to predation (Rikardsen & Dempson, 2011). Post-smolts appear to be opportunistic feeders, with variability observed in their stomach contents and fullness between years and locations (Rikardsen *et al.*, 2004; Rikardsen & Dempson, 2011; Utne *et al.*, 2021b; Hellenbrecht *et al.*, 2023), suggesting they adapt their feeding depending on the availability of different prey items. During this time, their main prey item is fish larvae, of various species including sandeels (*Ammodytes spp.*), herring (*Clupea harengus*), and gadoids such as blue whiting (*Micromesistius poutassou*) and cod (*Gadus morhua*) (Rikardsen *et al.*, 2004; Haugland *et al.*, 2006; Utne *et al.*, 2021a). Post-smolts also consume amphipods and euphausiids in lesser quantities, and an even smaller amount of copepods and decapods (Utne *et al.*, 2021b; Hellenbrecht *et al.*, 2023).

Several sources of evidence suggest that feeding opportunities for post-smolts have declined in quantity and quality. Utne *et al.* (2021b) found that the condition factor and stomach fullness of post-smolts in the Norwegian Sea had shown a declining trend between 2003 and 2012 (condition factor dropped from around 1.16 to 0.87 over this period). Both Utne *et al.* (2021b) and Utne *et al.* (2022) also revealed recent declines in the quantity of fish larvae and amphipods in post-smolt stomachs (fish larvae content dropped from 90% in 1997-1998 to 20% in 2019). With consumption of these high-energy prey items linked to increased body size and stomach fullness (Hellenbrecht *et al.*, 2023), this change may be detrimental to the overall growth and survival of post-smolts. In the face of ongoing declines in salmon populations (ICES, 2024a), further investigation of this potential driver of low marine survival rates is required.

With planktivorous fish larvae being of high importance to post-smolts, it might be hypothesised that any changes in their distribution or abundance might align with observed declines in post-smolt feeding and growth. However, the investigation of this hypothesis is hindered by data availability. Data on the abundance and distribution of planktivorous fish (that constitute prey for post-smolts) within our study region are generally limited to stock assessments (e.g. ICES, 2025c). These are aggregated over large spatial scales and typically focused on spawning stock biomass (SSB) rather than larval abundance, meaning they are poor measures of prey availability for salmon post-smolts (Vollset *et al.*, 2022; Tyldesley *et al.*, 2024). Instead, examining data from lower marine trophic levels may be useful in explaining the declines in consumption of fish larvae by post-smolts. The prey items of planktivorous fish, of both larval and adult stages, include copepods, crustacean larval stages, fish eggs and larvae (Utne *et al.*, 2021a; Olin *et al.*, 2022), and there is evidence suggesting that declines in zooplankton abundance are driving declines in planktivorous fish abundance (Beaugrand & Reid, 2003; Capuzzo *et al.*, 2018). Notably, Olin *et al.* (2022) found that zooplankton energy relevant to sandeels in the North Sea had decreased by over 50% in the past 60 years, but trends and absolute values of energy varied between locations, suggesting the importance of looking at prey fields on a regional-scale.

The continuous plankton recorder (CPR) is a long-term and large-scale programme in the North Atlantic where plankton samples are collected via reels of silk towed by ships of opportunity (Richardson *et al.*, 2006). Tyldesley *et al.* (2024) used the CPR data to investigate zooplankton availability in the salmon post-smolt food chain, finding that declines in zooplankton energy over broad spatial regions were correlated with declines in the marine survival rates of salmon. This chapter developed the work of Tyldesley *et al.* (2024) by using modelled post-smolt migrations to generate metrics of zooplankton energy within population-specific migration space-time domains.

CPR-derived zooplankton energy was selected for use in this study due to its long-term availability and coverage across the study domain (Figure 5.1). The CPR programme is the largest long-term plankton monitoring programme in the world (Richardson *et al.*, 2006), and the existence of sampling every year throughout our study period (1993-2019) means this dataset is a good candidate for trialling a river- and year-specific indicator of zooplankton energy. Furthermore, sampling is still ongoing, so a CPR-derived indicator could continue to be updated; this may be important in understanding ongoing declines and fluctuations in salmon marine survival rates.

Other zooplankton datasets were available, but were less suited to this work. For example, approaches to generate smooth modelled zooplankton fields from the CPR dataset have been developed (Beare & McKenzie, 1999; Castant *et al.*, 2025). However, the model outputs retain some of the uncertainty generated by CPR sampling (which is patchy in space and time, as seen in Figure 5.1 and discussed later in this chapter) and, at present, these models have only been developed for specific taxa (not including all of those relevant to the post-smolt food chain), so we elect to use CPR data, though we note that modelled CPR approaches might prove useful in future if these methods are developed further. Zooplankton models coupled to lower trophic levels and physical models are also available at various levels of spatial and temporal coverage. Global

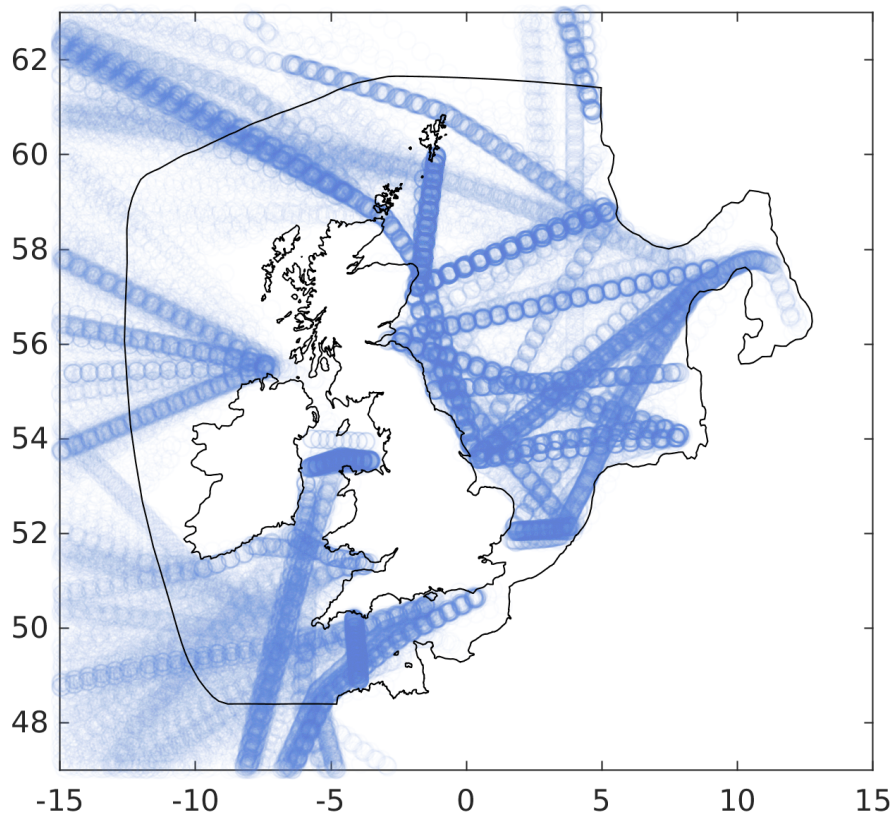


Figure 5.1: All CPR transects. The Scottish Shelf Model (SSM) domain is outlined.

models provide data on a coarse spatial scale, representing large-scale processes (e.g. Petrik *et al.*, 2022), but this scale is not necessarily relevant to the spatial scale of this study. Finer scale, local models are available across parts of our study domain, or parts of the time period, or certain relevant zooplankton taxa (e.g. Broekhuizen *et al.*, 1995; Maar *et al.*, 2014; Daewel *et al.*, 2019), but these models do not compare to the broad spatial, temporal and taxonomic coverage of the CPR.

Satellite-derived primary production or chlorophyll concentration datasets are readily available, and some previous studies have investigated relationships between salmon and phytoplankton abundance. For example, Olmos *et al.* (2020) found a positive correlation between primary production averaged over a wide spatial region in the north Atlantic and salmon post-smolt survival. However, they found negative or non-significant correlations between survival and primary production when considering smaller, stock-specific regions representing the first three months at sea (comparable to the scales considered in this study). Similarly, Friedland & Todd (2012) found no relationship between salmon marine growth rates west of Greenland and satellite-derived chlorophyll concentration or net primary production. These studies suggest that phytoplankton abundance is not a robust indicator of salmon growth or survival, and it may not be relevant on smaller spatial scales, as considered here.

In this chapter, the following questions were addressed:

- Q1. Is the coverage of the Continuous Plankton Recorder data sufficient (with low enough spatial and temporal variability) to develop a river- and year-specific indicator of marine prey energy availability for salmon post-smolts along modelled migration paths?
- Q2. How do modelled encountered zooplankton energy values differ with:
- a) interannually varying modelled migration paths, or
 - b) varying modelled migration paths from different migration behaviours
- Q3. Overall, how applicable is the CPR data on the relatively small scale of along-migration paths? What spatial and temporal scales are most relevant for future work?

Question 2 here directly addresses our hypothesis **H3**.

5.2 Methods

5.2.1 Continuous Plankton Recorder data

In this study, we use the measure of zooplankton energy (Z_E) available to forage fish in the post-smolt food chain derived from CPR data by Tyldesley *et al.* (2024). Z_E included the CPR taxonomic groups: copepods (*Acartia* spp., *Calanus finmarchicus*, *Calanus helgolandicus*, *Calanus* spp., *Centropages hamatus*, *Centropages typicus*, *Centropages* spp., copepod nauplii, *Metridia lucens*, *Oithona* spp., *Para-Pseudocalanus* spp., and *Temora longicornis*), larvaceans, crustacean larvae (cirripede and decapods), euphausiids (*Hyperiidea* spp. and unclassified), fish eggs, and fish larvae. The sampling efficiency of the CPR varies with size, with both smaller and larger zooplankton being underestimated (Richardson *et al.*, 2006). Furthermore, the diel vertical migration of zooplankton alters their sampling rates at night compared to during the day. Z_E was corrected for taxa-specific sampling efficiency differences using correction factors calculated by Olin *et al.* (2022) based on in-situ plankton sampling at Stonehaven in eastern Scotland and L4 in Plymouth, with separate corrections for day and night.

5.2.2 Evaluating consistency in CPR sampling

To address Q1, Z_E and the total number of CPR samples were evaluated between March and September (covering the main feeding seasons of forage fish in the northeast Atlantic, Hamre, 1980; Dalpadado *et al.*, 2000; Iversen, 2002; Gislason & Astthorsson, 2002; Utne *et al.*, 2021a; Olin *et al.*, 2022) from 1993 to 2019 (the period over which post-smolt migrations were simulated) within the SSM spatial domain. Energy (Z_E) and sampling were aggregated into rectangular boxes of 1° latitude $\times$ 2° longitude, as in Tyldesley *et al.* (2024): it was noted here that reducing the box size any further would cause a very low number of samples in some boxes (<5 over the 27-year study period). Mean Z_E per box was considered across the whole time period (March-September 1993-2019) and the whole SSM domain, then mean Z_E per box was considered spanning only the area covered by modelled migrations in individual years (i.e. considering the interannual consistency, or conversely variability, in CPR sampling across specific migration

paths). For the latter, river 12 (Thames) was selected to consider annual CPR sampling along migration paths (only a single river is presented in the results for brevity), as this river has a relatively long migration within the SSM domain, which includes the relatively consistently sampled region in the southern North Sea. Therefore, it was expected that sampling along this river’s migration paths had the greatest chance of finding a positive result to Q1 (i.e. this river was selected as a ‘best-case scenario’).

5.2.3 Interannual variability in Z_E

To address Q2a, a post-smolt ‘occupancy matrix’ for each river and each year was generated by counting the number of occurrences of all modelled post-smolts within each 1° latitude $\times$ 2° longitude box, and then normalising per river such that the entries of the matrix for the ‘highest occupancy’ year (i.e. the slowest migration year) summed to 1. This normalisation approach was taken so that absolute differences in occupancy between years were retained. The occupancy matrices combined simulated migrations from the full 25 parameter sets for each river rather than the optimal sets selected in Chapter 3. This created occupancy matrices spread over a larger spatial area for each river, acting as ‘error bars’ on the simulated migration locations, and ensuring that CPR energy values were considered over a wide area (making estimates more robust by including a larger number of samples). The resulting occupancy matrices were multiplied by the mean energy per box and summed to create time series of occupancy-weighted Z_E per year. Occupancy-weighted energy is presented for three North Sea rivers; again, the North Sea was selected due to the relatively high sampling effort there.

5.2.4 Inter-behavioural variability in Z_E

Another factor likely to alter the energy fields experienced by fish is their migratory behaviour (Humston *et al.*, 2004). To address Q2b, occupancy matrices were calculated separately for each migratory behaviour of the 25 parameter sets for each river, each combining the 27 years of simulations. The occupancy matrices were then multiplied by the mean zooplankton energy field. As before, we focused on river 12 due to the relatively high sampling along its migration route. The modelled migration spatial densities correlated with the lowest and highest occupancy-weighted energy values were compared. Then, the occupancy-weighted energy values were compared against the weights of the behavioural components in the movement model, w_c , w_s , and w_d .

5.3 Results

5.3.1 CPR energy and sampling consistency

Throughout the 27-year study time period, the total number of CPR samples taken varied spatially throughout the SSM domain (Figure 5.2 a). Certain locations had no CPR samples over the entire period, while others had several hundred. There was relatively high sampling effort in the Celtic Sea, the southern North Sea and patches of the northern North Sea, particularly

near Orkney and Shetland. The locations with high sampling (>350 samples over the study period) had relatively lower interannual variability in sampling (Figure 5.2 b), i.e. they were sampled consistently. However, most of the domain exhibited highly variable sampling ($CV \geq 1$).

The consistently-sampled areas of the southern North Sea had relatively low mean energy (Figure 5.2 c). The areas with few samples were more variable: a rarely-sampled area west of Scotland had relatively low mean energy values, while contrastingly, there was an isolated high-energy box southeast of Orkney, where mean energy was calculated from only two samples over the full 27-year period.

Despite the modelled migration route of river 12 (Thames) being relatively well sampled, the number of samples taken still varied interannually, with a minimum of 441 in 1994 and a maximum of 757 in 2001 (Figure 5.3 a). The spatial distribution of CPR sampling also varied between years (Figure 5.3 b-c), with many boxes having zero samples in individual years. Note that the number of CPR samples over the area spanned by modelled migrations varied with interannual differences in simulated migration paths; in 1994, with a minimum number of CPR samples, the area spanned was smaller than in 2001, with the maximum number of samples (black outlines in Figure 5.3 b-c).

5.3.2 Post-smolt occupancy-weighted zooplankton energy: interannual variability

With notable variability in sampling (both in magnitude and in distribution) between years (Section 5.3.1), we choose to use the mean energy per box over the whole time period (Figure 5.2 c) for the remainder of this analysis. Spatial and temporal aggregation of CPR data can help to minimise any bias driven by patchy sampling, but the larger the scale of aggregation, the less precise the measurements will be (Richardson *et al.*, 2006). Sampling still varies regionally when considering the full time period, but the overall higher number of samples means this version of the dataset is likely to be less biased by sampling. In this investigation, the CPR field is not considered to provide an absolute representation of the zooplankton energy field, but instead it provides a viable representation of a variable and patchy energy field, as is observed empirically (e.g. van Deurs *et al.*, 2013).

Assuming a constant energy field across years, the post-smolt occupancy-weighted CPR energy varied between rivers of origin and years (Figures 5.4-5.5). The absolute magnitudes of each of the time series were not comparable against each other, as the occupancy matrix was normalised per river (i.e. this did not account for the fact that post-smolts from river 5 took less time to migrate to the exit region than those from river 12). As discussed above, these time series represent the potential variability in cumulative along-migration prey energy with typical year-to-year variations in migration paths.

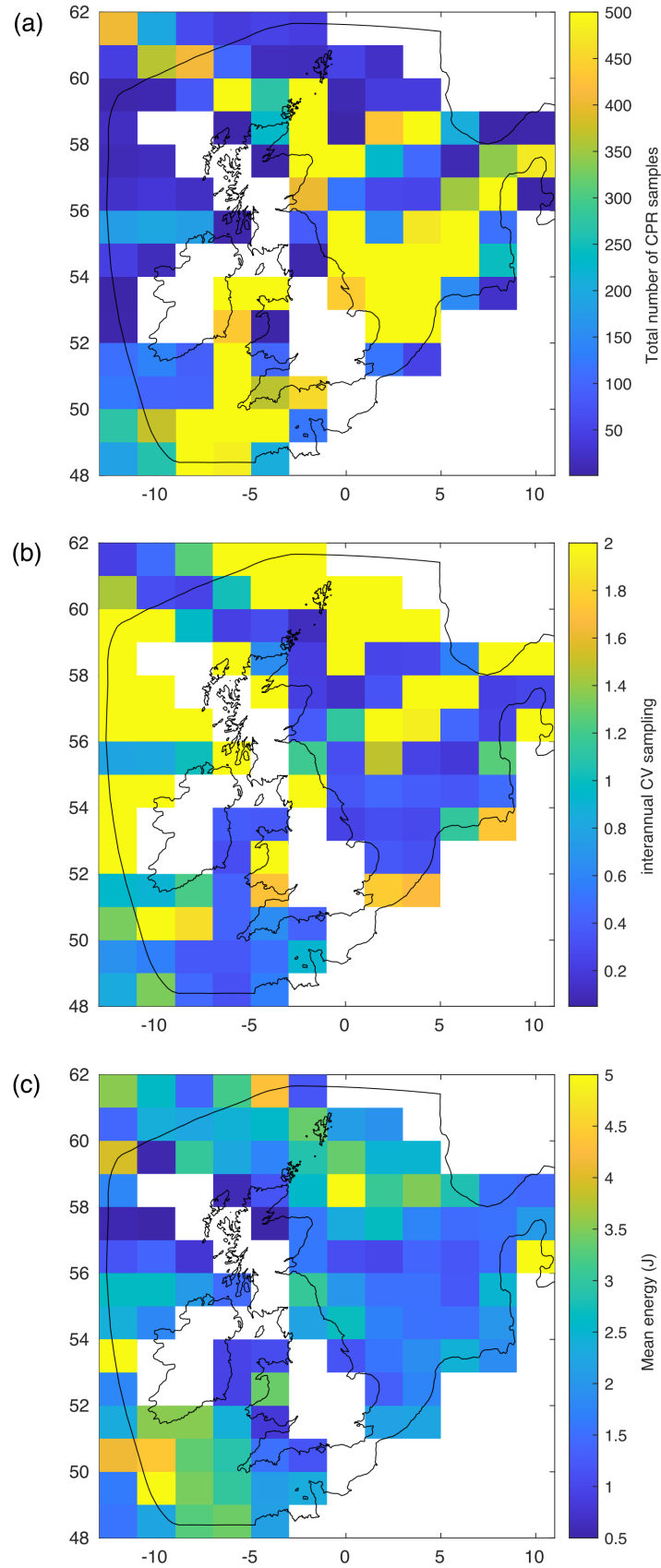


Figure 5.2: Between March and September 1993-2019: (a) the total number of Continuous Plankton Recorder (CPR) samples per box; (b) the coefficient of variation (CV) in the number of samples taken each year; (c) the mean energy per box.

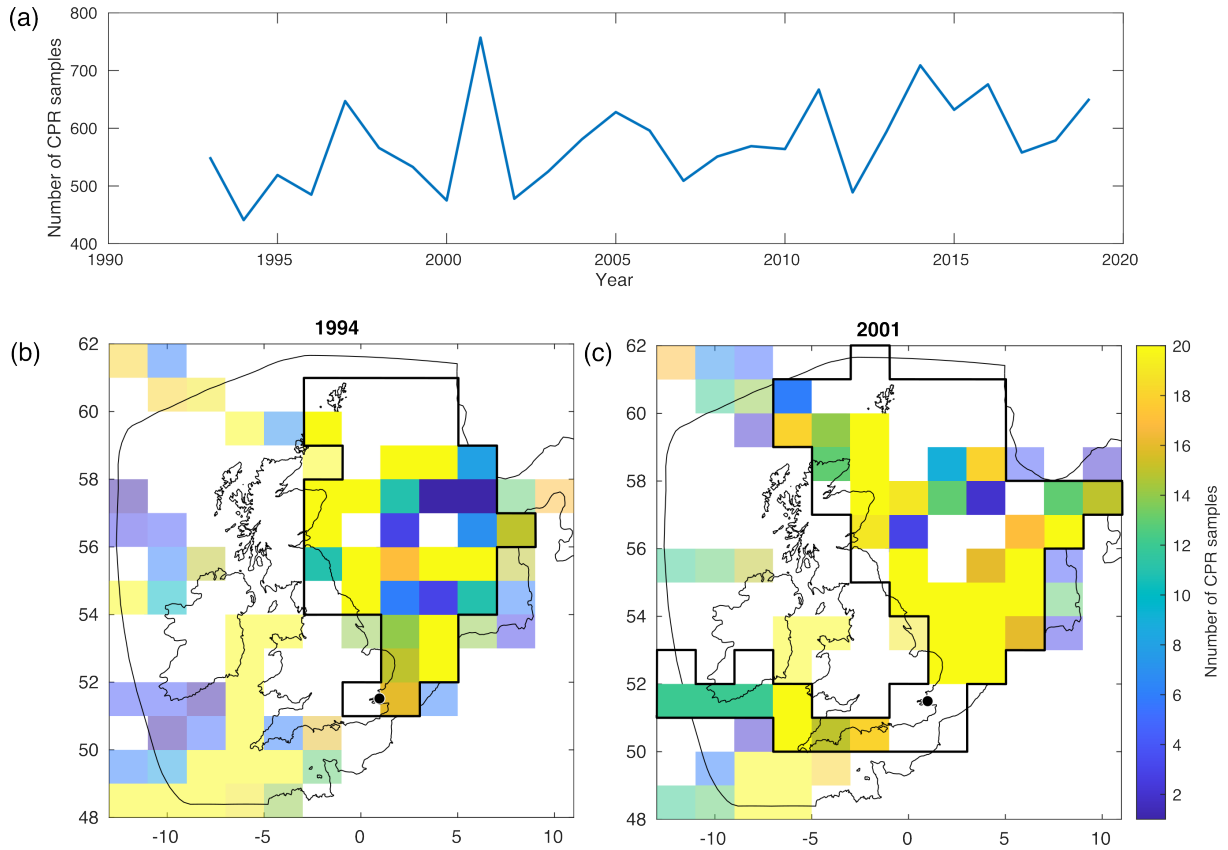


Figure 5.3: (a) Total CPR samples between March and September each year summed over the area spanned by the modelled migrations of river 12 (southern North Sea); (b) CPR samples per box March-September 1994; (c) CPR samples per box March-September 2001. Black outlines in (b) and (c) indicate the area spanned by the simulated migrations.

5.3.3 Post-smolt occupancy-weighted zooplankton energy: variation in migration behaviours

For river 12 in the southern North Sea, the migration behaviour generating the lowest total weighted energy used directional (compass) navigation cues primarily, with a smaller amount of currents and salinity ($w_c = 0.45, w_s = 0.32, w_d = 0.83$). The directional component for this behaviour was a bearing of 0° . Contrastingly, the migration behaviour generating the lowest total weighted energy used less directional movement (at a bearing of -45°) and more currents and salinity ($w_c = 0.79, w_s = 0.46, w_d = 0.41$). The simulated migrations for this behaviour were spread over a wider spatial region, with higher occupancy values overall (i.e. the total migration period was longer). Additionally, this behaviour resulted in a higher occupancy in the northwest North Sea (including south of Shetland), where there were locations of apparent high energy. These differences in occupancy resulted in a total summed occupancy-weighted energy of 0.5 J for the former behaviour and over 2 J for the latter, a larger range than was found between years, as explored in the previous section.

Looking across all 25 parameter sets for the River Thames, there was evidence of a positive relationship between the proportion of navigation dedicated to following ocean currents (w_c) and

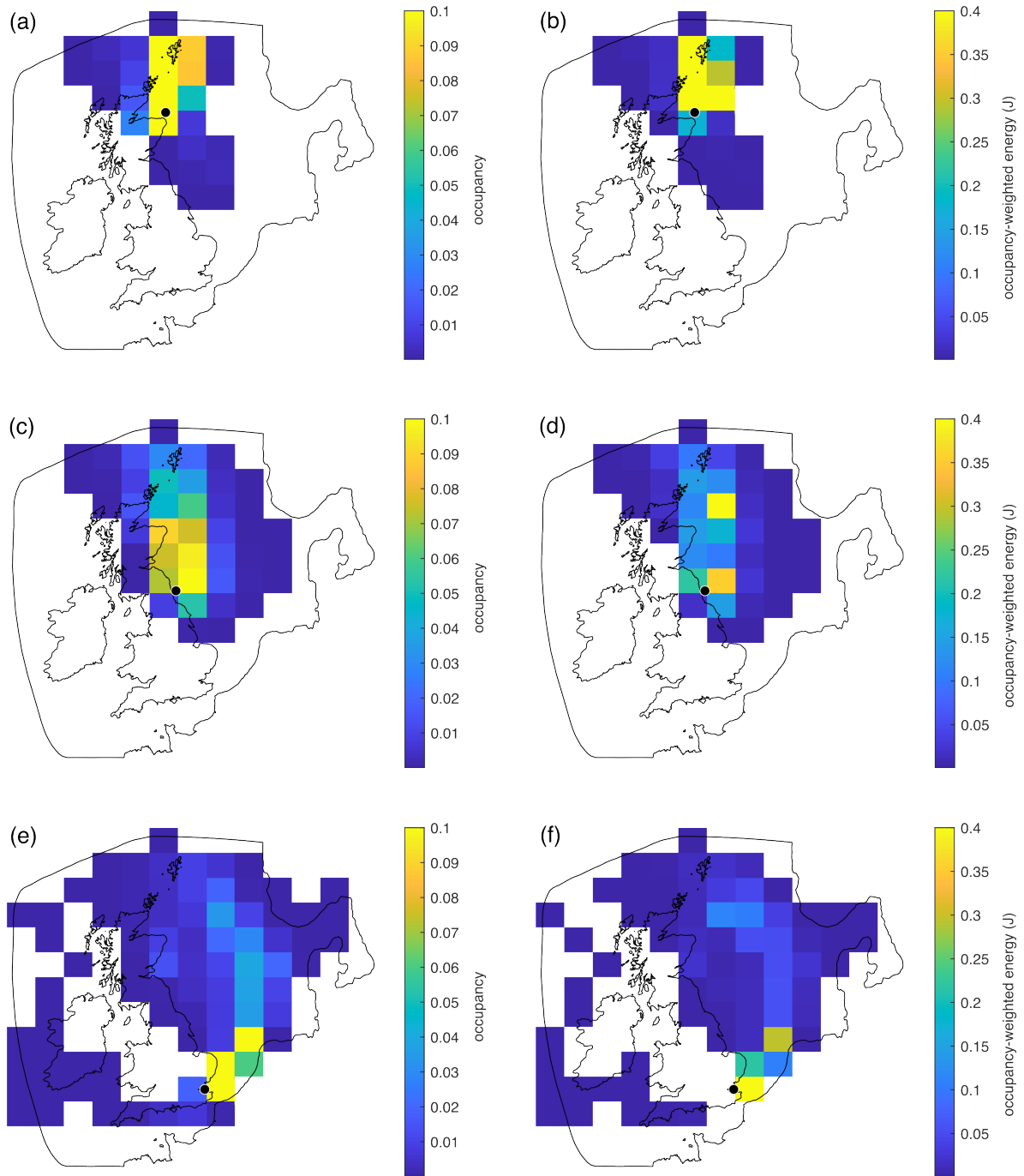


Figure 5.4: Simulated post-smolt occupancy (left) and occupancy-weighted zooplankton energy (right) between March and October from 1993 to 2019 for: (a)-(b) river 5 (Ugie) in the northern North Sea; (c)-(d) river 8 (Tyne) in the mid North Sea; (e)-(f) river 12 (Thames) in the southern North Sea.

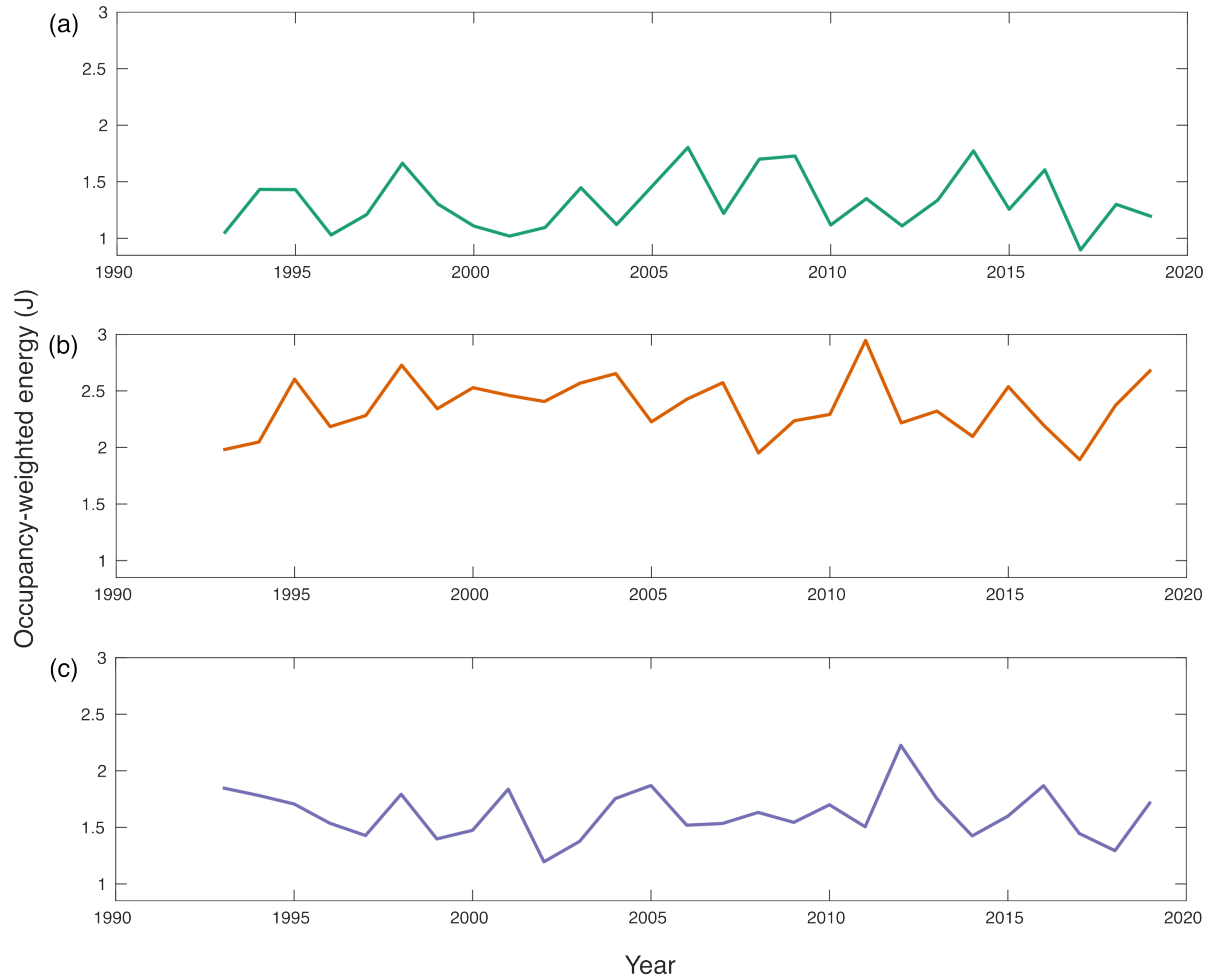


Figure 5.5: Simulated post-smolt occupancy weighted zooplankton energy between March-October from 1993 to 2019 for: (a) river 5 (Ugie) in the northern North Sea; (b) river 8 (Tyne) in the mid North Sea; (c) river 12 (Thames) in the southern North Sea.

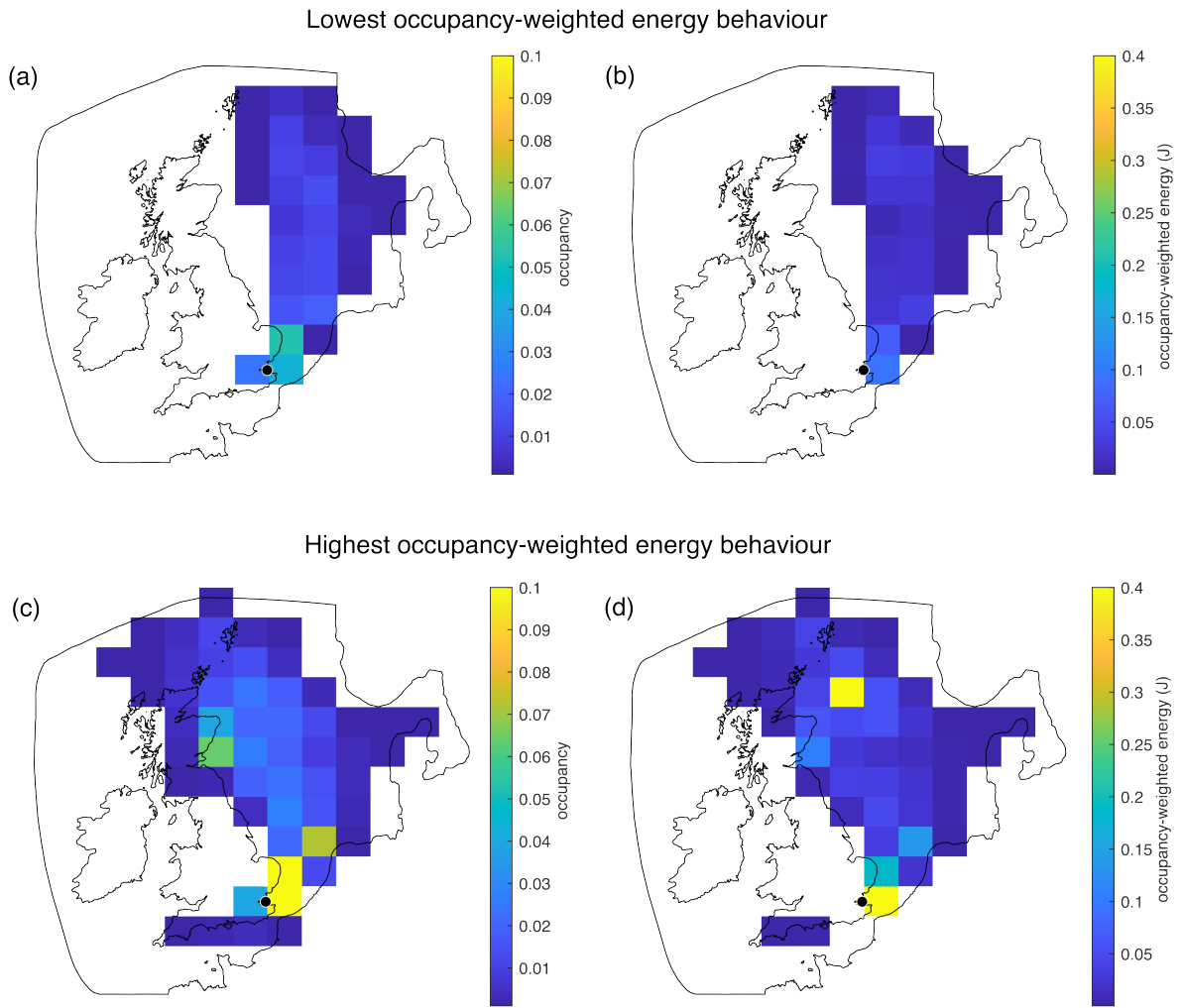


Figure 5.6: Simulated post-smolt occupancy and occupancy-weighted zooplankton energy between March and October 1993 to 2019 for: (a)-(b) the parameter set giving the lowest summed occupancy-weighted energy for river 12 (Thames) in the southern North Sea; (c)-(d) the parameter set with the highest summed occupancy-weighted energy for river 12 (Thames).

the summed occupancy-weighted energy, and a negative relationship between the proportion of directional movement (w_d) and the summed energy (Figure 5.7). This implies that a migration prioritising the use of currents over directed swimming may provide post-smolts with access to increased energy resources (in this assumed energy field).

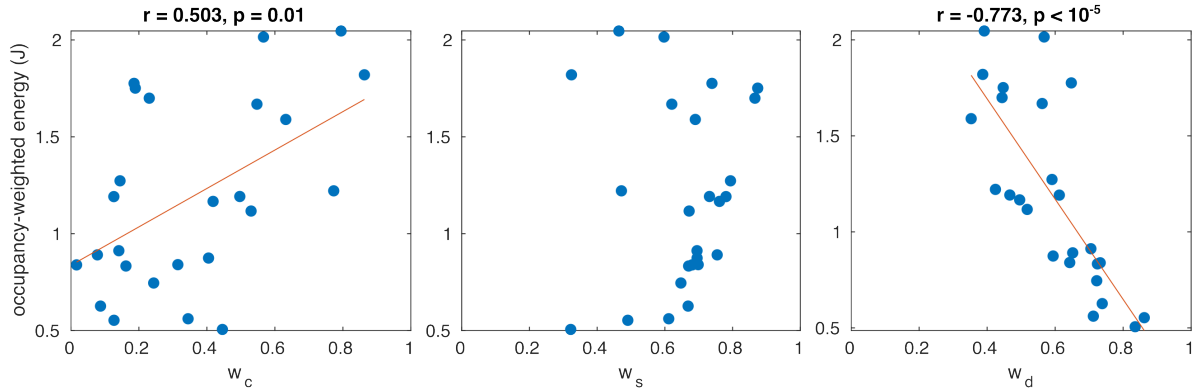


Figure 5.7: Summed occupancy-weighted energy for river 12 (Thames) against: (a) the weight of the current-following behaviour w_c ; (b) the weight of the salinity-gradient-following behaviour w_s ; (c) the weight of the directional swimming behaviour w_d .

5.4 Discussion

5.4.1 Variability in CPR sampling and potential implications (Q1)

With notable spatial and temporal variability in sampling along even the best-sampled migration route (River 12, Figure 5.3), it appears that the CPR sampling is too variable to be subsetting into individual years and boxes of this size. Relative consistency in sampling through space is of particular importance for creating occupancy-weighted measures of Z_E (Section 5.3.2) because areas of high occupancy are likely to generate sensitivity to sampling differences between years. Interannual consistency in sampling is hence important for considering interannual variability in encountered energy. Furthermore, sampling is lower and more variable across the migration paths of all of the other rivers (1-38, omitted for brevity). Figure 5.3 b-c shows that there are large unsampled areas in the northern North Sea in individual years, so estimates of occupancy-weighted energy for modelled post-smolts from rivers transiting through this region (particularly those that have a shorter total modelled migration distance, and hence do not travel through the relatively well sampled southern North Sea) will be influenced by these differences. Certain rarely-sampled areas within the SSM domain had particularly low and high energy values (such as the particularly high energy value southeast of Orkney). This may be a result of the sampling, as the standard error of the mean decreases with increasing sample size (i.e. the mean energy taken in a box with few samples will be less precise), suggesting that CPR sampling differences throughout the domain might influence our results. It would be challenging to disentangle the spatial-temporal differences in Z_E by that are driven by actual mechanistic differences from those that are driven those sampling differences. Therefore, in response to Q1, we conclude that the coverage of the CPR dataset is not sufficient to create a river- and year-specific measure of marine prey availability along modelled migration paths.

5.4.2 Interannual variability in post-smolt occupancy weighted zooplankton energy (Q2a)

There was interannual variability in post-smolt occupancy weighted zooplankton energy, despite our use of time-mean energy. Annual values were dependent on differences in modelled occupancy, especially in boxes with particularly low or high energy values. For the River Ugie (river 5) in the northern North Sea, the highest occupancy-weighted energy values were found around Orkney and Shetland, where the modelled post-smolts spent most of their time prior to exiting the SSM domain and entering the Norwegian Sea. The amount of time spent in this region varied between years (not displayed), leading to differences in summed occupancy-weighted energy between years (Figure 5.5 a). The weighted energy time series was sensitive to the isolated high-energy box southeast of Orkney and Shetland: years with a slightly higher occupancy in this box yielded much higher weighted energy values, even if occupancy was similar throughout the rest of the domain. The River Tyne in the mid North Sea (river 8) was also somewhat sensitive to this location of apparent high energy, as seen in Figure 5.4 d, where this box had the highest occupancy-weighted energy, despite having a lower occupancy than the surrounding area.

Total occupancy-weighted energy for the River Thames (river 12), in the southern North Sea, was highly dependent on its occupancy in the mid- to northern North Sea, where mean energy values were higher than in the southern North Sea. However, most of the migration time of simulated post-smolts from this river was spent in the south, near the river mouth. This meant that simulated smolts from this river and in this assumed energy field would have to migrate further to obtain greater energy availability. If this energy field represented the real prey availability for post-smolts, this might result in initially reduced growth from this river, and others in the southern North Sea, in comparison to rivers further north.

With interannual variation in occupancy-weighted energy observed even with a constant energy field between years, and occupancy-weighted energy being sensitive to patches of high energy, we conclude in response to Q2a that interannual variation in migration paths has the potential to significantly alter the energy fields encountered by post-smolts transiting a patchy energy landscape, providing evidence to support **H3**.

5.4.3 Inter-behavioural variability in post-smolt occupancy weighted zooplankton energy (Q2b)

Behaviours prioritising currents as a navigational cue (high w_c) and using less directional navigational cues (low w_d) were found to have higher occupancy weighted energy values. This is related to the overall speed of migrations: across the 25 behaviours, those that prioritised w_c over w_d had a slower migration time, generating a higher occupancy-weighted energy value by allowing increased foraging time in locations of high zooplankton energy (Figure 5.8). In response to Q2b, we conclude that modelled energy encounters vary greatly between migration behaviours, with slower migrations leading to greater encountered energy values, under the assumptions of our calculations of occupancy-weighted energy. This adds further evidence to support **H3**.

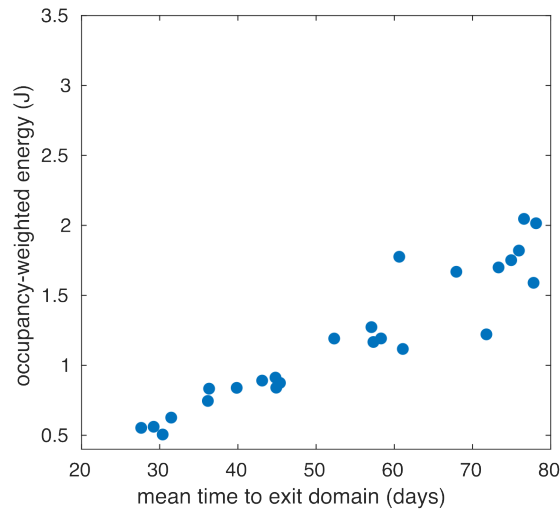


Figure 5.8: Mean time taken to exit the SSM domain against summed occupancy-weighted energy for the River Thames.

It should be noted that by summing zooplankton energy over the total time taken to migrate through this region, we assumed that migration time was a factor controlling foraging opportunities. The same assumption was made by Byron *et al.* (2014), who used a post-smolt movement model coupled with a bioenergetics model in the Gulf of Maine and showed that simulated fish that took longer to migrate had more feeding opportunities, and hence higher growth rates. Byron *et al.* (2014) also suggested that slower migrants risked not reaching their destination within an appropriate time frame, indicating a trade-off between short-term feeding opportunities and longer-term migration objectives.

Our results, and those of Byron *et al.* (2014), might be considered to imply that a slow initial migration is beneficial, as it enables an increased feeding potential during the first months at sea, where rapid growth of post-smolts is crucial to avoid predation. However, other unmodelled factors will affect the foraging opportunities of post-smolts. After exiting the area covered by the study domain here, post-smolts from rivers around the British Isles are known to migrate further north to feeding grounds in the central Norwegian Sea (Gilbey *et al.*, 2021). The potential trade-off, or prioritisation, between movement and foraging cannot be fully considered without acknowledging and comparing the prey availability and abundance across each section of the migration. If the feeding conditions in the central Norwegian Sea are far better than those immediately surrounding the British Isles (i.e. the study domain considered here), then a faster migration to the Norwegian Sea is likely to provide optimal feeding opportunities. A full comparison of post-smolt feeding opportunities would require integration of feeding conditions across the entire occupied space, from the river mouth to the Norwegian Sea.

Utne & Mousing (2025) simulated the migrations, feeding, and growth of post-smolts from Norwegian rivers (including some which enter into the North Sea). Prey fields - comprised of fish larvae, amphipods and mesozooplankton - were simulated using passive particle tracking. Modelled prey availability was found to be lower in the North Sea and southern Norwegian Sea

compared to the central and northern Norwegian Sea, meaning that simulated smolts from the more southern rivers experienced better growth rates if they migrated north as quickly as possible. These southern rivers were at a similar latitude to rivers 3-5 in the current study. If a similar interpretation as proposed by Utne & Mousing (2025) was applicable to these rivers, then post-smolts would experience better feeding and growth rates if they migrated quickly northward. Comparing energy values in the North Sea (and elsewhere in our study domain) with energy in the Norwegian Sea could shed light on whether the results of Utne & Mousing (2025) are applicable to the rivers considered here. Unfortunately the CPR data is extremely patchy, both spatially and temporally, in the southern Norwegian Sea, meaning that a comparison of zooplankton energy between our study domain and the Norwegian Sea is not currently possible.

Regardless of what might be considered an "optimal" migration strategy, it is unlikely that all post-smolts make the same migration choices. In reality, the decision to migrate in a fast and directed manner, or a slower, foraging-focused manner, is likely to be individual- or population-specific, and may also vary between years. Furthermore, an element of stochasticity is undoubtedly incorporated into this decision: if a post-smolt happens across a patch of high-energy feeding resources, it may be likely to spend additional time there (i.e. restricted area search, Dorfman *et al.*, 2022), though this decision may be further complicated in the presence of predators or competitors.

5.4.4 Applicability of CPR data on the spatial and temporal scales considered here (Q3)

This analysis provided an opportunity to evaluate the usefulness of a spatially specific measure of CPR zooplankton energy as a river-specific indicator of marine prey availability for Atlantic salmon post-smolts. It was concluded that a year-by-year analysis was not feasible on this relatively small spatial scale due to the sampling variability, both in abundance and distribution, between years, so a temporally explicit metric of river-specific zooplankton energy was not produced.

Considering a mean zooplankton energy field across all years (1993-2019) and focusing only on the variability created by varying modelled migration paths, either between years or between swimming behaviours, was likely to be less biased by the sampling due to the greater total sampling effort. Nevertheless, some boxes still only contained two samples across the entire 27-year period. Setting aside the sampling-associated bias and considering the energy field as a representation of a naturally patchy zooplankton field, this analysis revealed that the modelled zooplankton fields experienced by migrating post-smolts varied with both interannual and inter-behavioural changes in modelled migration paths, suggesting that both of these factors might significantly impact the prey fields encountered. With large differences in occupancy-weighted energy between swimming behaviours, we suggest that any future modelling studies examining prey encounters along post-smolt migration paths would benefit from modelling multiple swimming behaviours.

To consider trends and relationships between zooplankton energy and marine survival rates of salmon, a temporally explicit energy metric is required. By using larger spatial averaging

regions than considered here (and hence reducing the variability in sampling), Tyldesley *et al.* (2024) generated an annual measure of zooplankton energy availability. In response to Q3, we suggest that future work considering indicators of salmon marine survival maintains these larger averaging scales for CPR-derived zooplankton energy, to minimise bias and allow for an analysis of temporal trends and fluctuations.

Another possible future approach, which could allow for an investigation on smaller spatial scales, would be to use a modelled zooplankton field. Tyldesley *et al.* (2026) trained a machine learning model using CPR data to project future trends in zooplankton abundances. They used random forest machine learning, a non-parametric method using multiple “decision trees”, each trained on subsets of data. Using past oceanographic conditions as training data, Tyldesley *et al.* (2026) found the key explanatory variables of zooplankton abundance to include yearday, a proxy of sub-polar gyre strength, sea surface salinity, mixed layer depth, and sea surface temperature anomaly (the ranked variable importances varied between zooplankton taxa). The aim of Tyldesley *et al.* (2026) was to investigate long-term trends, and hence the model was not developed to depict interannual variability (time points were aggregated into decadal chunks). A similar approach could be developed in future to predict annual zooplankton abundances at locations with little or no CPR sampling, after training the model on well-sampled locations. The resulting modelled zooplankton abundances could be used to generate more robust post-smolt weighted zooplankton energy estimates.

However, we suggest that the use of larger averaging scales (e.g. Tyldesley *et al.*, 2024) could help to account for subtle differences between the density distributions of zooplankton and the fish larvae prey items of post-smolts. A key underlying assumption in the modelling was that zooplankton energy could act as a proxy for energy available to post-smolts, in line with the relationships between zooplankton energy summed over large regions and salmon marine survival rates found by Tyldesley *et al.* (2024). It was not possible to test whether these relationships held for specific occupancy-weighted zooplankton energy, as we did not create specific annual measures, as discussed above; it may be that the relationships break down when zooming in further than Tyldesley *et al.* (2024), possibly driven by changes in the distribution and abundance of fish larvae compared to zooplankton. These differences may be strengthened if there is some lag between the consumption of zooplankton by the fish larvae and the consumption of the larvae by a post-smolt, as both trophic levels will be advected by ocean currents, so the density distribution fields will not remain stationary. Maintaining larger averaging regions might encompass the advection of prey items prior to consumption by post-smolts.

Chapter 6

Using similarity in modelled migration densities to estimate marine survival rates

6.1 Introduction

Effective management for salmon conservation requires the provision and communication of relevant scientific knowledge, but directing science towards action can be challenging. The Likely Suspects Framework (LSF) concept, introduced by Crozier *et al.* (2018), aims to address gaps in scientific knowledge and communication for management of salmon populations. This examines the multiple drivers (i.e. likely suspects) behind mortality of salmon across the life-cycle and aims to evaluate their cumulative effects. Bull *et al.* (2022) expanded on this concept, discussing the scientific and communicative requirements for salmon management decisions. They emphasised that the existing large-scale stock assessments of salmon abundance (pre-fishery abundance, as calculated annually by the ICES Working Group on North Atlantic Salmon, e.g. ICES, 2024a) are currently too generalised to advise management actions, which typically occur on a population-specific scale. Furthermore, these stock assessments include limited consideration of the impact of environmental fluctuations on salmon stocks. The authors promote the adoption of a more ecosystem-based management approach for salmon, taking into account a range of abiotic (e.g. physical oceanographic conditions) and biotic (e.g. prey and predation) drivers that influence survival. With geographic and phenotypic differences between populations, the authors emphasise that no single set of drivers will explain salmon mortality for all, but a suite of larger-scale and smaller-scale drivers may be applicable, as suggested by Pardo *et al.* (2021).

One of the specific aims of the LSF is to develop management-focused decision support tools, which provide a bridge between scientific advances and management practice (Bull *et al.*, 2022). Managed by the Atlantic Salmon Trust, the LSF programme is producing a decision support tool (DST) that allows river managers and other stakeholders to visually explore the population-level effects of variation in processes affecting different stages of the lifecycle through an online

interface. The DST allows managers to test the impacts of different possible scenarios, such as reduced marine survival rates, and combinations of changes impacting various life stages simultaneously. Marine survival rates are parameterised within the model underlying the DST using marine return rates from several salmon index rivers (ICES, 2024a). A challenge arises from the fact that return rates are not counted for all salmon populations, and the DST is in development for a number of rivers with unknown return rates.

The marine return rates of salmon are measured in seven rivers around the British Isles, referred to as ‘indexed’ or ‘monitored’ salmon rivers (Figure 6.1). Common methods of counting outmigrating smolts and returning adults include trapping, netting, or resistivity counters, which use the electrical resistance differential between water and fish to identify fish (Dunkley & Shearer, 1982). Full or partial counts may be undertaken, with mark-recapture methods used to estimate the proportion of the population caught for the latter (Tyldesley *et al.*, 2024). Return rates are typically separated into sea age components: one-sea-winter (1SW) and multi-sea-winter (MSW) (ICES, 2024a).

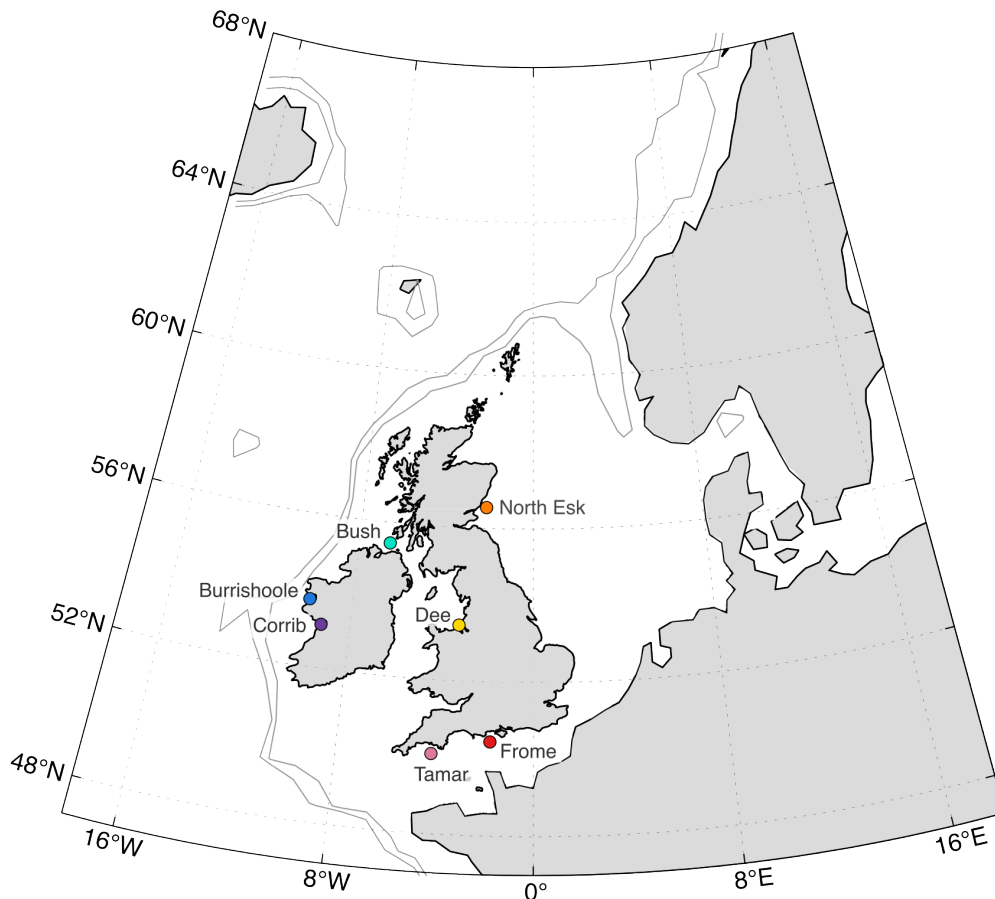


Figure 6.1: The seven monitored salmon rivers around the British Isles: North Esk, Frome, Tamar, Dee, Corrib, Burrishoole, Bush.

Marine return rates are often used as a proxy for marine survival rates. In this manner, they can be used to examine possible drivers of variation in marine survival. For example, Peyronnet *et al.* (2008) found a positive relationship between salmon return rates and the abundance of *Calanus*

finmarchicus across the northeast Atlantic (similar to the later study by Tyldesley *et al.*, 2024). Return rates have also been linked to individual and interannual variation in salmon traits: Armstrong *et al.* (2018) found a relationship between body condition of outmigrating smolts and their eventual marine return rates, while Jonsson *et al.* (2003) and Peyronnet *et al.* (2007) found a positive correlation between return rates and marine growth rates in the northeast Atlantic. These results collectively emphasise the importance of feeding opportunities and growth in both the freshwater and marine life stages. Many studies have considered relationships between return rates and sea surface temperature, with contrasting results. For example, Peyronnet *et al.* (2008) found a negative relationship between the SST at ocean entry of post-smolts and return rates (Ireland), while Hvidsten *et al.* (2009) found a positive correlation (Norway). These discrepancies indicate that SST is not a consistent driver of marine survival fluctuations, possibly suggesting that sea surface temperature is not a direct driver of survival, but rather a proxy for other factors, such as prey availability (Wilson *et al.*, 2021; Tyldesley *et al.*, 2025).

To address Q4, the simulated post-smolt migrations developed in this thesis were evaluated for use in developing spatially-interpolated estimates of marine survival, aiming to inform the DST and aid future exploration of management scenarios. For this analysis, it was assumed that post-smolts with overlapping marine migration routes were likely to experience similar foraging and predation conditions, and hence similar patterns in growth and survival. In the following, we calculated metrics of similarity and dissimilarity between modelled migrations from each combination of rivers and indexed rivers, and then evaluated whether similarity in modelled migrations could be used to estimate marine return rates for rivers where they are not known, informing the LSF DST.

6.2 Methods

A metric of similarity was calculated between the gridded occupancy matrices (1° latitude $\times$ 2° longitude) of pairs of rivers for individual years. The annual occupancy matrices were reshaped into vectors, and similarity was calculated as below, equivalent to $\cos(\theta)$ of the angle between occupancy vectors i and j in the year k . Only combinations of each of the 38 rivers with each of the 7 indexed rivers were considered (i.e. $i = 1 : 38$, $j = 1 : 7$, $k = 1 : 27$).

$$\text{similarity}(i, j, k) = \frac{\text{occupancy}_i \cdot \text{occupancy}_j}{\|\text{occupancy}_i\| \|\text{occupancy}_j\|}. \quad (6.1)$$

After calculating similarity for individual years k , the mean was taken across the 27-year period. A dissimilarity metric was also defined, combining the similarity metric between combinations of rivers and the relative contribution of each (i.e. the weight). This acts as a measure of dissimilarity to the seven indexed rivers together, rather than for each individual combination. If the similarity between the non-indexed rivers and the indexed rivers is used to infer marine survival rates (as discussed below), then dissimilarity in their migrations would propagate to uncertainty in the estimate. The following is similar to the dissimilarity metric of Rao (1982),

except here it is kept at the river-level, rather than a community-level metric (i.e. we do not sum over i):

$$dissimilarity(i) = \sum_j (1 - similarity(i, j)) \cdot w_{i,j} \quad (6.2)$$

$$w_{i,j} = \frac{similarity(i, j)}{\sum_j similarity(i, j)} \quad (6.3)$$

Additionally, $dissimilarity(i)$ is set to 0 when $similarity(i, j) = 1$ for some j (i.e. when a river is compared with itself).

To estimate return rates for non-indexed rivers, each row i of the similarity matrix was rescaled so that the row sum was 1. This row vector of ‘similarity weights’ was then used to take a weighted sum of the return rates time series, creating an estimate for each non-indexed river. Both annual and decadal estimates of return rates were generated. The uncertainty generated by dissimilarity to the indexed rivers was represented by a confidence interval, defined as the dissimilarity of a river i multiplied by its return rate estimate.

To evaluate the efficacy of this method, the return rates for the Burrishoole system (a monitored salmon river, Figure 6.1) were omitted and estimated using this method. The resulting estimates, which were based on the weighted sum of the other rivers’ return rates (annual and decadal), were then compared with the actual Burrishoole return rates. The Burrishoole was selected for this test to represent non-indexed rivers that are close to indexed rivers (here, the Corrib and the Bush), which is the scenario in which we anticipate this method would be most applicable.

6.3 Results

6.3.1 Similarity and dissimilarity

The similarity matrix and the dissimilarity vector comparing each river to the indexed rivers are shown in Figure 6.2. Certain rivers have high dissimilarity (>0.8) to all of the indexed rivers (rivers 1-5, 12-13, and 28), meaning that any estimates of their marine survival rates based on the monitored rivers are likely to be highly uncertain.

To summarise the similarity matrix, the ‘key’ indexed rivers for each of the non-indexed rivers were determined by identifying the minimum quantity of the weights $w_{i,j}$ needed to sum to > 0.7 , i.e. which of the indexed rivers explained 70% of the relative similarity for each of the non-indexed rivers. The regional patterns of similarity are summarised in Figure 6.3.

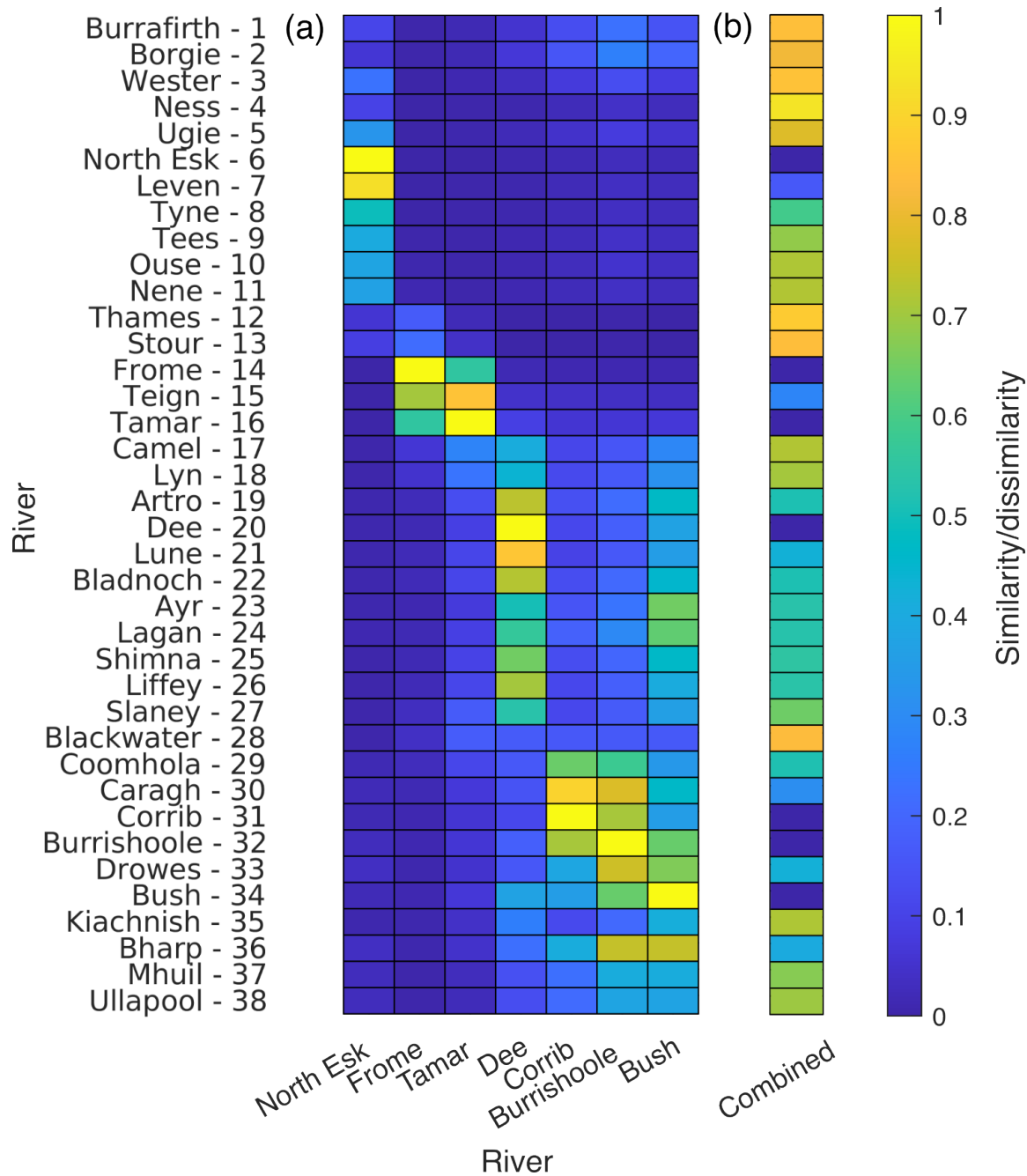


Figure 6.2: (a) Mean annual similarity between each combination of the 38 rivers and the 7 indexed rivers, (b) dissimilarity for each of the 38 rivers with the 7 indexed rivers combined.

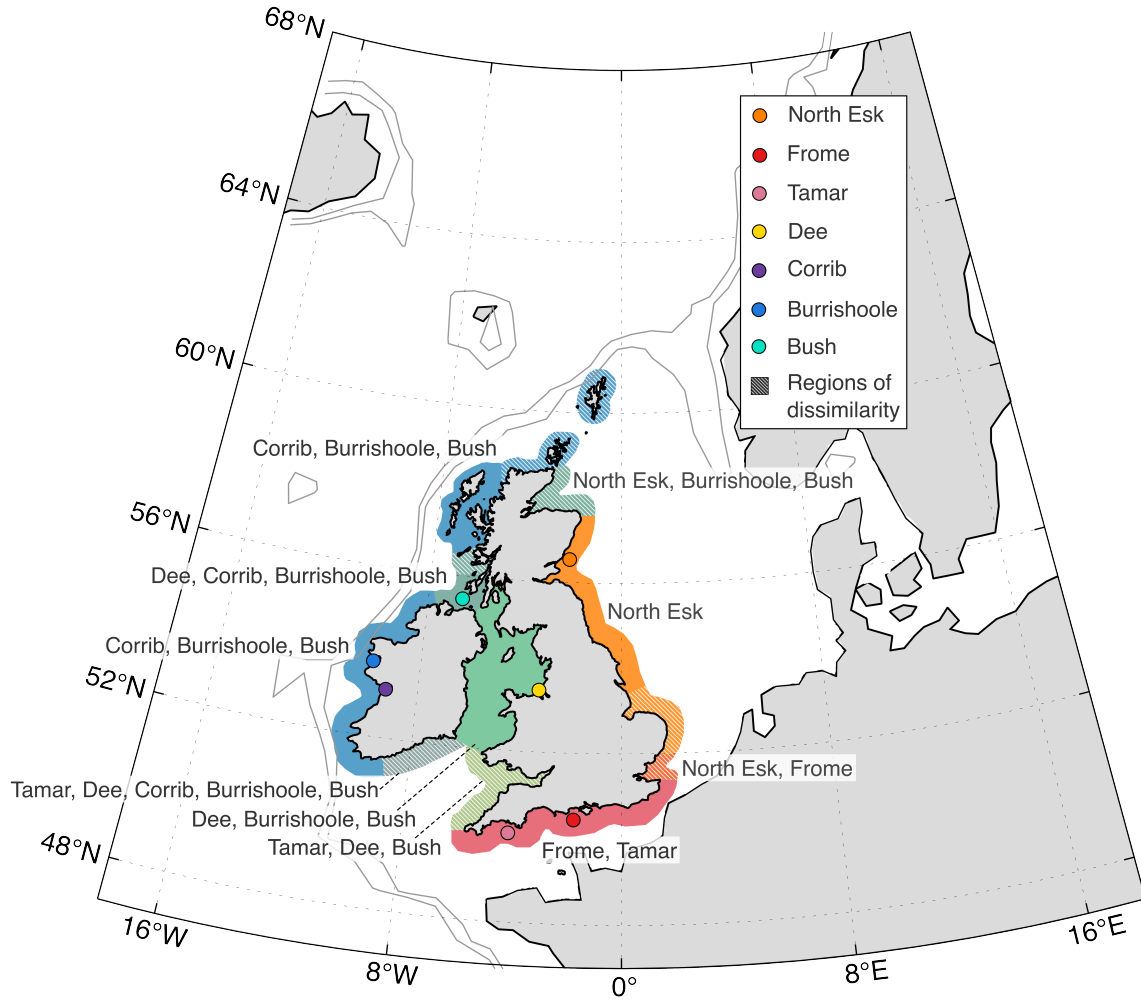


Figure 6.3: The most similar indexed rivers to each region, based on the similarity matrix for the modelled rivers and generalised to cover the areas between the modelled rivers. Areas with the highest dissimilarities to all of the indexed rivers are highlighted with thin dashed white lines.

6.3.2 Estimating unknown marine return rates

Marine return rates were estimated, and an example is displayed for the river Bharp in the Outer Hebrides in Scotland (Figure 6.4). Estimated returns initially increased from 1980 to 1987 and then declined, with some interannual fluctuations. Estimated return rates for the Burrishoole were generally lower than the real return rates, though the interannual trend was similar (Figure 6.5).

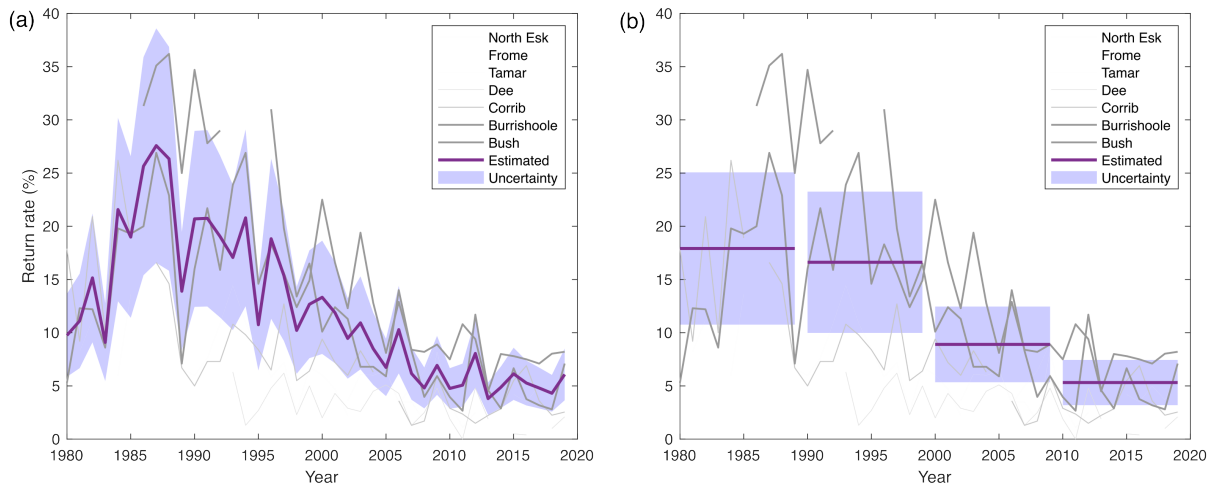


Figure 6.4: Estimated return rates, using the similarity-weighted sum, for the river Bharp (number 36), in the Outer Hebrides in Scotland: (a) year-by-year estimates; (b) decadal estimates. Each of the return rates time series is displayed (grey lines), with the line thicknesses weighted by their proportional contribution to the estimate, such that the more ‘important’ time series stand out clearly.

6.4 Discussion

In the development of this method, it was assumed that similarity in the spatial footprints of simulated migrations (i.e. where the post-smolts go and how long they spend there) drives similarity in the feeding conditions and predator encounters experienced. This assumption requires that there is some stability in prey and predator fields. While some spatial and temporal patchiness is expected in these fields (e.g. van Deurs *et al.*, 2013), the distribution and density of prey and predators will be influenced by both larger- and smaller-scale processes, with the larger-scale mechanisms generating slightly more stability over time and space. For example, physical bathymetric features drive large-scale patterns in prey availability: at the continental shelf-edge, upwelling of cool nutrient-rich water increases productivity and feeding opportunities for planktivorous fish (Simpson & Sharples, 2012). Another large-scale process that influences the North Atlantic is the expansion and contraction of the subpolar gyre, occurring over interannual timescales, which drives changes across trophic levels (Hátún *et al.*, 2009).

The simulated migrations in this work represented the first 1-3 months spent at sea. Deriving estimates of marine survival from the similarity in these simulated migrations assumes that this time period is key in driving trends in overall marine survival rates; this agrees with several studies suggesting that marine mortality is highest in the first months at sea (e.g. Hansen & Quinn, 1998; Klemetsen *et al.*, 2003; Thorstad *et al.*, 2012).

The other layer of assumptions in this work surrounds the application of return rates from monitored rivers to other rivers. Pardo *et al.* (2021) and Tyldesley *et al.* (2024) compared trends and fluctuations in marine return rates among nearby salmon populations (in eastern Canada and southern Europe respectively), both finding some degree of synchronicity. Neither considered

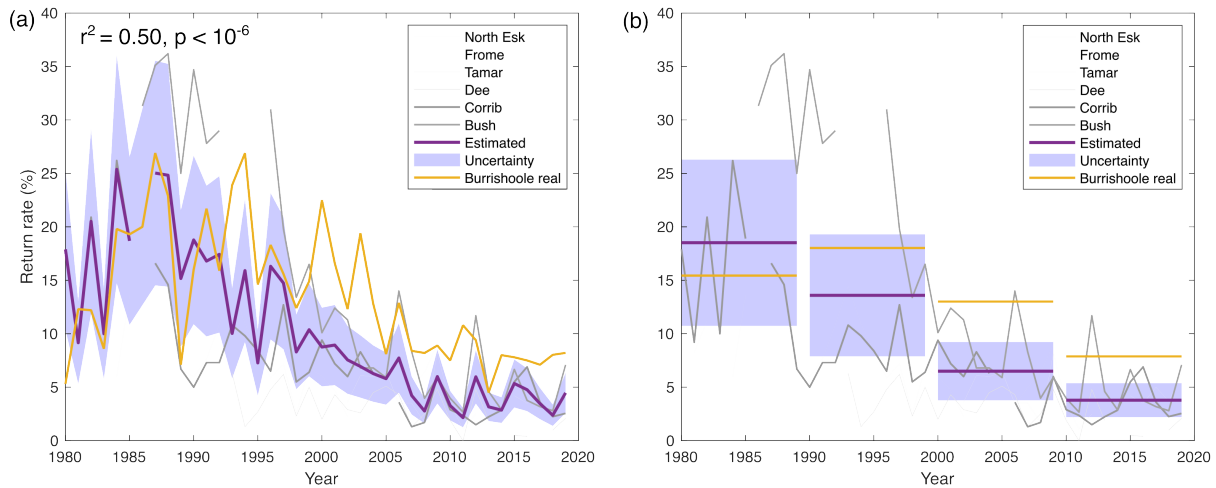


Figure 6.5: Estimated return rates for the Burrishoole, calculated using the other indexed rivers are shown in (a) year-by-year and (b) decadal formats. The yellow line in both indicates the real Burrishoole return rates. Correlation coefficients (r^2 and p) in (a) indicate the linear relationship between the estimated and real Burrishoole return rates. Each of the return rates time series is displayed (grey lines), with the line thicknesses weighted by their proportional contribution to the estimate, such that the more ‘important’ time series stand out clearly.

similarities or differences in the magnitudes of return rates. There are considerable differences in the mean magnitude of returns between the monitored rivers considered here (Figure 6.6). Note that the return rates are available over different time periods for each river, and the different periods of averaging per river in Figure 6.6 could have the potential to alter the results. For example, those rivers with return rates available pre-1990 might display higher means, as return rates were typically higher earlier in the time series. However, the mean return rates from 2002 onwards (when the Tamar and Frome time series began) displayed a similar between-river pattern, but with lower mean return rates for all of the rivers. On the other hand, the North Esk return rates ended in 2009, so the mean return rate might plausibly be lower than 7.5% had the time series extended to the present day.

Regardless, there are large differences in the mean magnitude of return rates between the monitored rivers. One striking comparison is the Dee compared to the Bush (3.0% versus 14.4%); these rivers are a similar distance apart as the Bush and the Burrishoole, which exhibit much more similar mean return rates. Many factors will drive differences in return rates between rivers, beginning with in-river differences that will impact marine survival, such as smolt size (McCormick *et al.*, 2009) and local predator populations. Furthermore, this method used 1SW return rates, which are influenced by maturation rates in addition to marine survival. Maturation itself is both environmentally- and genetically-driven (Thorpe *et al.*, 1998), with the latter factor also possibly driving between-river differences in return rates.

Finally, differences in sampling and counting methods are likely to explain some of the differences in mean return rates between rivers. The methods used to capture and count smolts and returning adults vary between rivers (Tyldesley *et al.*, 2024). The locations of counts (i.e. distance from

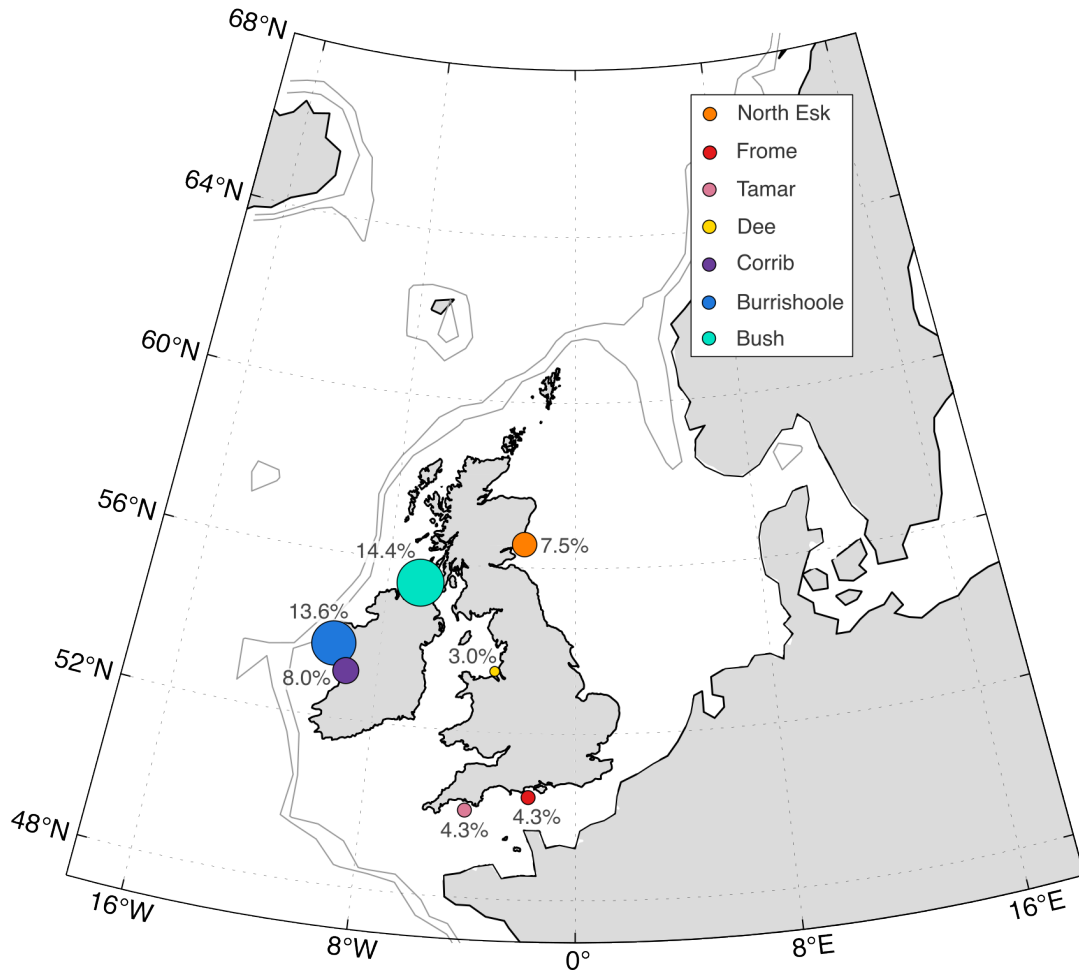


Figure 6.6: The mean 1SW return rate for each monitored salmon river across the whole period when return rates were measured: North Esk (1981-2009, with a few years unavailable inbetween); Frome (2002-2019); Tamar (2002-2019); Dee (1993-2019); Corrib (1980-2019); Burrishoole (1980-2019); Bush (1986-2019).

the sea) vary between rivers, and they are not all precisely at the river mouth. Flávio *et al.* (2020) presented the distances between smolt counting sites and the head of tide in each of the monitored rivers; these ranged between 0.1 km for the Burrishoole and the Corrib to 40 km for the Dee. High mortality rates have been found in the lower stretches of many rivers (e.g. Koed *et al.*, 2006; Barry *et al.*, 2024), and Flávio *et al.* (2020) found the loss rates of smolts in the Burrishoole after they were counted (3.5 km from sea) to range between 32% and 68%. The authors suggest that this late stage in-river mortality might be confounded with the marine survival rates. It is plausible that the differences in the relative locations of counting sites between the monitored rivers considered here may drive some of the quantitative differences in return rates.

It should also be noted that coastal fisheries are accounted for differently in the return rates for different rivers. For the Burrishoole, Bush, Dee, Corrib, and North Esk, returns are estimated prior to encounters with any fisheries (Tyldesley *et al.*, 2024). This is not true for the Tamar and the Frome; however, the homewater fisheries for these rivers ended in 2004 (Tyldesley *et al.*,

2024), shortly after the time series began in 2002, so these time series will largely be unaffected by the fishery. Therefore, it is not anticipated that differences in coastal fisheries between rivers will have driven differences in return rates between rivers.

Most of the North Sea modelled salmon rivers were only similar to the North Esk (Figure 6.3). Estimates of their return rates would therefore be entirely dependent on the North Esk return rate time series, which ended in 2009. This presents a considerable limitation in the application of this method to North Sea rivers. We note that Friedland *et al.* (2000) found that return rates from the North Esk and the Figgjo river in southern Norway were “highly correlated”, but the Figgjo return rates are not available through the ICES WGNAS reports (e.g. ICES, 2024a), as for the other monitored rivers, and it is not clear if the time series extends to the present day. If these data are available and can be obtained, the strength of the relationship between the Figgjo and the North Esk return rates might be investigated (over the time period in which they were both sampled); if a strong relationship were to be found, the Figgjo return rates could be used as a predictor of the North Esk return rates, and hence to estimate marine survival for the other North Sea rivers.

In the estimated return rates for the Bharp, there was an initial rise in estimated returns from 1980 to approximately 1987. This may have been related to the availability of data for the start of the period, as the Bush time series only started in 1986. The Burrishoole return rates were consistently underestimated, likely due to the magnitude differences of the rivers used to predict its returns (Figure 6.6), but the interannual pattern of the estimated return rates was similar to the real Burrishoole return rates ($r^2=0.50$, $p<10^{-6}$). Based on this, and the factors discussed here that may drive differences in the absolute values of return rates between rivers, we conclude that this method is better suited to predicting trends than absolute values in return rates. However, decision-making must make use of the best available information, even if it is imperfect. In response to Q4, we conclude that, as long as the caveats relating to our method and the data sources are considered, this approach considering similarity in modelled migrations can be used to estimate return rates in the DST. This will help develop a considered approach to the population dynamics of non-index river salmon populations in the DST, informing appropriate management actions.

Overall conclusion and future outlook

In the first two chapters of this thesis, a set of models was developed to describe the migration of Atlantic salmon post-smolts in their first months at sea. Interannual variability in simulated migrations from Scottish, Northern Irish and Irish rivers was quantified and compared with variability in oceanographic conditions. Then, the modelling approach was updated with additional swimming behaviours, and optimal portfolios of behaviours were selected for 38 rivers around the British Isles. This revealed the value of each salmon population having a diversity of migratory swimming behaviours to dampen interannual fluctuations in migration success, on both river-specific and stock-wide scales. The environmental and oceanographic drivers of migration variability were not further explored in Chapter 3, after the model was developed for all of the rivers. Further work could identify regions over which oceanographic conditions were correlated with migration metrics, similar to the shelf and shelf-edge regions in Chapter 2. This could improve understanding of the oceanographic influence on post-smolt migrations, which might be particularly relevant in the face of ongoing global climate change. For example, identifying relationships between ocean conditions in the North Sea and modelled migrations from relevant rivers could allow for a prediction of how migration patterns might change, or salmon might have to adapt, in the event of projected declines in circulation and salinity in the North Sea (Holt *et al.*, 2018). Further, the differing responses of different migration behaviours tested in Chapter 3 to oceanographic variability could be considered, further clarifying why a portfolio of migration behaviours is beneficial (and which strategies work well under which conditions).

The model developed in Chapter 3 produced modelled densities of post-smolts that were spatially and temporally consistent with empirical data on post-smolt locations on the west side of the British Isles, but there were some spatial differences between modelled and observed post-smolt distributions in specific locations in the North Sea. Any future developments of this model could use the correspondence with the available data in addition to the Sharpe scores to select migration behaviours (i.e. multi-objective optimisation). For example, f-scores, which can measure the predictive ability of a model in relation to presence-absence data (e.g. Jacobson *et al.*, 2013; Knight *et al.*, 2017), could be used to quantify the precision of the model in reference to the epipelagic trawls data (Newton *et al.*, 2026).

The start points in all of the post-smolt migration models were set to 30 km away from the coastline, as the larger-scale modelled movement cues were not applicable to fine-scale movements near the coastline. Animals sense and respond to the environment on multiple scales,

meaning movement processes occur over different scales (Benhamou, 2014). Modelling of movement processes, therefore, requires a consideration of scales, with different models required for different scales of movement (e.g. Johnson *et al.*, 2002; Yackulic *et al.*, 2011). Developing new models to simulate the first 30 km of the post-smolt marine migration, including transit of sea lochs and nearshore coastal areas, could help inform analyses of the exposure of post-smolts to potential stressors such as aquaculture sites or nearshore marine energy structures. A similar model structure as those developed in this thesis might be used, with oceanographic variables sensed over smaller scales (such as the detection area of surface salinity ϵ introduced in Chapter 2), and perhaps the inclusion of other movement mechanisms (such as an active response to tidal variability). There is a wealth of recent, relevant telemetry data available in nearshore environments around the British Isles (e.g. Newton *et al.*, 2021; Lilly *et al.*, 2022, 2023; Barry *et al.*, 2024; Rodger *et al.*, 2025), which could be used to parameterise small-scale movement models. Using these telemetry data, the model development might take an approach like Burke *et al.* (2016b), which parameterised an individual-based model of Chinook salmon to reproduce observed at-sea locations and timings.

A similar but opposite expansion of the model could consider the movement of post-smolts further north into the Norwegian Sea. This would require a different ocean model with a larger domain. If the selected ocean model was on a rectangular grid, rather than an FVCOM grid, then a different particle tracking software (other than FISCAM) would be required, such as Parcels (Delandmeter & Van Sebille, 2019). This modelling approach might also consider the return migration of adult salmon. Throughout most of our study region, there was limited empirical data with which to compare the modelled migrations. With future advances in at-sea data collection, the simulated migrations could be compared with more data, and the model could be adapted if desired.

In Chapter 4 of this thesis, the exposure of migrating post-smolts to pelagic fisheries was quantified, providing a proxy for bycatch risk within spatio-temporal migration regions. We suggested that environmental DNA (eDNA) collection from pelagic trawls or landings port observations of catches for human consumption (which are already individually inspected) should be used in future to quantify bycatch rates of post-smolts. Ideally, these would provide estimates of sensitivity (i.e. the bycatch rates of salmon per tonne of landings), which could be combined with our estimates of exposure to complete a full risk analysis (e.g. Samhoury & Levin, 2012). One of the limitations of the exposure analysis was that it relied on landings data, whereas fishing effort data would have provided a better measure of bycatch risk (a high number of fishing hours that caught a small mass of the target species could still have caught non-target bycatch species). Any future data calls for fisheries-dependent data to further this analysis might consider requesting fishing effort data, rather than landings. It is also possible that the fisheries landings data could be combined with gridded modelled migration densities to create occupancy-weighted exposure estimates. However, this would reduce the area of focus of the bycatch analysis, as the modelled migrations do not cover the full area considered in Chapter 4, and reducing the spatial scale of the exposure quantification might highlight any inconsistencies in the data (such as the lack of Russian landings). Alternatively, future expansion of the post-smolt movement model could

allow for occupancy-weighted exposure estimates across the wider region.

In Chapter 5, an occupancy-weighted measure of zooplankton energy was created. With low and variable CPR sampling across most of the study domain, we concluded that the larger-scale previous analysis of Tyldesley *et al.* (2024) was less likely to be impacted by sampling bias, and hence was a more robust analysis. The challenges caused by the patchy sampling could be mitigated by using a smooth modelled zooplankton field (e.g. Tyldesley *et al.*, 2026). Yet, given the trophic level difference between the considered energy field and the actual prey field of post-smolts, we also considered that subtle differences in the density distributions of these fields might be minimised by considering the zooplankton energy over larger spatial regions. Perhaps a fine-scale zooplankton field would not benefit this analysis. However, if there existed a zooplankton dataset or model that included sufficient spatial and temporal coverage throughout the SSM domain and into the Norwegian Sea, this could be combined with an expansion of the movement model (as discussed above) to provide an estimate of prey energy availability throughout the post-smolt life stage. This would allow for further clarification of the ‘prioritising movement versus foraging’ concept discussed in 5. The potential future applications of this model, along with the required developments of the model, are summarised in Table 6.1.

Future research theme	Expansion of model and data requirements
Interactions between wild salmon post-smolts and farmed salmon aquaculture sites.	Fine-scale movement model simulating the first section (~30 km) of the coastal migration, developed using relevant telemetry data.
Bycatch risk of post-smolts weighted by occupancy.	Expansion of the model into the Norwegian Sea, requiring forcing by a different physical ocean model, and likely a different particle tracking model.
Along-migration feeding opportunities for the remainder of the post-smolt life stage.	As above. Additionally, a different zooplankton energy dataset would be required, given the paucity of CPR data in the southern Norwegian Sea, or (best-case scenario) a spatially and temporally resolved dataset on larval planktivorous fish.

Table 6.1: A summary of potential future research opportunities based on expanding the post-smolt movement model developed in this thesis.

In Chapter 6, the similarities between modelled migrations from each of the 38 study rivers and the 7 monitored salmon rivers around the British Isles were evaluated, and the application of this method to estimate unknown marine survival rates in the Likely Suspects Framework Decision Support Tool was discussed. This method provides new information to aid decision-making, but uncertainties are associated with the return rate estimation due to the differences between rivers; some of which will be driven by population-specific factors, and some of which might be an artefact of the different sampling regimes between rivers. Given the uncertainties, this method is better suited to predicting trends, rather than absolute values, of return rates. Building upon the theme of similarity, future work focused on identifying the at-sea factors that drive salmon

mortality could consider similarity in these factors by dividing them into ‘local’ and ‘global’ drivers and considering the relative influence of both on return rates (as per Pardo *et al.*, 2021).

Much of the work in this thesis could be placed within a larger framework that combines multiple global and local drivers to explain salmon marine mortality. Sobocinski *et al.* (2021) provided an example of this with their holistic ecosystem approach to explaining marine survival rates of Pacific salmon (coho and Chinook). They developed hypotheses relating survival rates to predation, food availability, water quality, and anthropogenic factors (including human population size and salmon fishing pressure). Specific indicators were developed to test each hypothesis (such as seal abundance for predation and herring biomass for food abundance), and generalised additive models (GAMs) were used to identify relationships between the indicators and survival rates. A similar hypothesis-testing framework could be used to understand variability in Atlantic salmon marine survival rates. From this thesis, the interannually varying metrics of migratory “success” (domain exit rates) and pelagic fisheries exposure rates could act as indicators in the testing process, along with the prey energy availability metrics of Tyldesley *et al.* (2024). Any other potential drivers that are uncovered in future research could also be included, such as variables describing predation risk, encounters with anthropogenic stressors (including salmon farms and marine energy structures), or the return migratory success rates of adult salmon. Each piece of work contributing to the overall understanding of salmon migration and survival at sea could gradually expand the framework, incrementally improving understanding of salmon marine survival rates and encouraging ongoing management action based on the best available scientific advice.

Appendices

Appendix A

Modelled post-smolt migrations from Scottish, Northern Irish and Irish rivers

A.1 Model assumptions

Model assumption	Empirical evidence
Post-smolts can detect and follow currents, salinity, and magnetic cues.	Quinn (1980); Taylor (1986); Moore <i>et al.</i> (1990); Lacroix & McCurdy (1996); Døving & Stabell (2003); Lacroix <i>et al.</i> (2004); Hedger <i>et al.</i> (2008); Martin <i>et al.</i> (2009); Dadswell <i>et al.</i> (2010); Putman <i>et al.</i> (2014); Minkoff <i>et al.</i> (2020); Main (2021); Lilly <i>et al.</i> (2022).
Post-smolt swimming speed is increased with a stronger salinity gradient (i.e. the magnitude of $\mathbf{g}_s$ is not constant).	Hedger <i>et al.</i> (2008).
Magnetic cues are not used for the entire post-smolt migration.	None available; we hypothesise that currents and salinity might be preferable cues for post-smolts as they are related to different water masses and perhaps hence prey fields.
Post-smolts know when they reach a depth of 200m.	None available; we hypothesise that changes in chemical or optical cues could signal this.
Post-smolts can cover a radius of 10km in each 12-hour timestep, sensing salinity conditions, and then choose which direction to continue in.	None available; we use the suggestion of Dolmaire (2022) to determine this radius.
Smolt migration timing is determined by latitude.	Hvidsten <i>et al.</i> (1998); Otero <i>et al.</i> (2014); Vollset <i>et al.</i> (2021).
Post-smolts remain at a depth of 5m.	Renkawitz <i>et al.</i> (2012); Newton <i>et al.</i> (2021).
Post-smolts should exit our domain of modelling within 100 days of entering the sea.	Gilbey <i>et al.</i> (2021).

Table A.1: Assumptions used in the development of the Atlantic salmon post-smolt (*Salmo salar*) migration model.

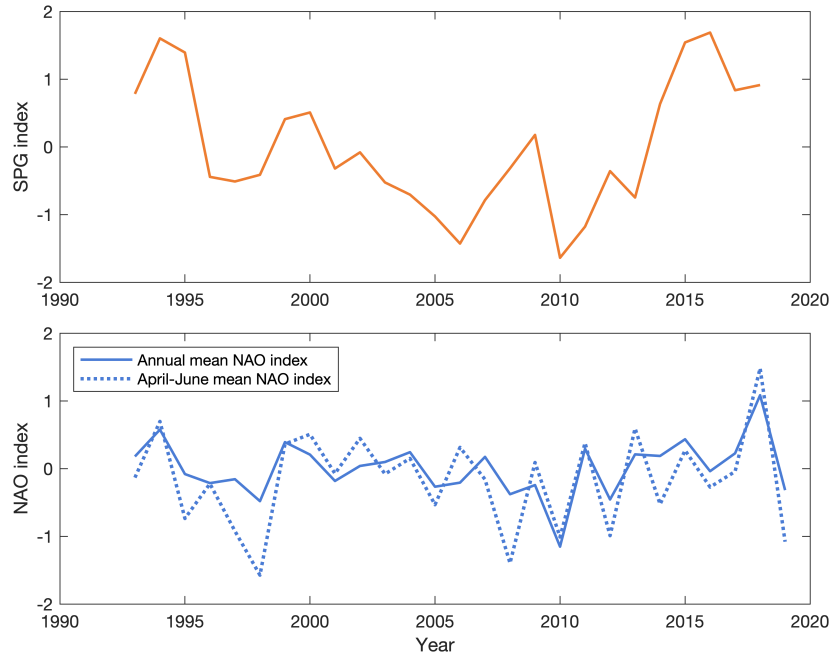


Figure A.1: Subpolar gyre (SPG) index annual mean from 1993-2018. North Atlantic Oscillation (NAO) index annual mean and April-June mean from 1993-2019.

A.2 Subpolar gyre and North Atlantic Oscillation indices

A.3 Annual particle concentrations 1993-2019

A.3. ANNUAL PARTICLE CONCENTRATIONS 1993-2019

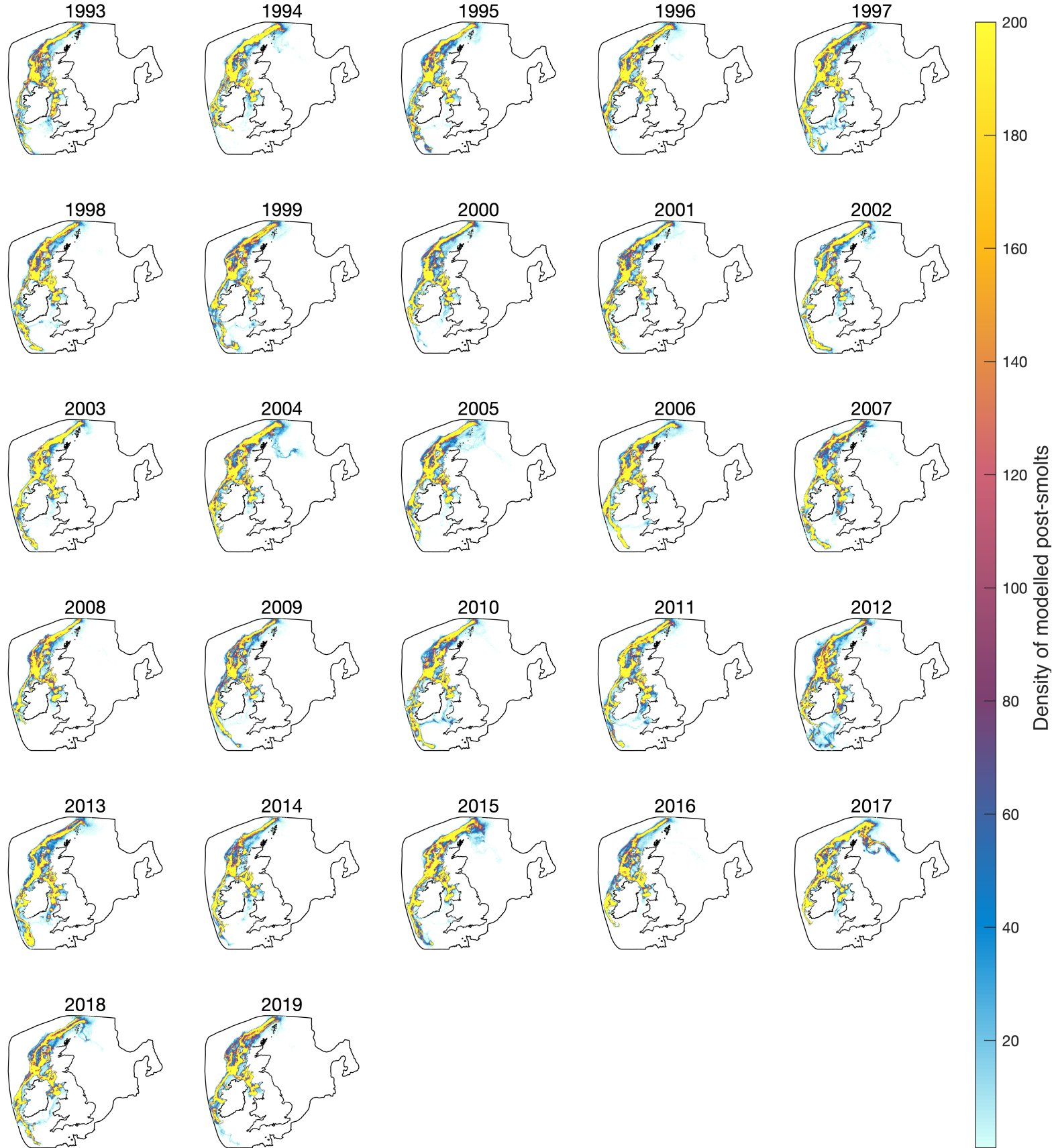


Figure A.2: Density of modelled Atlantic salmon (*Salmo salar*) post-smolts (total number per 30 km² bin) for all timesteps of modelled migrations each year (1993-2019).

Appendix B

Migration behaviour portfolio analysis

B.1 Ranges of optimal portfolio sizes

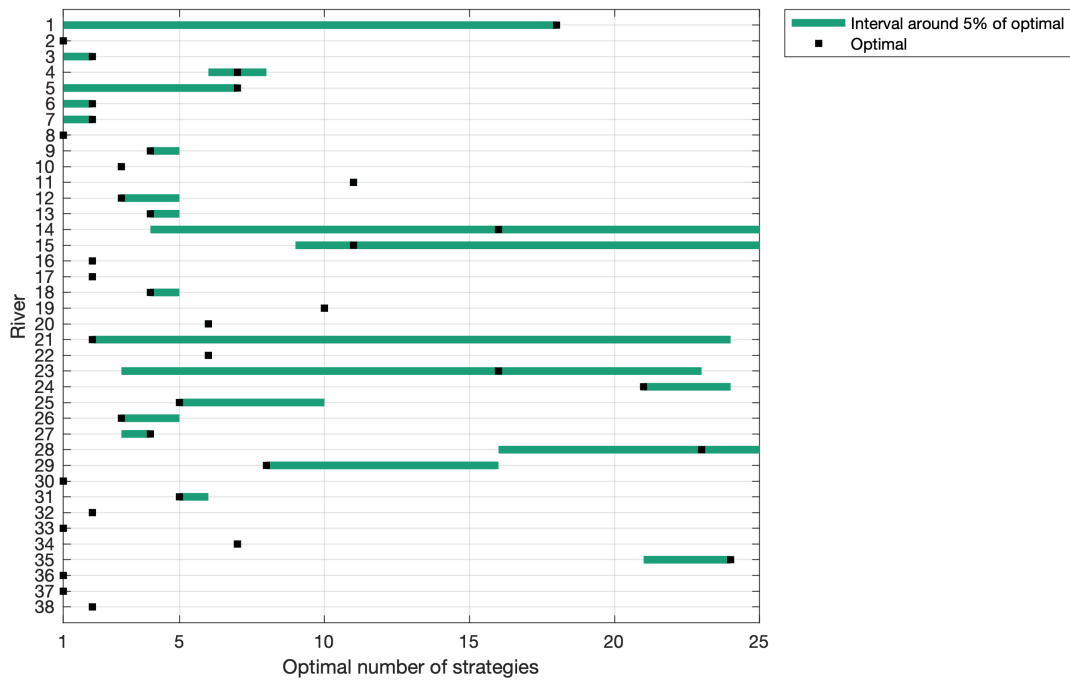


Figure B.1: The range of portfolio sizes per river giving a Sharpe ratio within 5% of the optimal. The optimal portfolio size is shown by a black square. In the case of infinite Sharpe ratios (as for river 1), the interval of portfolio sizes giving infinite Sharpe ratios is displayed.

B.2 Portfolio component examples

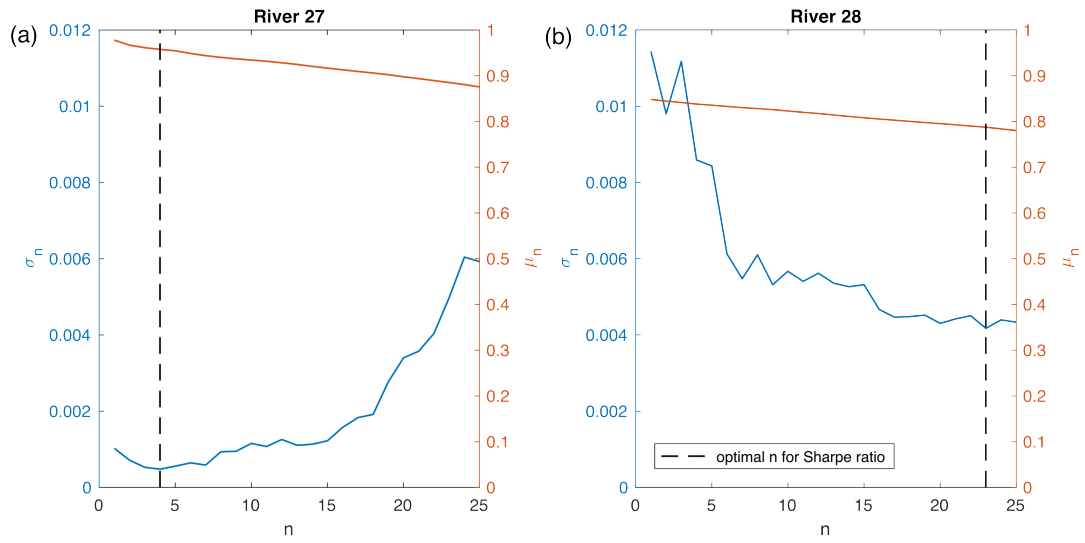


Figure B.2: Standard deviation σ_n and mean return μ_n of different portfolio sizes for (a) river 27 and (b) river 28. A vertical black dashed line indicates the value of n for the optimal Sharpe ratio.

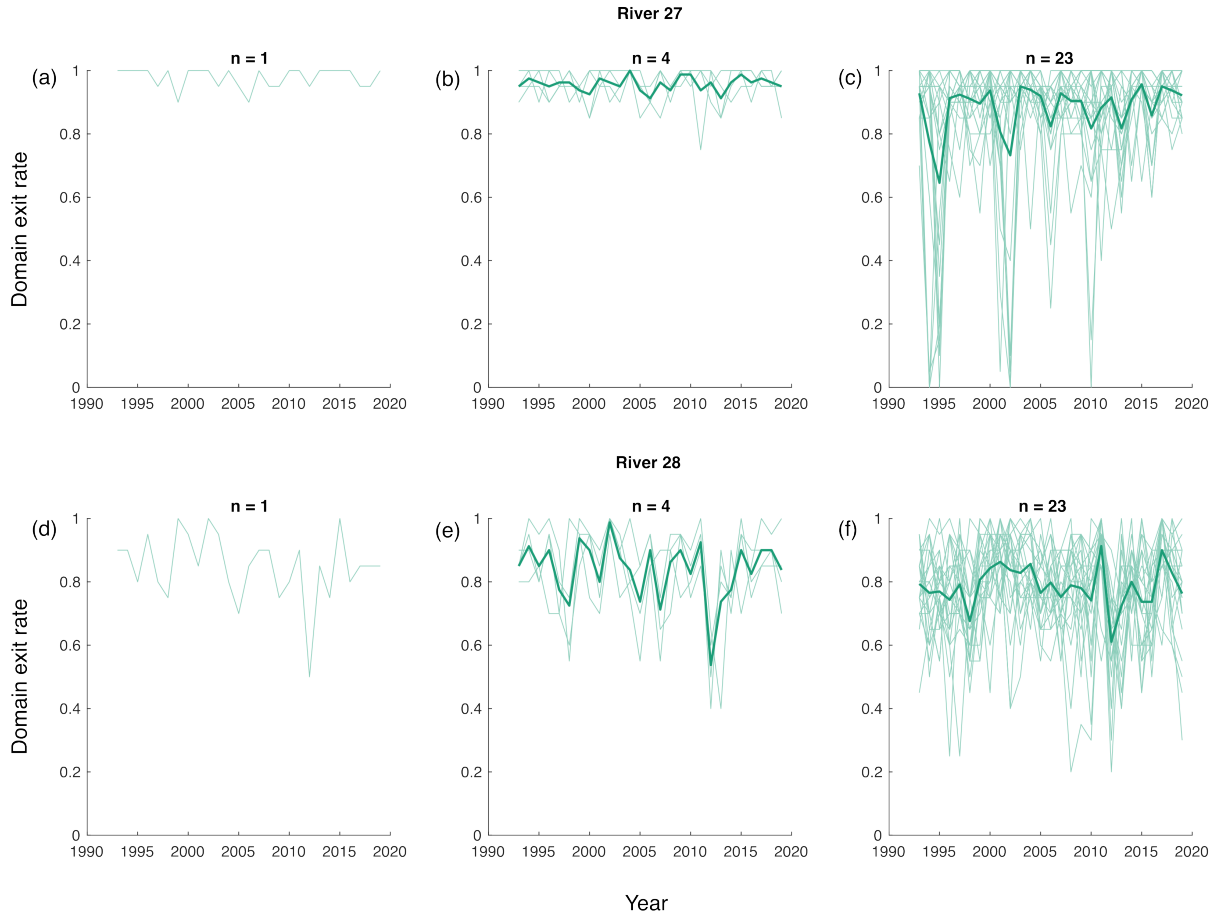


Figure B.3: Domain exit rate for each component of portfolios (thin lines) and the combined portfolio means (thick line) for river 27 and river 28 for: (a), (d) $n = 1$; (b), (e) $n = 4$, the optimal portfolio size for river 27; (c), (f) $n = 23$, the optimal portfolio size for river 28.

B.3 Coefficients of variation without rivers 4-7

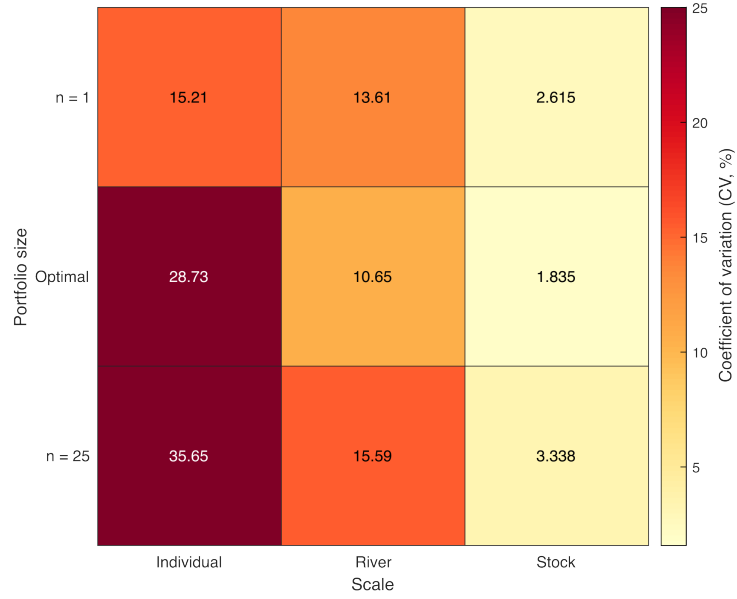


Figure B.4: The coefficient of variation (CV) on individual-, river- and stock-levels, calculated without the domain exit rates of rivers 4-7, for: $n = 1$, i.e. the single best swimming behaviour per river; the selected optimal portfolio per river; and $n = 25$, i.e. the set of all modelled swimming behaviours per river.

B.4 Optimal portfolio components with migration distance

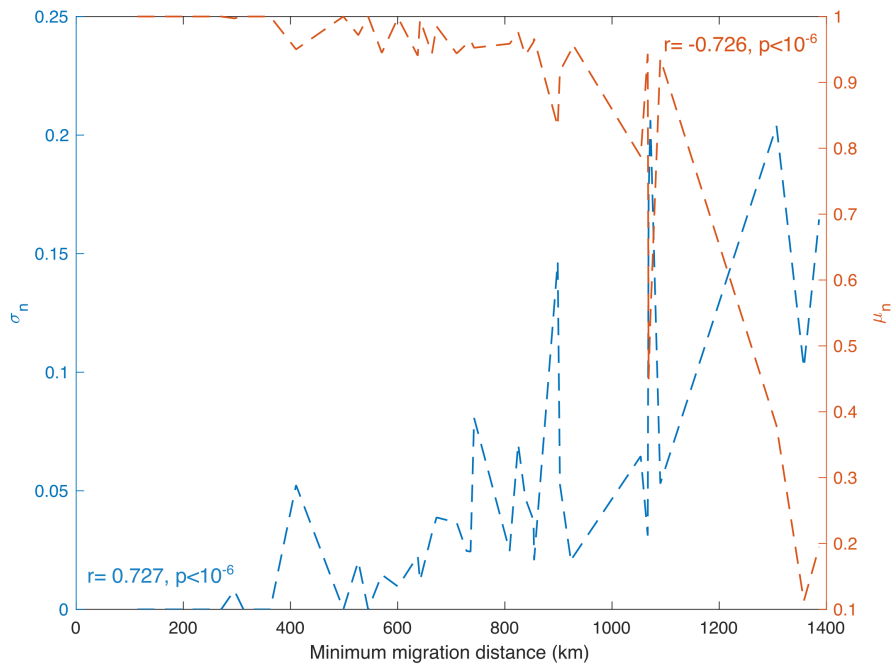


Figure B.5: Standard deviation σ_n and mean return μ_n for the optimal portfolio for each river against the minimum migration distance to the domain exit region.

Appendix C

Fisheries exposure analysis

C.1 Fisheries overview

	Primary gear	Operational fishing depth	Additional gear types
Mackerel (<i>Scomber scombrus</i>)	Pelagic trawlers and purse-seine (ICES, 2023g).	0-50m in Celtic Sea and in northern North Sea April-June; surface fishery in the Norwegian Sea July-September (ICES, 2004).	Handlines and gillnets (ICES, 2023g).
Herring (<i>Clupea harengus</i>)	Pelagic trawlers and purse-seine (ICES, 2007; ICES, 2013b).	>20m in several regions; surface fishery in the Norwegian Sea in July-September (ICES, 2004).	
Horse mackerel (<i>Trachurus trachurus</i>)	Pelagic trawlers and purse-seine (ICES, 2023g).	From a 1992-2017 survey: catches focused around 20-50m, particularly high CPUE at 20m (ICES, 2023g).	Artisanal fisheries along the coasts of Spain and Portugal (ICES, 2010).
Capelin (<i>Mallotus villosus</i>)	Purse-seine (ICES, 2023d).		Pelagic trawlers (ICES, 2023d).
Chub mackerel (<i>Scomber colias</i>)	Purse-seine (ICES, 2021b).	Species depth distribution between surface and 500m (ICES, 2021b).	
Sardine (<i>Sardina pilchardus</i>)	Purse-seine (ICES, 2023f).		Pelagic trawlers (ICES, 2023f).

Table C.1: A summary of the target species, gear types, and operational fishing depths of the pelagic fisheries considered in this study. Cells are left blank where the information was not available within any ICES Scientific Reports.

C.2 Estimation of pelagic landings from Russia and the Faroe Islands

Fishing effort expressed in hours was obtained for this analysis from Global Fishing Watch (<https://globalfishingwatch.org/>) from April to August of 2012-2020 (all of the available years) across the northeast Atlantic (latitudinal range 40°-70°, longitudinal range -30°-20°) for the eleven nations which provided landings data for this study and for Russia and the Faroe Islands. Effort data was binned into ICES statistical rectangles. Gear types considered were purse seines, seines, and trawls. Unfortunately, the trawl gear type in Global Fishing Watch data does not differentiate between pelagic and demersal trawls, but most trawling in this region is pelagic (ICES, 2021a), and hence relevant to the species of focus in this study. The location of fishing effort for Russia and the Faroe Islands (Figures C.1 and C.2) suggests that these fisheries will primarily overlap with the post-smolt migration regions from May onwards, hence we estimate landings from May to August.

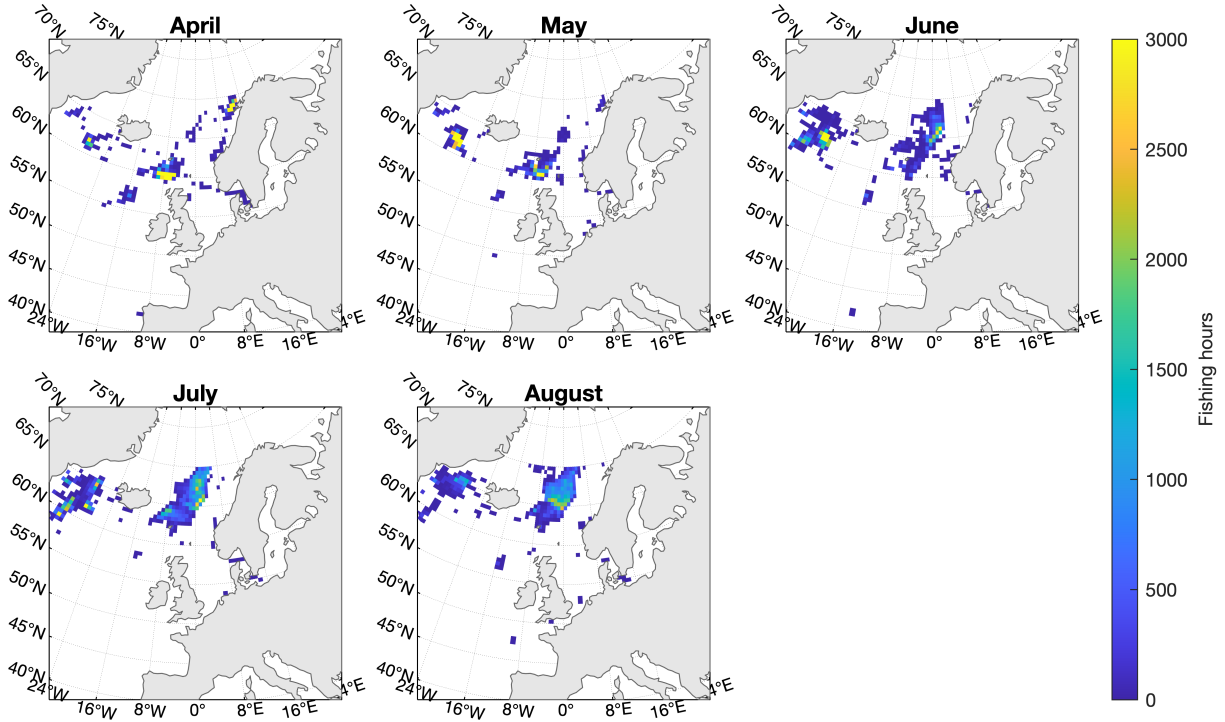


Figure C.1: Fishing hours of Russian fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.

Fishing hours for the Norwegian fleets (Figure C.3) and the Icelandic fleets (Figure C.4) showed the most similar spatial distributions of fishing in the Norwegian Sea to the Russian (Figure C.1) and Faroese fleets (Figure C.2). This suggested that it was appropriate to calculate monthly catch per unit effort (CPUE) from these two nations to extrapolate landings for Russia and the Faroe Islands, using the above fishing hours per ICES rectangle from Global Fishing Watch (GFW) and the tonnage of landings (of all species considered in this study) per ICES rectangle. By comparing effort from GFW with officially reported pelagic landings for Iceland and Norway

C.2. ESTIMATION OF PELAGIC LANDINGS FROM RUSSIA AND THE FAROE ISLANDS

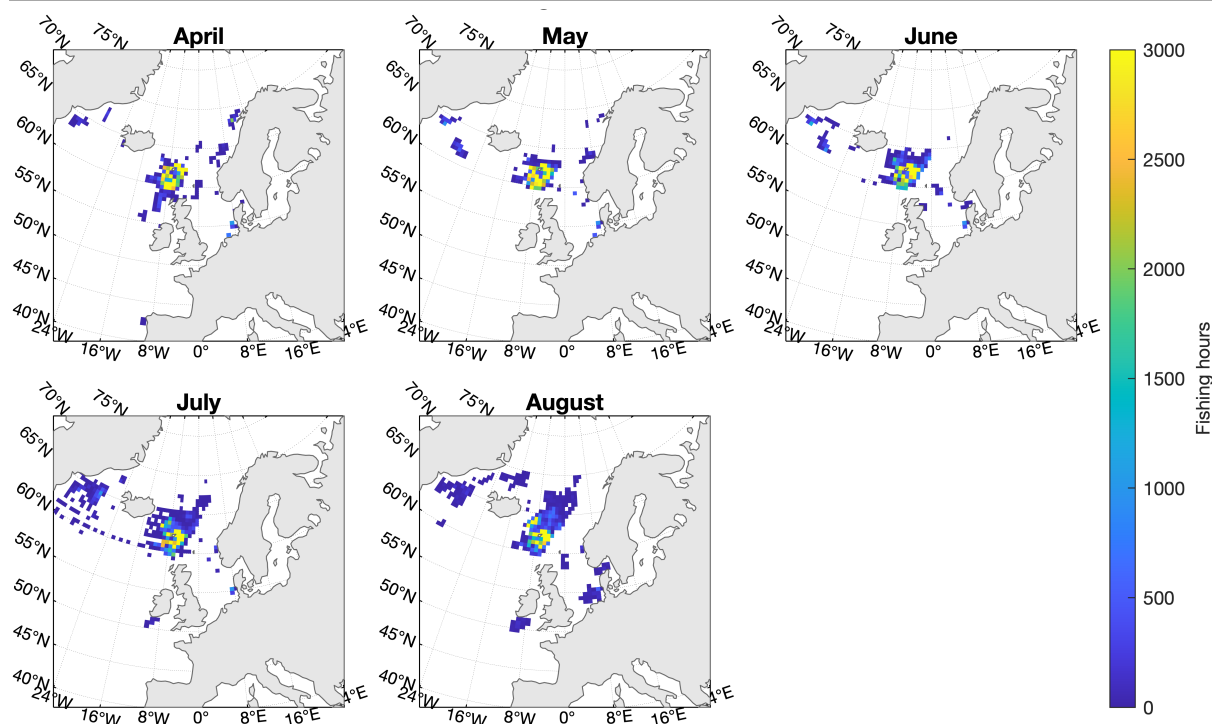


Figure C.2: Fishing hours of Faroese fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.

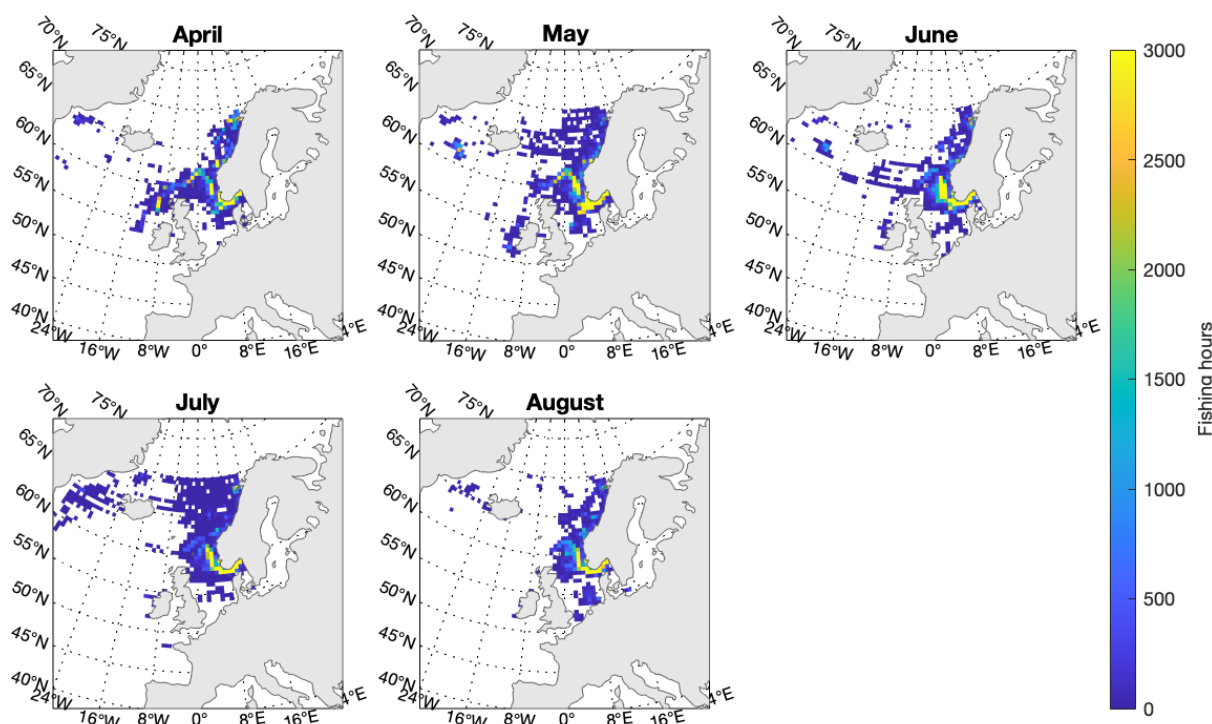


Figure C.3: Fishing hours of Norwegian fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.

C.2. ESTIMATION OF PELAGIC LANDINGS FROM RUSSIA AND THE FAROE ISLANDS

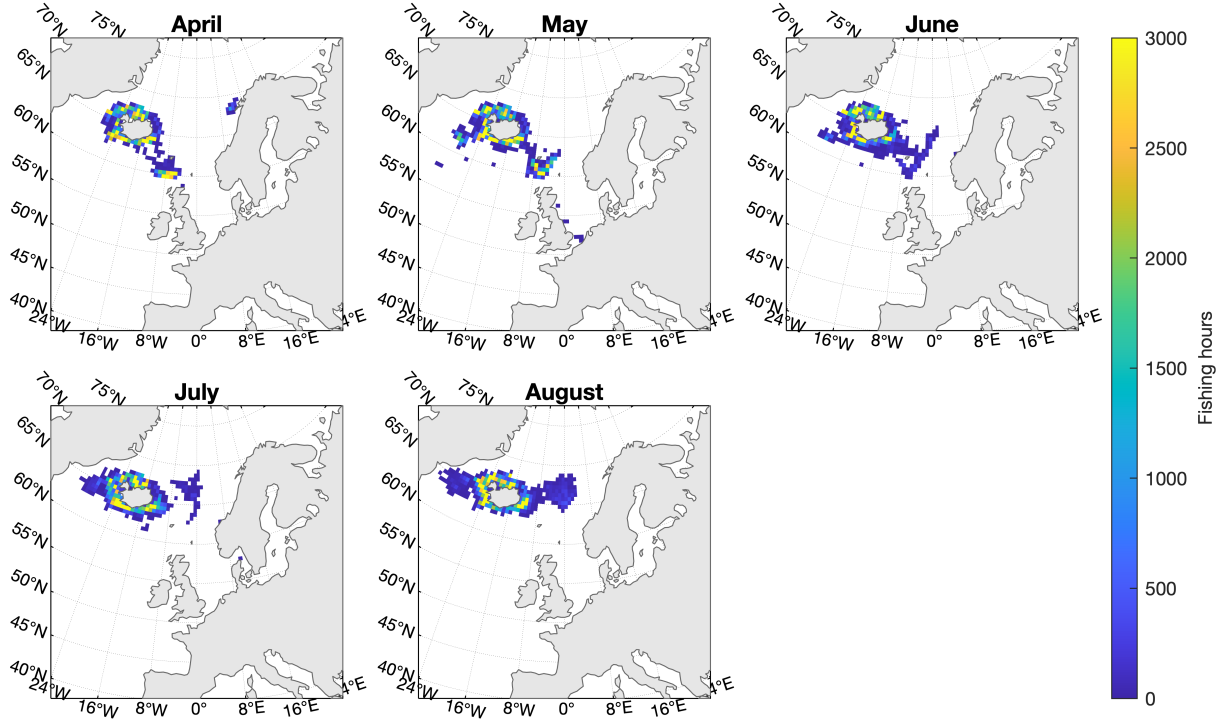


Figure C.4: Fishing hours of Icelandic fleets by ICES rectangle for gear types: seiners, purse-seiners, trawlers. Data from April-August 2012-2020, downloaded from Global Fishing Watch.

in this way, we must assume that the effort data is representative of all pelagic fishing. A large proportion ($>99\%$) of small vessels (<12 m) do not have Automatic Identification Systems (AIS), meaning they are not included in this dataset (Kroodsma *et al.*, 2018). We therefore excluded effort and landings from on-shelf waters from the CPUE estimation, with the aim of excluding landings from these smaller vessels. A region was hence defined to sum the effort and landings from each of these nations over the central Norwegian Sea, excluding most waters less than 400m deep (Figure C.5).

The time series of Norwegian effort and landings over the central Norwegian Sea region (Figure C.6) are not correlated in May, July or August (little to no evidence; $p > 0.1$), hence these time series are not appropriate for calculating catch per unit effort. One potential reason for these time series not being correlated is that some of the Norwegian effort might be from an industrial fishery targeting a lower-priced species (i.e. not one of our six focus species and hence not included in our landings time series) for fishmeal production.

Contrastingly, the Icelandic effort from Global Fishing Watch and the pelagic landings time series over this region are strongly ($r^2 > 0.78$) and significantly (strong evidence; $p < 0.01$) correlated for each month from May-August, meaning these time series are appropriate for calculating CPUE. The strong effort-landings relationships here could be because the main Icelandic pelagic fisheries (capelin and herring) are made up of a small number of large vessels (Arnason, 1996), all of which would likely have AIS.

Linear models were fitted to square root transformed Icelandic effort and landings, with this

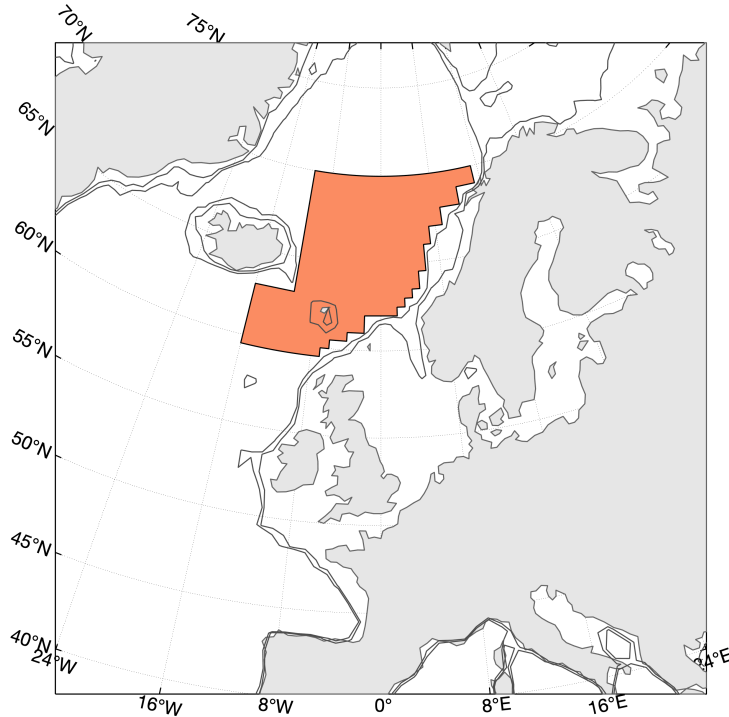


Figure C.5: Region excluding waters less than 400m deep used for summing Global Fishing Watch (GFW) effort and pelagic landings.

transformation applied to prevent outlying data points having a disproportionately large influence on the model fit. The models were constrained to have a zero intercept to provide a realistic estimate of CPUE (zero effort = zero landings). Estimated CPUE was taken as the slope of each fitted model, which was subsequently transformed back to the original units (tonnes/hour).

The CPUE varies between months, with the highest value in August (Figure C.8). Landings from the Faroe Islands and Russia were estimated by multiplying effort by this monthly estimated CPUE.

To validate the estimated pelagic landings for Russia and the Faroe Islands, they were compared with annual landings of mackerel, herring, and blue whiting for the Faroe Islands and Russia from ICES (2023g). There are, however, a few key differences to be noted when drawing comparisons between these time series: (1) the total landings from ICES (2023g) are per year, while the estimated landings are per month; (2) the total landings are over the entire northeast Atlantic, while the estimated landings are only over a specific region in the Norwegian Sea (however this region covers the majority of fishing effort from these nations, Figures C.1-C.2); and (3) the estimated landings are for all pelagic fisheries, while the total landings are for specific individual species only. For example, we did not otherwise consider blue whiting landings in this study, but the GFW effort data included blue whiting fisheries, hence the estimated landings included blue whiting and were compared to time series of total landings including blue whiting.

Estimated landings for the Faroe Islands in the Norwegian Sea were generally higher than those

C.2. ESTIMATION OF PELAGIC LANDINGS FROM RUSSIA AND THE FAROE ISLANDS

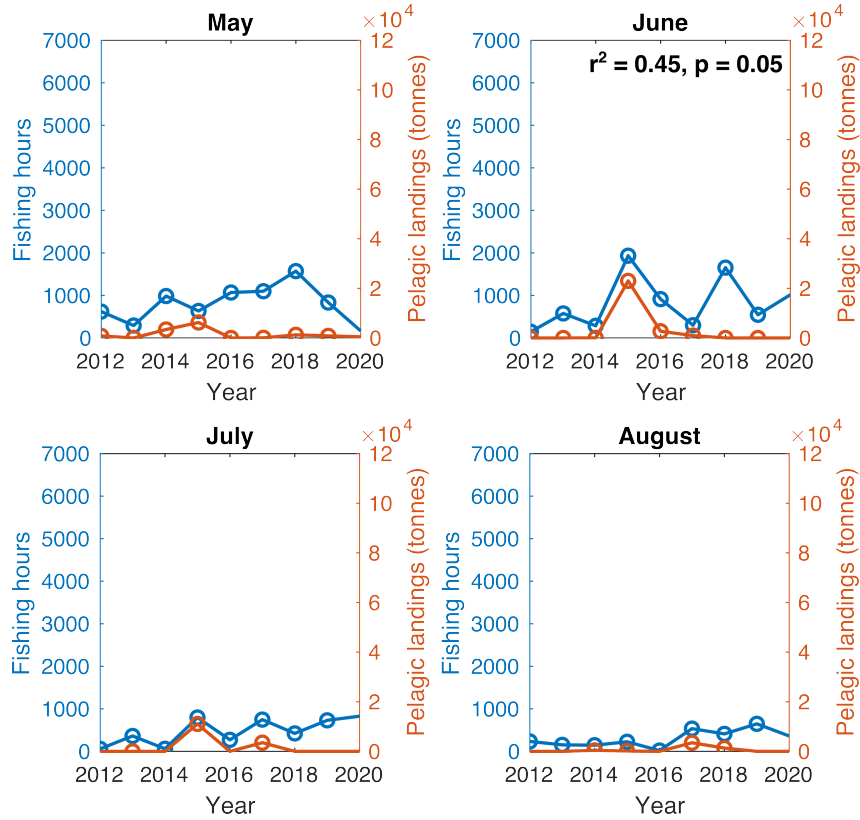


Figure C.6: Hours of Norwegian fishing effort from Global Fishing Watch (blue) and Norwegian pelagic landings (orange) over the region defined in Figure S5. Correlation coefficients r^2 and p are displayed where there is at least moderate evidence of a relationship ($p < 0.05$).

for Russia and displayed a different interannual pattern (Figure C.9). There was an increasing trend in the estimated Faroese landings from 2012-2015 for each month, but not in the estimated Russian landings.

The mean monthly estimated landings for the Faroe Islands were 4-150 times greater than the monthly landings from the other nations considered in this study, with the greatest differences seen in July and August. The mean monthly estimated landings for Russia were lower than the mean landings from the other nations in May but were 8-100 times greater than the mean landings of the other nations in the other months.

The estimated landings of the Faroe Islands showed a similar interannual pattern to their total annual landings of mackerel, herring and blue whiting as reported by ICES (2023g) (Figure C.9). While we chose not to focus on blue whiting landings in this study, the GFW effort data did include blue whiting fishing activity, and so the estimated landings included blue whiting landings. Estimated Russian landings in July and August were very similar, in terms of trends rather than magnitude, to their total annual mackerel, herring and blue whiting landings, with some slight differences in May and June.

The interannual pattern of estimated landings from the Faroe Islands in the Norwegian Sea was very different to the interannual pattern of total landings from other nations (blue line)

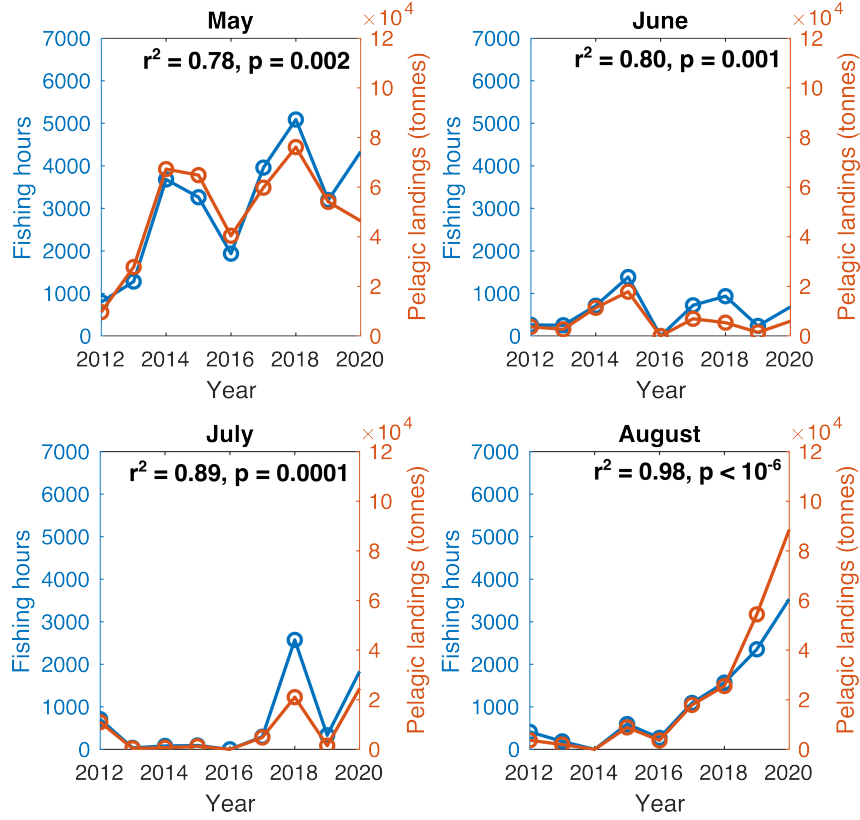


Figure C.7: Hours of Icelandic fishing effort from Global Fishing Watch (blue) and Icelandic pelagic landings (orange) over the region defined in Figure S5. Correlation coefficients r^2 and p are displayed where there is at least moderate evidence of a relationship ($p < 0.05$).

considered in this study. Estimated Russian landings showed a similar interannual pattern to landings from other nations in May and June, but not in the other months.

Our estimated landings from the Faroese fleet in the Norwegian Sea are certainly overestimated, given that the sum of our monthly estimated landings from May-August would be higher than the total annual landings by the Faroe Islands of mackerel, herring and blue whiting as reported by ICES (2023g). This might be because the summed effort used to estimate landings included the shelf around the Faroe Islands, where there is a trawl demersal fishery (ICES, 2023b). The estimated landings for the Russian fleets were lower than the Faroese fishery and generally did not appear to be overestimated (when comparing our estimated landings with the total annual landings by Russia of mackerel, herring and blue whiting). The interannual patterns were similar between the estimated monthly Faroese/Russian landings and their reported total annual mackerel, herring and blue whiting landings, suggesting that our method captured the interannual fluctuations in these fisheries.

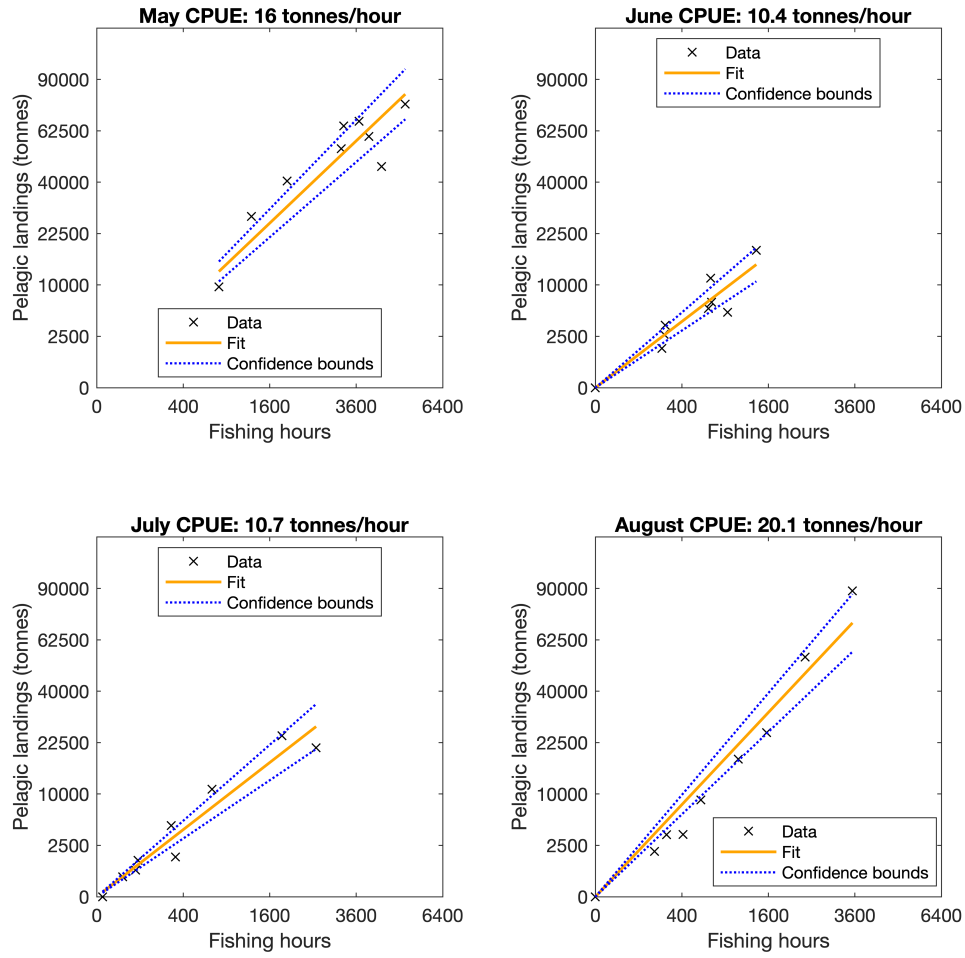


Figure C.8: Linear models fitted to monthly Icelandic fishing effort (from Global Fishing Watch) and landings in the central Norwegian Sea region per month, with the gradient of these being the estimated CPUE in tonnes per hour. Fishing hours axes are on a square root scale.

C.3 Spatial overlap of pelagic fishing activity with monthly post-smolt migration regions

C.3. SPATIAL OVERLAP OF PELAGIC FISHING ACTIVITY WITH MONTHLY POST-SMOLT MIGRATION REGIONS

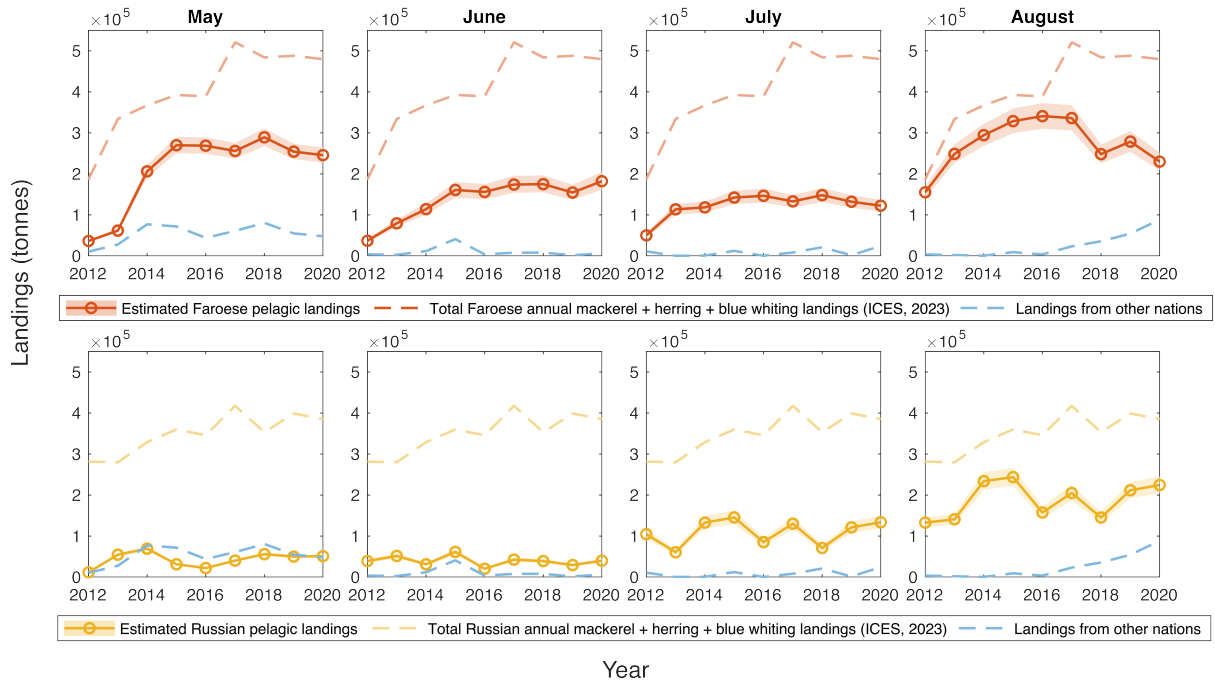


Figure C.9: Estimated pelagic landings of the Faroe/Russian fleets (red/yellow line with circles, shaded confidence interval) per month alongside the summed annual Faroese/Russian mackerel, herring, and blue whiting landings (red/yellow dashed line) from ICES (2023g). Total monthly landings across the same area in the Norwegian Sea from the other nations considered in this study (all species, including blue whiting) are displayed as a dashed blue line.

Mackerel landings in post-smolt regions 2000-2022

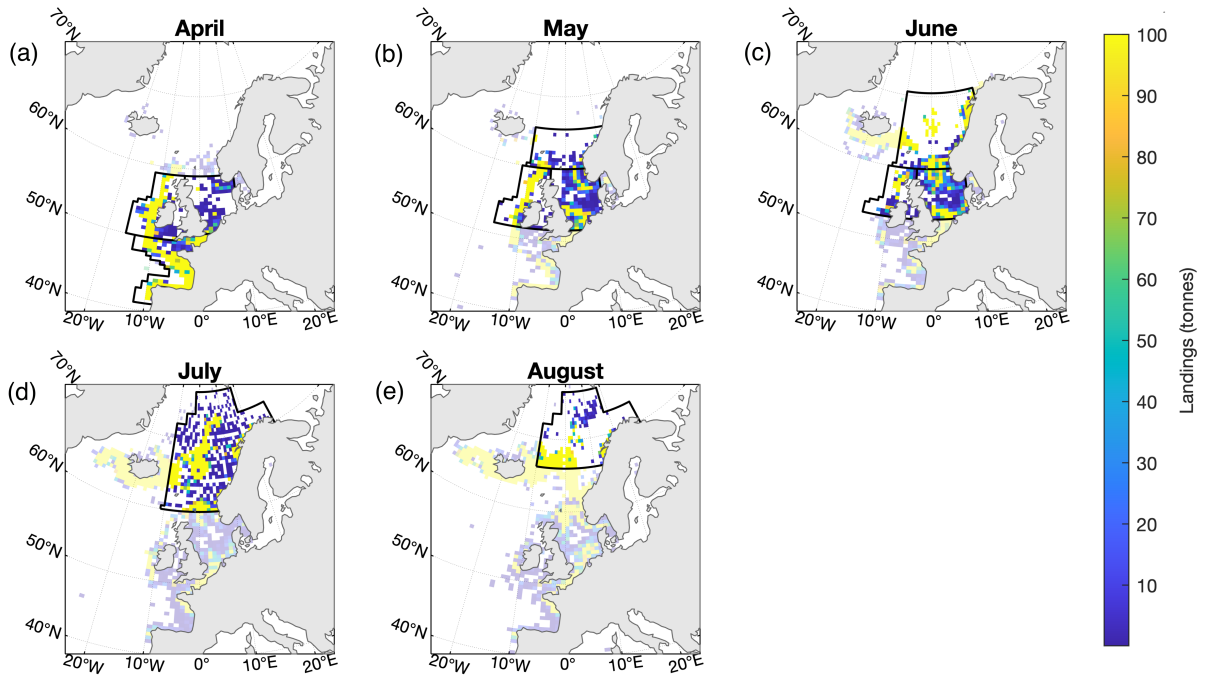


Figure C.10: Landings of mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

C.3. SPATIAL OVERLAP OF PELAGIC FISHING ACTIVITY WITH MONTHLY POST-SMOLT MIGRATION REGIONS

Herring landings in post-smolt regions 2000-2022

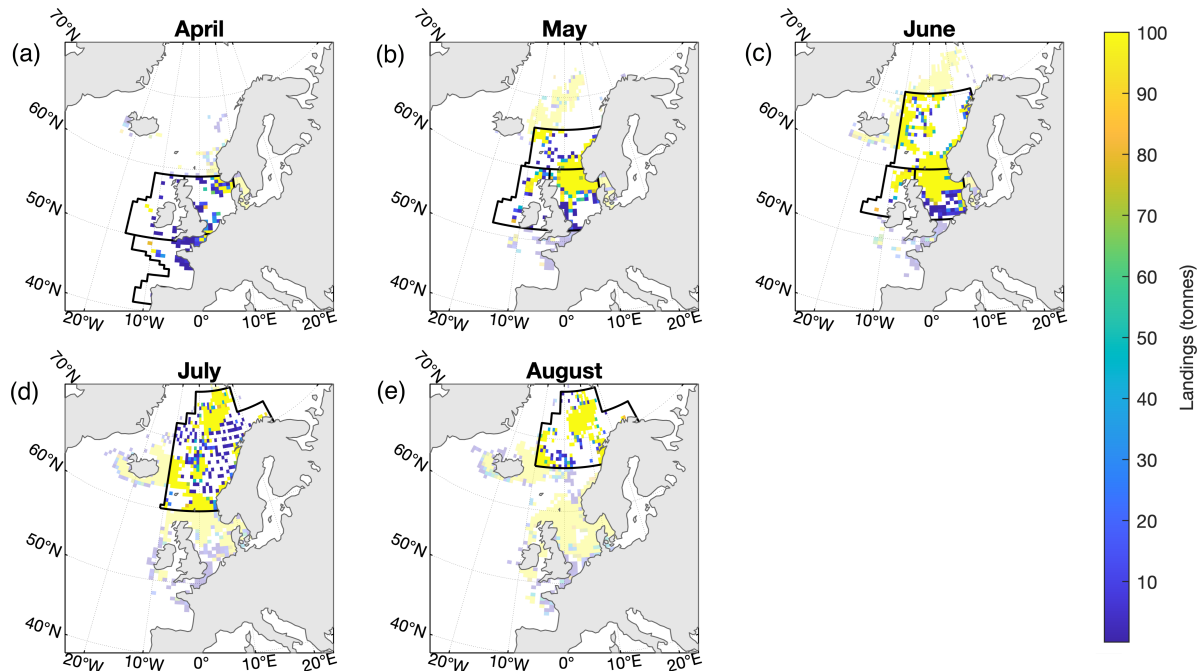


Figure C.11: Landings of herring by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

Horse mackerel landings in post-smolt regions 2000-2022

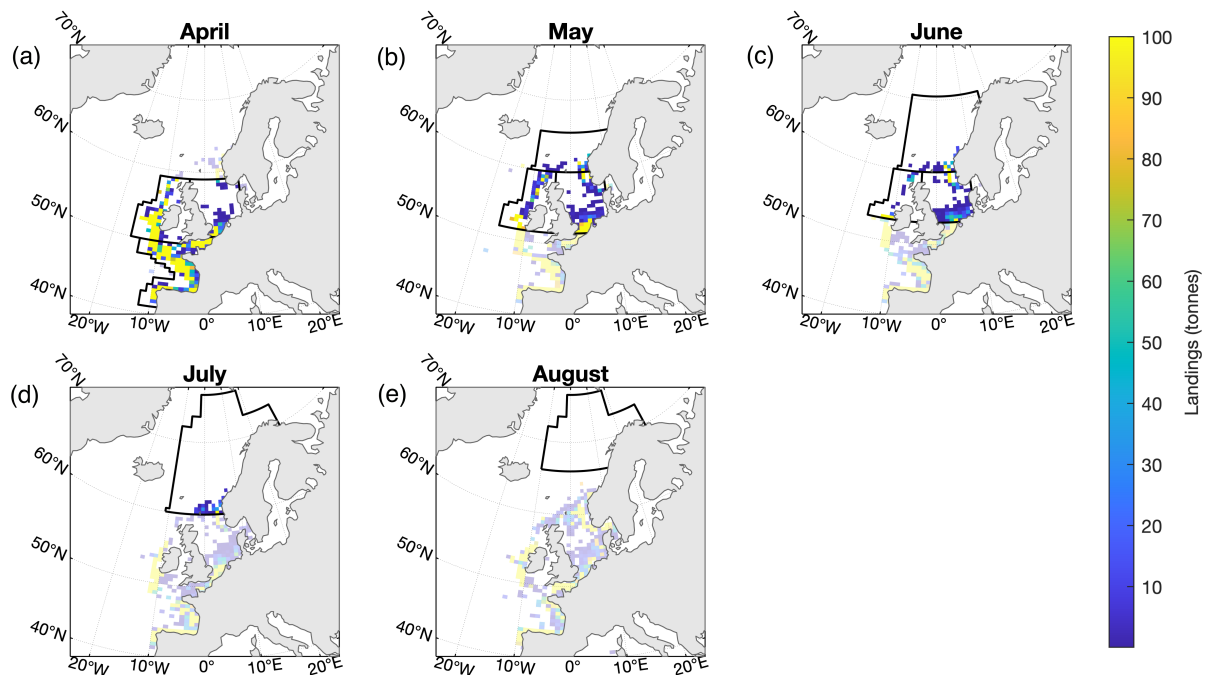


Figure C.12: Landings of horse mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

C.3. SPATIAL OVERLAP OF PELAGIC FISHING ACTIVITY WITH MONTHLY POST-SMOLT MIGRATION REGIONS

Sardine landings in post-smolt regions 2000-2022

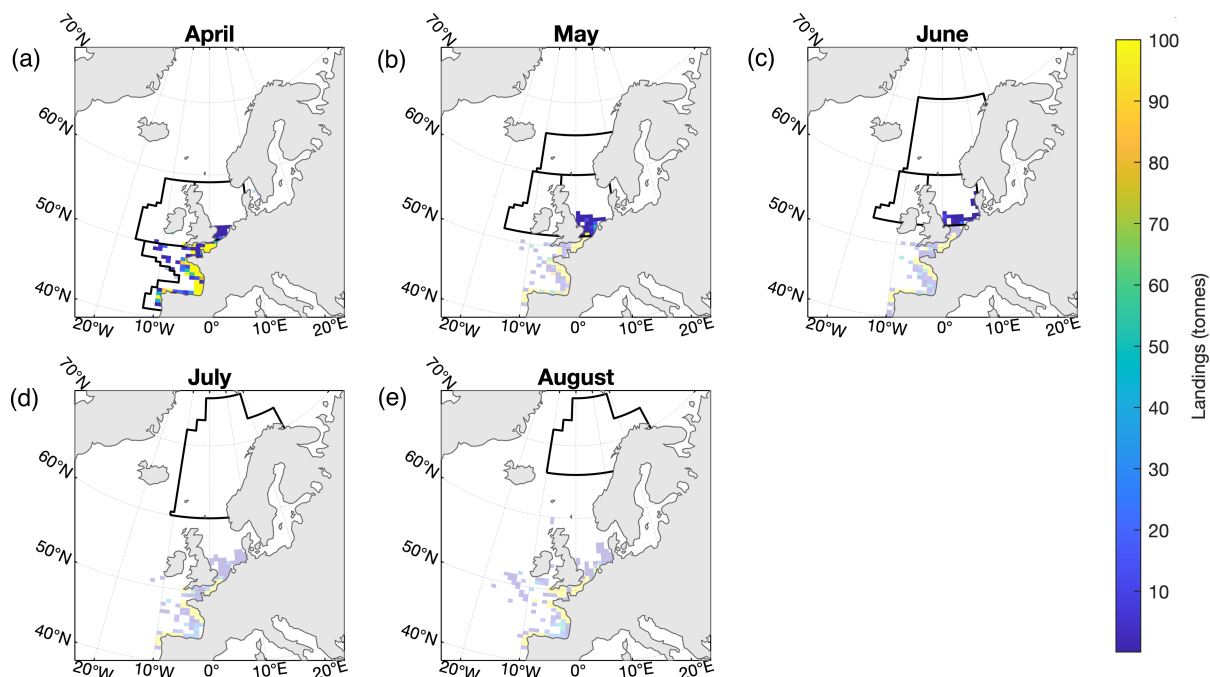


Figure C.13: Landings of sardine by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

Capelin landings in post-smolt regions 2000-2022

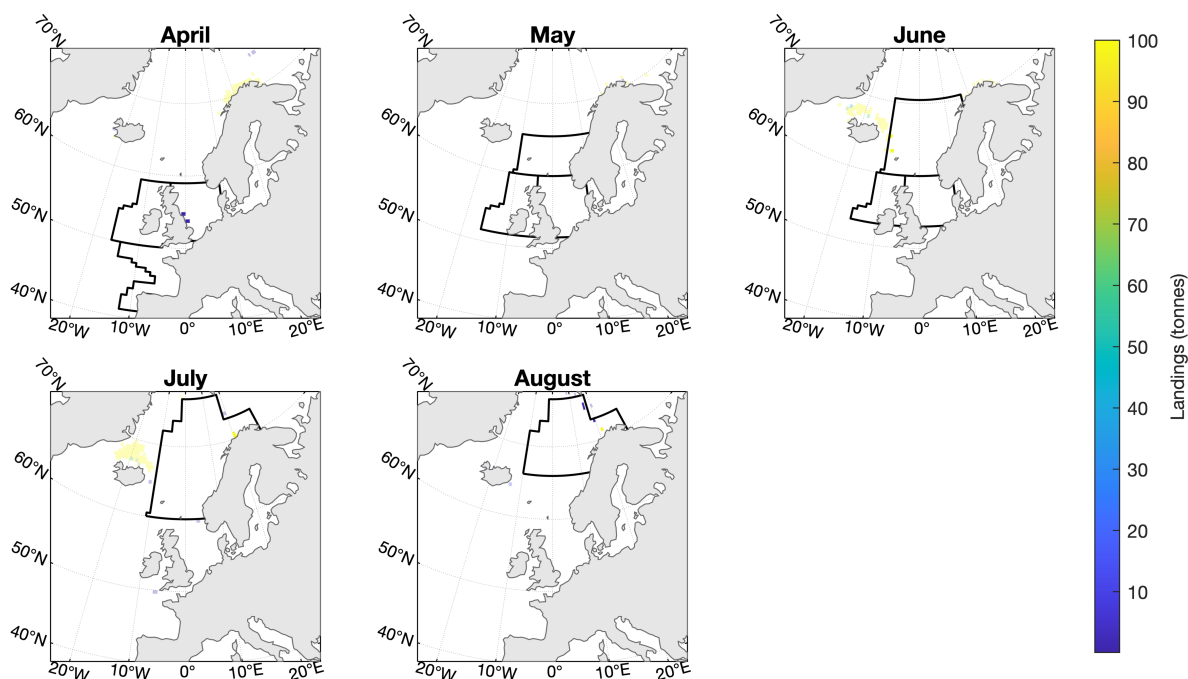


Figure C.14: Landings of capelin by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

C.3. SPATIAL OVERLAP OF PELAGIC FISHING ACTIVITY WITH MONTHLY POST-SMOLT MIGRATION REGIONS

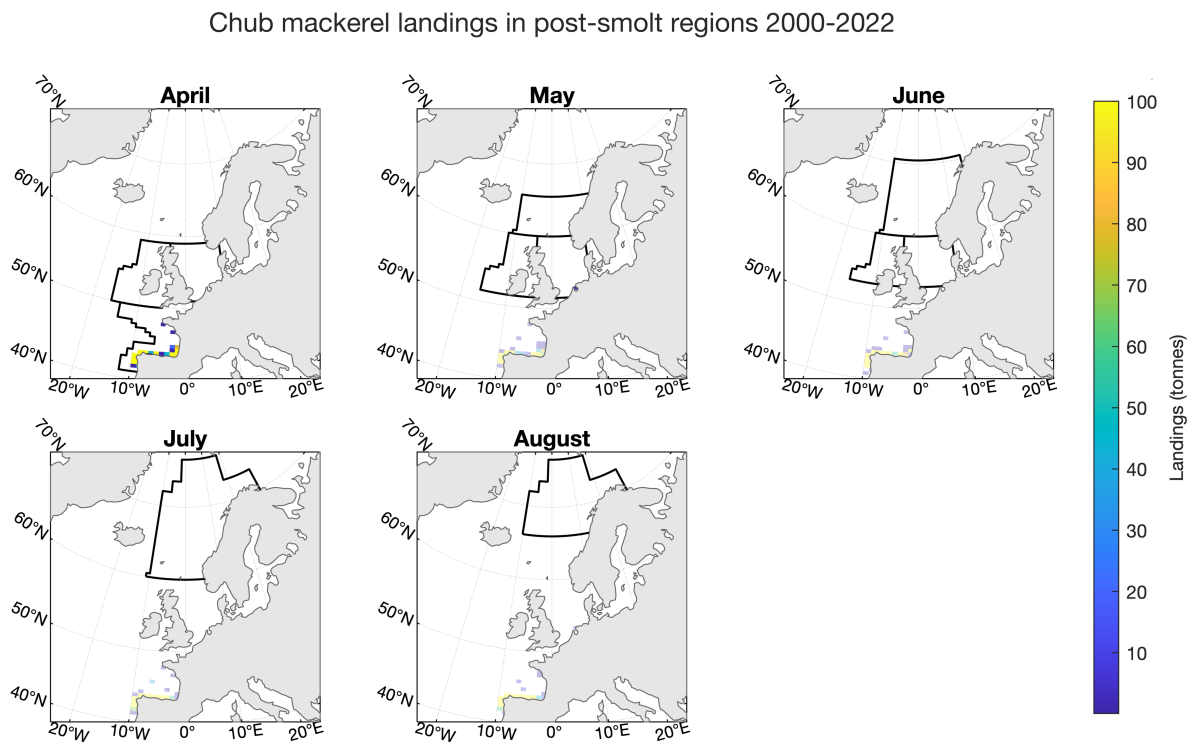


Figure C.15: Landings of chub mackerel by ICES rectangle within the post-smolt regions (outlined) per month across 2000-2022.

Bibliography

- Aas, Øystein, Klemetsen, Anders, Einum, Sigurd, & Skurdal, Jostein. 2010. *Atlantic salmon ecology*. John Wiley & Sons.
- Adams, Colin E, Chavarie, Louise, Rodger, Jessica R, Honkanen, Hannele M, Thambithurai, Davide, & Newton, Matthew P. 2022. An opinion piece: the evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon. *Journal of Fish Biology*, **100**(4), 860–867.
- Adams, Colin E, Forrester, Ruaidhri, Newton, Matthew, Lothian, Angus J, Honkanen, Hannele M, Thambithurai, Davide, Wilkie, Lorna, Smith, Melanie A, Walters, Marcus, Miller, Richard, *et al.* 2025. Inshore marine coastal zone migration patterns in Atlantic salmon post-smolts emigrating from eight rivers in north-east Scotland. *Journal of fish biology*.
- Albonetti, L. 2023. DNA metabarcoding of trawling bycatch reveals diversity and distribution patterns of sharks and rays in the central Tyrrhenian Sea. *ICES Journal of Marine Science*, **80**(4), 664–674.
- Alerstam, Thomas, & Lindström, Åke. 1990. Optimal bird migration: the relative importance of time, energy, and safety. *Pages 331–351 of: Bird migration: physiology and ecophysiology*. Springer.
- Alerstam, Thomas, Hedenström, Anders, & Åkesson, Susanne. 2003. Long-distance migration: evolution and determinants. *Oikos*, **103**(2), 247–260.
- Allan, IRH, & Ritter, JA. 1977. Salmonid terminology. *ICES Journal of Marine Science*, **37**(3), 293–299.
- Alne, Henriette, Oehme, Maike, Thomassen, Magny, Terjesen, Bendik, & Rørvik, Kjell-Arne. 2011. Reduced growth, condition factor and body energy levels in Atlantic salmon *Salmo salar* L. during their first spring in the sea. *Aquaculture Research*, **42**(2), 248–259.
- Anderson, James J, Gurarie, Eliezer, & Zabel, Richard W. 2005. Mean free-path length theory of predator–prey interactions: application to juvenile salmon migration. *Ecological Modelling*, **186**(2), 196–211.

- Antonsson, Thorolfur, Heidarsson, Thorkell, & Snorrason, Sigurdur S. 2010. Smolt emigration and survival to adulthood in two Icelandic stocks of Atlantic salmon. *Transactions of the American Fisheries Society*, **139**(6), 1688–1698.
- Arheimer, Berit, Pimentel, Rafael, Isberg, Kristina, Crochemore, Louise, Andersson, Jafet CM, Hasan, Abdulghani, & Pineda, Luis. 2020. Global catchment modelling using World-Wide HYPE (WWH), open data, and stepwise parameter estimation. *Hydrology and Earth System Sciences*, **24**(2), 535–559.
- 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. *Journal of Fish Biology*, **92**(3), 569–578.
- Armstrong, Richard A. 2014. When to use the Bonferroni correction. *Ophthalmic and physiological optics*, **34**(5), 502–508.
- Arnason, R. 1996. On the ITQ fisheries management system in Iceland. *Reviews in Fish Biology and Fisheries*, **6**(1), 63–90.
- Artero, C. 2023. Survival of Atlantic salmon and sea trout smolts in transitional waters. *Marine Ecology Progress*, **709**, 91–108.
- Autret, E, Piollé, J. F., Tandéo, P, & Prévost, C. 2020. ODYSSEA Level 4 Sea Surface Temperature Reprocessing over the European North West Shelf / Iberia Biscay Irish Seas Reprocessing SST-ATL-SST-L4-REP-OBSERVATIONS-010-026. *Tech. Rep. 1.4*.
- Bacon, PJ, Malcolm, IA, MacLean, JC, McLaren, I, & Thorne, A. 2012. Female length and mass quantify the difference between Atlantic salmon ova fecundity and ova deposition. *North American Journal of Fisheries Management*, **32**(3), 491–498.
- Bandara, Kanchana, Varpe, Øystein, Wijewardene, Lishani, Tverberg, Vigdis, & Eiane, Ketil. 2021. Two hundred years of zooplankton vertical migration research. *Biological Reviews*, **96**(4), 1547–1589.
- Barry, J, Fitzgerald, C, Callaghan, JO, Kennedy, R, Rosell, R, & Roche, W. 2024. Interannual variation in survival of wild Atlantic salmon smolts through a dynamic estuarine habitat. *Fisheries Management and Ecology*, e12685.
- Barry, James, Kennedy, Richard J, Rosell, Robert, & Roche, William K. 2020. Atlantic salmon smolts in the Irish Sea: first evidence of a northerly migration trajectory. *Fisheries Management and Ecology*, **27**(5), 517–522.
- Barton, B, De Dominicis, M, O'Hara Murray, R, & Campbell, L. 2022. Scottish Shelf Model 3.02 - 27 Year Reanalysis.
- Barton, Benjamin I, De Dominicis, Michela, O'Hara Murray, Rory, Wolf, Judith, & Gallego, Alejandro. 2024. Formation and dynamics of a coherent coastal freshwater influenced system. *Earth and Space Science*, **11**(2), e2023EA002872.

- Bartsch, J, & Coombs, S. 1997. A numerical model of the dispersion of blue whiting larvae, *Micromesistiuspoutassou* (Risso), in the eastern North Atlantic. *Fisheries Oceanography*, **6**(3), 141–154.
- Batista, M. 2015. Assessment of catches, landings and fishing effort as useful tools for MPA management. *Fisheries Research*, **172**, 197–208.
- Beare, DOUG, & McKenzie, Eddie. 1999. The multinomial logit model: a new tool for exploring Continuous Plankton Recorder data. *Fisheries Oceanography*, **8**, 25–39.
- Beaugrand, Grégory, & Reid, Philip C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, **9**(6), 801–817.
- Beaugrand, Grégory, & Reid, Philip C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, **69**(9), 1549–1562.
- Béguier-Pon, Mélanie, Benchetrit, José, Castonguay, Martin, Aarestrup, Kim, Campana, Steven E, Stokesbury, Michael JW, & Dodson, Julian J. 2012. Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence.
- Bell, VA, Kay, AL, Jones, RG, Moore, RJ, & Reynard, NS. 2009. Use of soil data in a grid-based hydrological model to estimate spatial variation in changing flood risk across the UK. *Journal of Hydrology*, **377**(3-4), 335–350.
- Benhamou, Simon. 2014. Of scales and stationarity in animal movements. *Ecology letters*, **17**(3), 261–272.
- Bicknell, Anthony WJ, Gierhart, Samuel, Newton, Matthew, Main, Robert, Thompson, Paul, & Witt, Matthew J. 2025. The role of acoustic telemetry to assess the effects of offshore wind infrastructure on fish behaviour, populations and predation. *Renewable and Sustainable Energy Reviews*, **212**, 115306.
- Bisch, A. 2024. *Atlas des Chondrichthyens de France métropolitaine - Cartographier la présence et la sensibilité des espèces réglementées dans le cadre du programme de mesures D01-PC-OE01-AN1 (sous-action 1) de la DCSMM cycle 2*. Rapport d’expertise de PatriNat et de l’Université de Corse.
- Bohlin, Torgny, Hamrin, Stellan, Heggberget, Tor G, Rasmussen, Gorm, & Saltveit, Svein Jakob. 1989. Electrofishing—theory and practice with special emphasis on salmonids. *Hydrobiologia*, **173**(1), 9–43.
- Booker, Douglas J, Wells, Neil C, & Smith, I Philip. 2008. Modelling the trajectories of migrating Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **65**(3), 352–361.

- Borland, Aislinn, Banas, Neil, Gallego, Alejandro, Speirs, Douglas, Tyldesley, Emma, & Bull, Colin. 2025. Modelled marine migrations of Atlantic salmon post-smolts from Irish and Scottish rivers vary interannually with local currents and salinity. *ICES Journal of Marine Science*, **82**(5), fsae185.
- Bourret, Vincent, Kent, Matthew P, Primmer, Craig R, Vasemägi, Anti, Karlsson, Sten, Hindar, Kjetil, McGinnity, Philip, Verspoor, Eric, Bernatchez, Louis, & Lien, Sigbjørn. 2013. SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Molecular ecology*, **22**(3), 532–551.
- Broekhuizen, N, Heath, MR, Hay, SJ, & Gurney, WSC. 1995. Modelling the dynamics of the North Sea's mesozooplankton. *Netherlands Journal of Sea Research*, **33**(3-4), 381–406.
- Brunsdon, Eric Blake, Daniels, Jason, Hanke, Alex, & Carr, Jonathan. 2019. Tag retention and survival of Atlantic salmon (*Salmo salar*) smolts surgically implanted with dummy acoustic transmitters during the transition from fresh to salt water. *ICES Journal of Marine Science*, **76**(7), 2471–2480.
- Buck, RJG, & Hay, DW. 1984. The relation between stock size and progeny of Atlantic salmon, *Salmo salar* L., in a Scottish stream. *Journal of Fish Biology*, **24**(1), 1–11.
- Bull, Colin D, Metcalfe, Neil B, & Mangel, Marc. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **263**(1366), 13–18.
- Bull, Colin D, Gregory, Stephen D, Rivot, Etienne, Sheehan, Timothy Francis, Ensing, Dave, Woodward, Guy, & Crozier, Walter. 2022. The likely suspects framework: the need for a life cycle approach for managing Atlantic salmon (*Salmo salar*) stocks across multiple scales. *ICES Journal of Marine Science*, **79**(5), 1445–1456.
- Burke, Brian J, Anderson, James J, Miller, Jessica A, Tomaro, Londi, Teel, David J, Banas, Neil S, & Baptista, António M. 2016a. Estimating behavior in a black box: how coastal oceanographic dynamics influence yearling Chinook salmon marine growth and migration behaviors. *Environmental biology of fishes*, **99**, 671–686.
- Burke, Brian J., Anderson, James J., Miller, James A., Tomaro, Lisa, Teel, David J., Banas, Neil S., & Baptista, Antonio M. 2016b. Estimating behavior in a black box: how coastal oceanographic dynamics influence yearling Chinook salmon marine growth and migration behaviors. *Environmental Biology of Fishes*, **99**(8), 671–686.
- Butler, JRA, Middlemas, SJ, Graham, Isla Margaret, Thompson, Paul Michael, & Armstrong, JD. 2006. Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: a tool for targeting conflict resolution. *Fisheries Management and Ecology*, **13**(5), 285–291.
- Byron, Carrie J, & Burke, Brian J. 2014. Salmon ocean migration models suggest a variety of population-specific strategies. *Reviews in fish biology and fisheries*, **24**(3), 737–756.

- Byron, Carrie J, Pershing, Andrew J, Stockwell, Jason D, Xue, Huijie, & Kocik, John. 2014. Migration model of post-smolt Atlantic salmon (*Salmo salar*) in the Gulf of Maine. *Fisheries Oceanography*, **23**(2), 172–189.
- Capuzzo, Elisa, Lynam, Christopher P, Barry, Jon, Stephens, David, Forster, Rodney M, Greenwood, Naomi, McQuatters-Gollop, Abigail, Silva, Tiago, van Leeuwen, Sonja M, & Engelhard, Georg H. 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global change biology*, **24**(1), e352–e364.
- Carlson, Stephanie Marie, & Satterthwaite, William Hallowell. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**(9), 1579–1589.
- Carss, DN, Kruuk, H, & Conroy, JWH. 1990. Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, **37**(6), 935–944.
- Castant, Jérôme, Vantrepotte, Vincent, Thibault, Hélène, & Beaugrand, Grégory. 2025. Long-term changes in depth distribution and phenology of four North Atlantic plankton species. *Marine Ecology Progress Series*, **771**, 33–53.
- Cauwelier, E, Stewart, DC, Millar, CP, Gilbey, J, & Middlemas, SJ. 2018. Across rather than between river genetic structure in Atlantic salmon *Salmo salar* in north-east Scotland, UK: Potential causes and management implications. *Journal of fish biology*, **92**(3), 607–620.
- Chapman, Ben B, Hulthén, Kaj, Wellenreuther, Maren, Hansson, Lars-Anders, Nilsson, Jan-Åke, & Brönmark, Christer. 2014. Patterns of animal migration. *Animal movement across scales*, **1**, 11–35.
- Chapman, Jason W, Klaassen, Raymond HG, Drake, V Alistair, Fossette, Sabrina, Hays, Graeme C, Metcalfe, Julian D, Reynolds, Andrew M, Reynolds, Don R, & Alerstam, Thomas. 2011. Animal orientation strategies for movement in flows. *Current Biology*, **21**(20), R861–R870.
- Chaput, Gérald. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, **69**(9), 1538–1548.
- Chaput, Gérald, Carr, Jonathan, Daniels, Jason, Tinker, Steve, Jonsen, Ian, & Whoriskey, Frederick. 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 Journal of Marine Science*, **76**(4), 1107–1121.
- Chavarie, Louise, Honkanen, Hannele M, Newton, Matthew, Lilly, Jessie M, Greetham, Hannah R, & Adams, Colin E. 2022. The benefits of merging passive and active tracking approaches: New insights into riverine migration by salmonid smolts. *Ecosphere*, **13**(5), e4045.

- Chen, Changsheng, Liu, Hedong, & Beardsley, Robert C. 2003. An unstructured grid, finite-volume, three-dimensional, primitive equations ocean model: application to coastal ocean and estuaries. *Journal of atmospheric and oceanic technology*, **20**(1), 159–186.
- Clark, Matthew, Marsh, Robert, & Harle, James. 2022. Weakening and warming of the European Slope Current since the late 1990s attributed to basin-scale density changes. *Ocean Science*, **18**(2), 549–564.
- Clay, T. 2019. A comprehensive large-scale assessment of fisheries bycatch risk to threatened seabird populations. *Journal of Applied Ecology*, **59**(8), 1882–1893.
- Coombs, Sheryl, Bak-Coleman, Joe, & Montgomery, John. 2020. Rheotaxis revisited: a multi-behavioral and multisensory perspective on how fish orient to flow. *Journal of Experimental Biology*, **223**(23), jeb223008.
- Cresci, Alessandro. 2020. A comprehensive hypothesis on the migration of European glass eels (*Anguilla anguilla*). *Biological Reviews*, **95**(5), 1273–1286.
- Crozier, Walter, Whelan, Ken, Buoro, Mathieu, Chaput, Gerald, Daniels, Jason, Grant, Sue, Hyatt, Kim, Irvine, James, Ó'Maoiléidigh, Niall, Prévost, Etienne, *et al.* 2018. Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework. *Atlantic Salmon Trust report*.
- Cushing, DH. 1973. Dependence of recruitment on parent stock. *Journal of the Fisheries Board of Canada*, **30**(12), 1965–1976.
- Cushing, DH. 1990. Plankton production and year-class strength in fish populations: an upyear of the match/mismatch hypothesis. *Pages 249–293 of: Advances in marine biology*, vol. 26. Elsevier.
- Dadswell, MJ, Spares, AD, Reader, JM, & Stokesbury, MJW. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: The 'Merry-Go-Round' hypothesis. *Journal of Fish Biology*, **77**(3), 435–467.
- Daewel, Ute, Schrum, Corinna, & Temming, Axel. 2011. Towards a more complete understanding of the life cycle of brown shrimp (*Crangon crangon*): modelling passive larvae and juvenile transport in combination with physically forced vertical juvenile migration. *Fisheries Oceanography*, **20**(6), 479–496.
- Daewel, Ute, Schrum, Corinna, & Macdonald, Jed I. 2019. Towards end-to-end (E2E) modelling in a consistent NPZD-F modelling framework (ECOSMO E2E_v1. 0): application to the North Sea and Baltic Sea. *Geoscientific Model Development*, **12**(5), 1765–1789.
- Dalpadado, P, Ellertsen, B, Melle, W, & Dommasnes, A. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES Journal of Marine Science*, **57**(4), 843–857.

- Dammhahn, Melanie, Dingemanse, Niels J, Niemelä, Petri T, & Réale, Denis. 2018. *Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history*.
- Daniels, Jason, Chaput, Gérald, & Carr, Jonathan. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, **75**(11), 1811–1822.
- Daniels, Jason, Sutton, Stephen, Webber, Dale, & Carr, Jonathan. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. *Animal Biotelemetry*, **7**(1), 16.
- Daniels, Jason, Breau, Cindy, Carr, Jon, Castonguay, Martin, Chassé, Joël, Lavoie, Diane, Roloson, Scott, & Ouellet, Valerie. 2026. An individual based modelling approach to simulating Atlantic salmon post smolt migration in the Gulf of St. Lawrence. *ICES Journal of Marine Science*, **83**(1), fsaf239.
- Darwall, W. 2023. *IUCN Red List of Threatened Species: Salmo salar*. *IUCN Red List of Threatened Species*.
- Davidson, J. 2008. Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, **73**(4), 1065–1074.
- de Eyto, Elvira, & McGinnity, Philip. 2023. Fish lengths of juvenile Atlantic salmon from the Burrishoole catchment, Co. Mayo, Ireland (1997-2019). *Marine Institute, Ireland*.
- DeAngelis, Donald L, & Grimm, Volker. 2014. Individual-based models in ecology after four decades. *F1000prime reports*, **6**, 39.
- Delandmeter, Philippe, & Van Sebille, Erik. 2019. The Parcels v2. 0 Lagrangian framework: new field interpolation schemes. *Geoscientific Model Development*, **12**(8), 3571–3584.
- Den Boer, Pieter J. 1968. Spreading of risk and stabilization of animal numbers. *Acta biotheoretica*, **18**(1-4), 165–194.
- Diack, Graeme. 2021. Atlantic salmon smolt migration timing for 9 rivers across UK, Ireland and France. *Knowledge Network for Biocomplexity*. <https://doi.org/10.5063/F1HQ3XD1>.
- Dieperink, C, Bak, BD, Pedersen, L-F, Pedersen, Michael Ingemann, & Pedersen, Stig. 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology*, **61**(3), 848–852.
- Dingle, Hugh. 1996. *Migration: the biology of life on the move*. Oxford University Press.
- Dingle, Hugh, & Drake, V Alistair. 2007. What is migration? *Bioscience*, **57**(2), 113–121.
- Doak, Daniel F, Bigger, D, Harding, EK, Marvier, MA, O'malley, RE, & Thomson, D. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist*, **151**(3), 264–276.

- Dolmaire, Emma. 2022. Spatial modelling of blue whiting population dynamics in the north-east Atlantic. *PhD thesis, University of Strathclyde*.
- Dorfman, Arik, Hills, Thomas T, & Scharf, Inon. 2022. A guide to area-restricted search: a foundational foraging behaviour. *Biological Reviews*, **97**(6), 2076–2089.
- Døving, Kjell B, & Stabell, Ole B. 2003. Trails in open waters: sensory cues in salmon migration. *Pages 39–52 of: Sensory processing in aquatic environments*. Springer.
- Dreujou, Elliot, Beauchesne, David, Daigle, Rémi M, Carrière, Julie, Noisette, Fanny, McKindsey, Christopher W, & Archambault, Philippe. 2023. Multiple human activities in coastal benthic ecosystems: Introducing a metric of cumulative exposure. *Elem Sci Anth*, **11**(1), 00024.
- Drinkwater, Kenneth F, Belgrano, Andrea, Borja, Angel, Conversi, Alessandra, Edwards, Martin, Greene, Charles H, Ottersen, Geir, Pershing, Andrew J, & Walker, Henry. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *Geophysical Monograph-American Geophysical Union*, **134**, 211–234.
- Dubost, G. 2014. *Rapport du projet «MigrenMer»: Synthèse et valorisation des connaissances disponibles sur les migrants amphihalins en mer Rapport final*. Office Français de la Biodiversité.
- Ducharme, LJA. 1969. Atlantic salmon returning for their fifth and sixth consecutive spawning trips. *Journal of the Fisheries Board of Canada*, **26**(6), 1661–1664.
- Dunkley, DA, & Shearer, WM. 1982. An assessment of the performance of a resistivity fish counter. *Journal of fish biology*, **20**(6), 717–737.
- Einum, Sigurd, & Nislow, Keith H. 2011. Variation in population size through time and space: theory and recent empirical advances from Atlantic salmon. *Atlantic salmon ecology*, 277–298.
- Elliott, S. 2023. Modelling the distribution of rare and data-poor diadromous fish at sea for protected area management. *Progress in Oceanography*, **210**, 102924.
- Elliott, Sophie AM, Aebischer, Nicholas J, Gillson, Jonathan P, Utne, Kjell R, Beaumont, William A, Boraiah, Keerthan, & Roberts, Dylan E. 2026. Atlantic salmon survival during different life-stages: time to focus on improving marine survival to slow population declines. *Frontiers in Ecology and Evolution*, **14**.
- English, Greg, Wilson, Brent M, Lawrence, Michael J, Black, Matt, Hawkes, James P, Hardie, David C, Daniels, Jason M, Carr, Jonathan W, Rycroft, Claire, Crossin, Glenn T, *et al.* 2023. Determining early marine survival and predation by endothermic predators on acoustically tagged Atlantic salmon (*Salmo salar*) post-smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, **81**(4), 387–402.

- Erich, Magdalena, Ringler, Max, Hödl, Walter, & Ringler, Eva. 2015. Brood-partitioning behaviour in unpredictable environments: hedging the bets? *Behavioral Ecology and Sociobiology*, **69**(6), 1011–1017.
- Falkegård, Morten, Lennox, Robert J, Thorstad, Eva B, Einum, Sigurd, Fiske, Peder, Garmo, Øyvind A, Garseth, Ase, Skoglund, Helge, Solberg, Monica Favnebøe, Utne, Kjell Rong, *et al.* 2023. Predation of Atlantic salmon across ontogenetic stages and impacts on populations. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Feist, Blake E, Anderson, James Jay, & Miyamoto, Robert. 1991. Potential impacts of pile driving on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon behavior and distribution.
- Finstad, Anders G, Einum, Sigurd, Ugedal, Ola, & Forseth, Torbjørn. 2009. Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. *Journal of Animal Ecology*, 226–235.
- Finstad, Anders G, Armstrong, John D, & Nislow, Keith H. 2011. Freshwater habitat requirements of Atlantic salmon. *Atlantic salmon ecology*, 67–87.
- Fisheries, Eastern Inshore, & Authority, Conservation. 2018. *Strategic Assessment 2017-18. Appendix 1 - Methodology and outputs from initial assessment*.
- Flávio, Hugo, Kennedy, Richard, Ensing, Dennis, Jepsen, Niels, & Aarestrup, Kim. 2020. Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fisheries Management and Ecology*, **27**(1), 92–101.
- Flávio, Hugo, Caballero, Pablo, Jepsen, Niels, & Aarestrup, Kim. 2021. Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho. *Ecology of Freshwater Fish*, **30**(1), 61–72.
- Floyd, Trevor A, MacInnis, Charles, & Taylor, Barry R. 2009. Effects of artificial woody structures on Atlantic salmon habitat and populations in a Nova Scotia stream. *River Research and Applications*, **25**(3), 272–282.
- Foldvik, Anders, & Kvingedal, Eli. 2018. Long-term PIT tag retention rates in Atlantic salmon (*Salmo salar*). *Animal Biotelemetry*, **6**(1), 1–4.
- Frantz, B. 2024. Combining potential and realized distribution modeling of telemetry data for a bycatch risk assessment. *Ecology and Evolution*, **14**(6), 11541.
- Fraser, Dylan J, Weir, Laura K, Bernatchez, Louis, Hansen, Michael Møller, & Taylor, Eric B. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity*, **106**(3), 404–420.

- Friedland, KD, Manning, JP, Link, Jason S, Gilbert, JR, Gilbert, AT, & O'Connell Jr, AF. 2012. Variation in wind and piscivorous predator fields affecting the survival of Atlantic salmon, *Salmo salar*, in the Gulf of Maine. *Fisheries Management and Ecology*, **19**(1), 22–35.
- Friedland, Kevin D, & Todd, Christopher D. 2012. Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biology*, **35**(4), 593–609.
- Friedland, Kevin D, Hansen, Lars P, & Dunkley, David A. 1998. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. *Fisheries Oceanography*, **7**(1), 22–34.
- Friedland, Kevin D, Hansen, Lars P, Dunkley, David A, & MacLean, Julian C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine science*, **57**(2), 419–429.
- Friedland, Kevin D, MacLean, Julian C, Hansen, Lars P, Peyronnet, Arnaud J, Karlsson, Lars, Reddin, David G, Ó Maoiléidigh, Niall, & McCarthy, Jennifer L. 2009. The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science*, **66**(2), 289–304.
- Furey, Nathan B, Vincent, Stephen P, Hinch, Scott G, & Welch, David W. 2015. Variability in migration routes influences early marine survival of juvenile salmon smolts. *PLoS One*, **10**(10), e0139269.
- Garnier, Soizic, Murray, Rory O'Hara, Gillibrand, Philip A, Gallego, Alejandro, Robins, Peter, & Moriarty, Meadhbh. 2025. Particle tracking modelling in coastal marine environments: Recommended practices and performance limitations. *Ecological Modelling*, **501**, 110999.
- Gilbey, John, Utne, Kjell Rong, Wennevik, Vidar, Beck, Alexander Christian, Kausrud, Kyrre, Hindar, Kjetil, Garcia de Leaniz, Carlos, Cherbonnel, Corrine, Coughlan, Jamie, Cross, Tom F, *et al.* 2021. The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, **22**(6), 1274–1306.
- Gillson, Jonathan P, Bašić, Tea, Davison, Phil I, Riley, William D, Talks, Lawrence, Walker, Alan M, & Russell, Ian C. 2022. A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. *Reviews in Fish Biology and Fisheries*, **32**(3), 879–919.
- Gislason, Astthor, & Astthorsson, Olafur S. 2002. The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia: North Atlantic Marine Science*, **87**(3), 236–247.
- Glover, Kevin A, Solberg, Monica F, McGinnity, Phil, Hindar, Kjetil, Verspoor, Eric, Coulson, Mark W, Hansen, Michael M, Araki, Hitoshi, Skaala, Øystein, & Svåsand, Terje. 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish and Fisheries*, **18**(5), 890–927.

- Godfrey, Jason D, Stewart, David C, Middlemas, Stuart J, & Armstrong, John D. 2015. Depth use and migratory behaviour of homing Atlantic salmon (*Salmo salar*) in Scottish coastal waters. *ICES Journal of Marine Science*, **72**(2), 568–575.
- Greene, Charles H, & Pershing, Andrew J. 2000. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES Journal of Marine Science*, **57**(6), 1536–1544.
- Greene, Correigh M, Hall, Jason E, Guilbault, Kimberly R, & Quinn, Thomas P. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters*, **6**(3), 382–386.
- Greenstreet, S. 2007. Relationship between TACs, fish landings and fishing effort in the North Sea. *Fisheries Research Services, Col. Report*.
- Greenstreet, S., Holland, G., Fraser, T., & Allen, V. 2009. Modelling demersal fishing effort based on landings and days absence from port, to generate indicators of “activity”. *ICES Journal of Marine Science*, **66**(5), 886–901.
- Gregory, Stephen D, Armstrong, John D, & Britton, J Robert. 2018. Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival. *Journal of Fish Biology*, **92**(3), 579–592.
- Gregory, Stephen D, Ibbotson, Anton T, Riley, William D, Nevoux, Marie, Lauridsen, Rasmus B, Russell, Ian C, Britton, J Robert, Gillingham, Phillipa K, Simmons, Olivia M, & Rivot, Etienne. 2019. Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, **76**(6), 1702–1712.
- Griffiths, Jennifer R, Schindler, Daniel E, Armstrong, Jonathan B, Scheuerell, Mark D, Whited, Diane C, Clark, Robert A, Hilborn, Ray, Holt, Carrie A, Lindley, Steven T, Stanford, Jack A, *et al.* 2014. Performance of salmon fishery portfolios across western North America. *Journal of Applied Ecology*, **51**(6), 1554–1563.
- Gudbergsson, G., Eiriksson, G., & Oskarsson, S. 2014. *Bycatch of Atlantic salmon in Pelagic Fisheries for Mackerel and Herring in Iceland 2010-2013*. ICES North Atlantic Salmon Working Group WP23.
- Gudjonsson, Sigurdur, Jonsson, Ingi Runar, & Antonsson, Thorolfur. 2005. Migration of Atlantic salmon, *Salmo salar*, smolt through the estuary area of River Ellidaar in Iceland. *Environmental Biology of Fishes*, **74**(3), 291–296.
- Guðjónsson, Sigurður, Einarsson, Sigurður Már, Jónsson, Ingi Rúnar, & Guðbrandsson, Jóhannes. 2015. Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. *Canadian Journal of Fisheries and Aquatic Sciences*, **72**(7), 1087–1098.
- Gunther, Erna. 1926. An analysis of the first salmon ceremony. *American Anthropologist*, **28**(4), 605–617.

- Guri, G. 2024. Predicting trawl catches using environmental DNA. *ICES Journal of Marine Science*, **81**(8), 1536–1548.
- Halfyard, EA, Gibson, AJF, Ruzzante, DE, Stokesbury, MJW, & Whoriskey, FG. 2012. Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, **81**(5), 1626–1645.
- Hamre, Johannes. 1980. Biology, exploitation, and management of the Northeast Atlantic mackerel.
- Hansen, Lars P, & Jonsson, Bror. 1989. Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. *Aquaculture*, **82**(1-4), 367–373.
- Hansen, LP, & Quinn, TP. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 104–118.
- Hanson, Nora, Ounsley, James, Burton, Tim, Auer, Sonya, Hunt, James H, Shaw, Brian, Henderson, Jim, & Middlemas, Stuart J. 2020. Hierarchical analysis of wild Atlantic salmon (*Salmo salar*) fecundity in relation to body size and developmental traits. *Journal of Fish Biology*, **96**(2), 316–326.
- Hanson, Nora, Ounsley, James, Middlemas, Stuart J, Gilbey, John, & Todd, Christopher D. 2022. Inferring individual marine migration from otolith ecogeochemical signatures of a wide-ranging fish. *Frontiers in Marine Science*, **9**, 1071081.
- Hanson, Nora Nell, Wurster, Christopher Martin, Todd, Christopher David, *et al.* 2013. Reconstructing marine life-history strategies of wild Atlantic salmon from the stable isotope composition of otoliths. *Marine Ecology Progress Series*, **475**, 249–266.
- Harvey, Alison, Skaala, Øystein, Borgstrøm, Reidar, Fjeldheim, Per Tommy, Christine Andersen, Kaja, Rong Utne, Kjell, Askeland Johnsen, Ingrid, Fiske, Peder, Winterthun, Synne, Knutar, Sofie, *et al.* 2022. Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecology and evolution*, **12**(4), e8780.
- Hatch, J. 2023. Evaluating simple measures of spatial-temporal overlap as a proxy for encounter risk between a protected species and commercial fishery. *Frontiers in Conservation Science*, **4**.
- Hátún, H, & Chafik, L. 2018. On the recent ambiguity of the North Atlantic subpolar gyre index. *Journal of Geophysical Research: Oceans*, **123**(8), 5072–5076.
- Hátún, H, Lohmann, Katja, Matei, Daniela, Jungclaus, Johann H, Pacariz, S, Bersch, M, Gislason, A, Ólafsson, J, & Reid, PC. 2016. An inflated subpolar gyre blows life toward the northeastern Atlantic. *Progress in Oceanography*, **147**, 49–66.

- Hátún, Hjálmar, Sandø, Anne Britt, Drange, Helge, Hansen, Bogi, & Valdimarsson, Heðinn. 2005. Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science*, **309**(5742), 1841–1844.
- Hátún, Hjálmar, Payne, MR, Beaugrand, G, Reid, PC, Sandø, AB, Drange, H, Hansen, B, Jacobsen, JA, & Bloch, D. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, **80**(3-4), 149–162.
- Haughland, M., Holst, J., Holm, M., & Hansen, L. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, **63**(8), 1488–1500.
- Haugland, Monika, Holst, Jens Christian, Holm, Marianne, & Hansen, Lars Petter. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, **63**(8), 1488–1500.
- Hedger, R.D., Kjellman, M., Thorstad, E.B., Strøm, J.F., & Rikardsen, A.H. 2022. Diving and feeding of adult Atlantic salmon when migrating through the coastal zone in Norway. *Environmental Biology of Fishes*.
- Hedger, Richard D, Martin, François, Hatin, Daniel, Caron, François, Whoriskey, Fred G, & Dodson, Julian J. 2008. Active migration of wild Atlantic salmon *Salmo salar* smolt through a coastal embayment. *Marine Ecology Progress Series*, **355**, 235–246.
- Hellenbrecht, Lea Marie, Utne, Kjell Rong, Karlsen, Ørjan, Glover, Kevin Alan, & Wennevik, Vidar. 2023. Diet analysis of Atlantic salmon (*Salmo salar*) post-smolts after the ecological regime shift in the Northeast Atlantic. *Fisheries Research*, **262**, 106672.
- Hersbach, Hans, Bell, Bill, Berrisford, Paul, Hirahara, Shoji, Horányi, András, Muñoz-Sabater, Joaquín, Nicolas, Julien, Peubey, Carole, Radu, Raluca, Schepers, Dinand, *et al.* 2020. The ERA5 global reanalysis. *Quarterly Journal of the Royal Meteorological Society*, **146**(730), 1999–2049.
- Hines, E. 2020. Getting to the bottom of bycatch: a GIS-based toolbox to assess the risk of marine mammal bycatch. *Endangered Species Research*, **42**, 37–57.
- Hodgson, Emma E, Wilson, Samantha M, & Moore, Jonathan W. 2020. Changing estuaries and impacts on juvenile salmon: A systematic review. *Global change biology*, **26**(4), 1986–2001.
- Høgåsen, Helga Rachel. 1998. *Physiological changes associated with the diadromous migration of salmonids*. NRC Research Press.
- Holliday, N Penny, Bersch, Manfred, Berx, Barbara, Chafik, Léon, Cunningham, Stuart, Florindo-López, Cristian, Hátún, Hjálmar, Johns, William, Josey, Simon A, Larsen, Karin Margretha H, *et al.* 2020. Ocean circulation causes the largest freshening event for 120 years in eastern subpolar North Atlantic. *Nature communications*, **11**(1), 585.

- Holm, M, Holst, J Chr, & Hansen, LP. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science*, **57**(4), 955–964.
- Holst, Jens Christian, Hansen, Lars Petter, & Holm, Marianne. 1996. Observations of abundance, stock composition, body size and food of postsmolts of Atlantic salmon in the NE Atlantic during summer. ICES.
- Holt, Jason, Hughes, Sarah, Hopkins, Joanne, Wakelin, Sarah L, Holliday, N Penny, Dye, Stephen, González-Pola, César, Hjøllø, Solfrid Sætre, Mork, Kjell Arne, Nolan, Glen, *et al.* 2012. Multi-decadal variability and trends in the temperature of the northwest European continental shelf: a model-data synthesis. *Progress in Oceanography*, **106**, 96–117.
- Holt, Jason, Polton, Jeff, Huthnance, John, Wakelin, Sarah, O’dea, Enda, Harle, James, Yool, Andrew, Artioli, Yuri, Blackford, Jerry, Siddorn, John, *et al.* 2018. Climate-driven change in the North Atlantic and Arctic Oceans can greatly reduce the circulation of the North Sea. *Geophysical Research Letters*, **45**(21), 11–827.
- Houpert, Loïc, Cunningham, Stuart, Fraser, Neil, Johnson, Clare, Holliday, N Penny, Jones, Samuel, Moat, Ben, & Rayner, Darren. 2020. Observed variability of the North Atlantic Current in the Rockall Trough from 4 years of mooring measurements. *Journal of Geophysical Research: Oceans*, **125**(10), e2020JC016403.
- Hubley, P Bradford, Amiro, Peter G, Gibson, A Jamie F, Lacroix, Gilles L, & Redden, Anna M. 2008. Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. *ICES Journal of Marine Science*, **65**(9), 1626–1634.
- Humston, Robert, Olson, Donald B, & Ault, Jerald S. 2004. Behavioral assumptions in models of fish movement and their influence on population dynamics. *Transactions of the American Fisheries Society*, **133**(6), 1304–1328.
- Hurrell, James W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science*, **269**(5224), 676–679.
- Hutchings, Jeffrey A, Ardren, William R, Barlaup, Bjørn T, Bergman, Eva, Clarke, Keith D, Greenberg, Larry A, Lake, Colin, Piironen, Jorma, Sirois, Pascal, Sundt-Hansen, Line E, *et al.* 2019. Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, **76**(10), 1697–1708.
- Hvidsten, NA, & Møkkelgjerd, PI. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. *Journal of fish biology*, **30**(3), 273–280.
- Hvidsten, NILS ARNE, Heggberget, TG, & Jensen, ARNE J. 1998. Sea water temperatures at Atlantic salmon smolt entrance. *Nordic Journal of Freshwater Research*, 79–86.
- Hvidsten, Nils Arne, Jensen, AJ, Rikardsen, AH, Finstad, B, Aure, J, Stefansson, S, Fiske, P, & Johnsen, BO. 2009. Influence of sea temperature and initial marine feeding on survival of

- Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. *Journal of Fish Biology*, **74**(7), 1532–1548.
- Ianelli, J., & Stram, D. 2015. Estimating impacts of the pollock fishery bycatch on western Alaska Chinook salmon. *ICES Journal of Marine Science*, **72**(4), 1159–1172.
- ICES. 2004. Report of the Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries (SGBYSAL). *ICES Expert Group reports*.
- ICES. 2005. Report of the Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries (SGBYSAL). *ICES Expert Group reports*.
- ICES. 2007. Report of the northern pelagic and blue whiting fisheries working group (WGNPBW). *ICES Expert Group reports*.
- ICES. 2010. Report of the Working Group on Widely-Distributed Stocks (WGWIDE). *ICES Expert Group reports*.
- ICES. 2013a. Report of the Baltic Salmon and Trout assessment Working Group (WGBAST). *ICES Expert Group reports*.
- ICES. 2013b. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG). *ICES Expert Group reports*.
- ICES. 2019. Working Group on Widely Distributed Stocks (WGWIDE). *ICES Scientific Reports*.
- ICES. 2020. Nasco Workshop for North Atlantic Salmon At-Sea Mortality (WKSALMON, outputs from 2019 meeting). *ICES Scientific Reports*, **69**(2), 175.
- ICES. 2021a. Norwegian Sea ecoregion - Fisheries overview. *ICES Advice: Fisheries Overviews*.
- ICES. 2021b. Second Workshop on Atlantic Chub Mackerel (*Scomber colias*) (WKCOLIAS2). *ICES Scientific Reports*.
- ICES. 2021c. Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*.
- ICES. 2023a. Atlantic salmon from the Northeast Atlantic. *ICES Advice on fishing opportunities, catch, and effort. Report of the ICES Advisory Committee. ICES advice*.
- ICES. 2023b. Northwestern Working Group (NWWG). *ICES Scientific Reports*.
- ICES. 2023c. The Second ICES/NASCO Workshop on Salmon Mortality at Sea (WKSALMON2; outputs from 2022 meeting). *ICES Scientific Reports*.
- ICES. 2023d. Stock annex: Capelin (*Mallotus villosus*) in subareas 1 and 2 (Northeast Arctic), excluding Division 2.a west of 5°W (Barents Sea capelin). *ICES Stock Annexes*.
- ICES. 2023e. Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*.

- ICES. 2023f. Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA). *ICES Scientific Reports*.
- ICES. 2023g. Working Group on Widely Distributed Stocks (WGWIDE). *ICES Scientific Reports*.
- ICES. 2024a. Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*.
- ICES. 2024b. Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA). *ICES Scientific Reports*.
- ICES. 2024c. Working Group on Widely Distributed Stocks (WGWIDE). *ICES Scientific Reports*.
- ICES. 2025a. WGBYC Data call 2025: Bycatch of protected species for ICES advisory work. *Data Calls*.
- ICES. 2025b. Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*.
- ICES. 2025c. Working Group on Widely Distributed Stocks (WGWIDE). *ICES Scientific Reports*.
- IPCC. 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. *Cambridge University Press*.
- Islam, Shahinur S, Wringe, Brendan F, Bradbury, Ian R, & Fleming, Ian A. 2020. Behavioural variation among divergent European and North American farmed and wild Atlantic salmon (*Salmo salar*) populations. *Applied Animal Behaviour Science*, **230**, 105029.
- Iversen, Svein A. 2002. Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. *ICES Marine Science Symposia*.
- Jacobsen, J. 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 Journal of Marine Science*, **69**(9), 1598–1608.
- Jacobson, Eiren K, Yack, Tina M, & Barlow, Jay. 2013. Evaluation of an automated acoustic beaked whale detection algorithm using multiple validation and assessment methods.
- Jensen, JLA, Strøm, JF, Nikolopoulos, A, Primicerio, R, Skarðhamar, J, Atencio, BJ, Strand, JET, Bjørn, PA, & Bøhn, T. 2022. Micro-and macro-habitat selection of Atlantic salmon, *Salmo salar*, post-smolts in relation to marine environmental cues. *ICES Journal of Marine Science*.
- Jepsen, Niels, Holthe, Espen, & Økland, F. 2006. Observations of predation on salmon and trout smolts in a river mouth. *Fisheries Management & Ecology*, **13**(5).

- Johnsen, Ingrid A, Harvey, Alison, Sævik, Pål Næverlid, Sandvik, Anne D, Ugedal, Ola, Ådlandsvik, Bjørn, Wennevik, Vidar, Glover, Kevin A, & Karlsen, Ørjan. 2021. Salmon lice-induced mortality of Atlantic salmon during post-smolt migration in Norway. *ICES journal of Marine science*, **78**(1), 142–154.
- Johnson, Chris J, Parker, Katherine L, Heard, Douglas C, & Gillingham, Michael P. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, **71**(2), 225–235.
- Jones, Sam, Cottier, Finlo, Inall, Mark, & Griffiths, Colin. 2018. Decadal variability on the Northwest European continental shelf. *Progress in Oceanography*, **161**, 131–151.
- Jonsson, B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science*, **54**(6), 1031–1039.
- Jonsson, Bror, & Jonsson, Nina. 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. *Journal of fish biology*, **75**(10), 2381–2447.
- Jonsson, Bror, & Jonsson, Nina. 2011. Smolts and smolting. *Pages 211–245 of: Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*. Springer.
- Jonsson, N, & Jonsson, B. 2004. Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). *Journal of fish biology*, **64**(1), 241–247.
- Jonsson, N, Jonsson, B, & Fleming, IA. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Functional Ecology*, 89–96.
- Jonsson, N, Jonsson, B, & Hansen, LP. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, 425–436.
- Jonsson, N, Jonsson, B, & Hansen, LP. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, **67**(5), 751–762.
- Jonsson, Nina, Jonsson, Bror, & Hansen, Lars Petter. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology*, **40**(5), 900–911.
- Kadri, S, Metcalfe, NB, Huntingford, FA, & Thorpe, JE. 1995. What controls the onset of anorexia in maturing adult female Atlantic salmon? *Functional Ecology*, 790–797.
- Kashetsky, Tovah, Avgar, Tal, & Dukas, Reuven. 2021. The cognitive ecology of animal movement: evidence from birds and mammals. *Frontiers in Ecology and Evolution*, **9**, 724887.
- Kennedy, Richard, Rosell, Robert, Hunter, Ewan, & del Villar-Guerra, Diego. 2023. Programmed acoustic tags reveal novel information on late-phase marine life in Atlantic salmon, *Salmo salar*. *Journal of Fish Biology*, **102**(3), 707–711.

- King, TL, Kalinowski, Steven T, Schill, WB, Spidle, AP, & Lubinski, BA. 2001. Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. *Molecular Ecology*, **10**(4), 807–821.
- Klemetsen, A, Amundsen, P-A, 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. *Ecology of freshwater fish*, **12**(1), 1–59.
- Knight, Elly C, Hannah, Kevin C, Foley, Gabriel J, Scott, Chris D, Brigham, R Mark, & Bayne, Erin. 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *ACE*, **12**(2), 14.
- Koed, Anders, Baktoft, Henrik, & Bak, Brian Daniel. 2006. Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River research and applications*, **22**(1), 69–78.
- Koed, Anders, Birnie-Gauvin, Kim, Sivebæk, Finn, & Aarestrup, Kim. 2020. From endangered to sustainable: Multi-faceted management in rivers and coasts improves Atlantic salmon (*Salmo salar*) populations in Denmark. *Fisheries Management and Ecology*, **27**(1), 64–76.
- Koul, Vimal, Tesdal, Jan-Erik, Bersch, Manfred, Hátún, Hjálmar, Brune, Sebastian, Borchert, Leonard, Haak, Helmuth, Schrum, Corinna, & Baehr, Johanna. 2020. Unraveling the choice of the north Atlantic subpolar gyre index. *Scientific Reports*, **10**(1), 1005.
- Kroodsma, David A, Mayorga, Juan, Hochberg, Timothy, Miller, Nathan A, Boerder, Kristina, Ferretti, Francesco, Wilson, Alex, Bergman, Bjorn, White, Timothy D, Block, Barbara A, *et al.* 2018. Tracking the global footprint of fisheries. *Science*, **359**(6378), 904–908.
- Kundegorski, Mikolaj E, Honkanen, Hannele M, Stephen, Alastair, Torney, Colin J, Killen, Shaun, & Adams, Colin E. 2025. Defining the water flow cues for navigation in migrating Atlantic salmon smolts. *Journal of Fish Biology*.
- Kurlansky, Mark. 2020. *Salmon: A fish, the earth, and the history of a common fate*. Simon and Schuster.
- Lacroix, Gilles L. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**(9), 2063–2079.
- Lacroix, Gilles L. 2013. Migratory strategies of Atlantic salmon (*Salmo salar*) postsmolts and implications for marine survival of endangered populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(1), 32–48.
- Lacroix, Gilles L, McCurdy, Paul, & Knox, Derek. 2004. Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society*, **133**(6), 1455–1471.

- Lacroix, GL, & McCurdy, P. 1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology*, **49**(6), 1086–1101.
- Lank, David B, Butler, Robert W, Ireland, John, & Ydenberg, Ronald C. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos*, **103**(2), 303–319.
- Larsen, Martin H, Thorn, Aske N, Skov, Christian, & Aarestrup, Kim. 2013. Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. *Animal Biotelemetry*, **1**(1), 19.
- Lawrence, MJ, Wilson, BM, Reid, GK, Hawthorn, C, English, G, Black, M, Leadbeater, S, McKindsey, CW, & Trudel, M. 2023. The fate of intracoelomic acoustic transmitters in Atlantic salmon (*Salmo salar*) post-smolts and wider considerations for causal factors driving tag retention and mortality in fishes. *Animal Biotelemetry*, **11**(1), 40.
- Lehnert, Sarah J, Kess, Tony, Bentzen, Paul, Kent, Matthew Peter, Lien, Sigbjørn, Gilbey, John, Clément, Marie, Jeffery, NW, Waples, Robin S, & Bradbury, Ian R. 2019. Genomic signatures and correlates of widespread population declines in salmon. *Nature Communications*, **10**(1), 2996.
- Lennox, Robert J, Eliason, Erika J, Havn, Torgeir B, Johansen, Martin R, Thorstad, Eva B, Cooke, Steven J, Diserud, Ola H, Whoriskey, Frederick G, Farrell, Anthony P, & Uglem, Ingebrigt. 2018. Bioenergetic consequences of warming rivers to adult Atlantic salmon *Salmo salar* during their spawning migration. *Freshwater Biology*, **63**(11), 1381–1393.
- Lennox, Robert J, Alexandre, Carlos M, Almeida, Pedro R, Bailey, Kevin M, Barlaup, Bjørn T, Bøe, Kristin, Breukelaar, André, Erkinaro, Jaakko, Forseth, Torbjørn, Gabrielsen, Sven-Erik, *et al.* 2021. The quest for successful Atlantic salmon restoration: perspectives, priorities, and maxims. *ICES Journal of Marine Science*, **78**(10), 3479–3497.
- Lerner, Darren T, Sheridan, Mark A, & McCormick, Stephen D. 2012. Estrogenic compounds decrease growth hormone receptor abundance and alter osmoregulation in Atlantic salmon. *General and comparative endocrinology*, **179**(2), 196–204.
- Lilly, Jessie, Honkanen, Hannele M, Bailey, David M, Bean, Colin W, Forrester, Ruaidhri, Rodger, Jessica R, & Adams, Colin E. 2022. Investigating the behaviour of Atlantic salmon (*Salmo salar* L.) post-smolts during their early marine migration through the Clyde Marine Region. *Journal of Fish Biology*, **101**(5), 1285–1300.
- Lilly, Jessie, Honkanen, Hannele H, Rodger, Jessica R, Del Villar, Diego, Boylan, Patrick, Green, Amy, Pereiro, Diego, Wilkie, Lorna, Kennedy, Richard, Barkley, Andrea, *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. *Journal of Fish Biology*, **104**(1), 265–283.
- Limburg, K., & Waldman, J. 2009. Dramatic declines in North Atlantic diadromous fishes. *Bioscience*, **59**(11), 955–965.

- Liu, Chang, Cowles, Geoffrey W, Churchill, James H, & Stokesbury, Kevin DE. 2015. Connectivity of the bay scallop (*Argopecten irradians*) in Buzzards Bay, Massachusetts, USA. *Fisheries Oceanography*, **24**(4), 364–382.
- Lothian, Angus J, Newton, Matthew, Barry, James, Walters, Marcus, Miller, Richard C, & Adams, Colin E. 2018. Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. *Ecology of Freshwater Fish*, **27**(2), 549–558.
- Lothian, Angus J, Rodger, Jessica, Wilkie, Lorna, Walters, Marcus, Miller, Richard, Muller, Karen, & Adams, Colin E. 2024. A comparison of acoustic tag sizes on wild Atlantic salmon *Salmo salar* L. smolt migration success and behaviour. *Ecology of Freshwater Fish*, **33**(4), e12798.
- Lucas, Martyn, & Baras, Etienne. 2008. *Migration of freshwater fishes*. John Wiley & Sons.
- Lux, Fred E. 1971. Age determination of fishes. *NOAA Professional Paper NMFS 13*.
- Maar, Marie, Rindorf, Anna, Møller, Eva Friis, Christensen, Asbjørn, Madsen, Kristine S, & van Deurs, Mikael. 2014. Zooplankton mortality in 3D ecosystem modelling considering variable spatial–temporal fish consumptions in the North Sea. *Progress in Oceanography*, **124**, 78–91.
- Maiello, G. 2024. Fishing in the gene-pool: implementing trawl-associated eDNA metaprobe for large scale monitoring of fish assemblages. *Reviews in Fish Biology and Fisheries*, 1–15.
- Main, Robert Andrew Kenneth. 2021. *Migration of Atlantic salmon (*Salmo salar*) smolts and post-smolts from a Scottish east coast river*. M.Phil. thesis, University of Glasgow.
- Malcolm, I, Millar, C, & Millidine, K. 2015. Spatio-temporal variability in the emigration times and sizes of Scottish Atlantic salmon (*salmo salar*) smolts. *Scottish Marine and Freshwater Science*.
- Malcolm, IA, Godfrey, J, & Youngson, AF. 2010. *Review of migratory routes and behaviour of Atlantic salmon, sea trout and European eel in Scotland’s coastal environment: Implications for the development of marine renewables*. Marine Scotland Science.
- Maoiléidigh, Niall Ó. 2018. *Fifty years of marine tag recoveries from Atlantic salmon*. International Council for the Exploration of the Sea.
- Markowitz, Harry M. 1959. *Portfolio selection: efficient diversification of investments*. Yale University Press.
- Marsh, Robert, Haigh, Ivan D, Cunningham, Stuart A, Inall, Mark E, Porter, Marie, & Moat, Ben I. 2017. Large-scale forcing of the European Slope Current and associated inflows to the North Sea. *Ocean Science*, **13**(2), 315–335.

- Martin, F, Hedger, RD, Dodson, JJ, Fernandes, L, Hatin, D, Caron, F, & Whoriskey, FG. 2009. Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. *Ecology of Freshwater Fish*, **18**(3), 406–417.
- Martín Míguez, Belén, Novellino, Antonio, Vinci, Matteo, Claus, Simon, Calewaert, Jan-Bart, Vallius, Henry, Schmitt, Thierry, Pititto, Alessandro, Giorgetti, Alessandra, Askew, Natalie, *et al.* 2019. The European Marine Observation and Data Network (EMODnet): visions and roles of the gateway to marine data in Europe. *Frontiers in Marine Science*, **6**, 313.
- Mathworks Inc. 2021. MATLAB version 9.11.0.1769968 (R2023b).
- May, Samuel A, Shedd, Kyle R, Gruenthal, Kristen M, Hard, Jeffrey J, Templin, William D, Waters, Charles D, Adkison, Milo D, Ward, Eric J, Habicht, Christopher, Wilson, Lorna I, *et al.* 2024. Salmon hatchery strays can demographically boost wild populations at the cost of diversity: quantitative genetic modelling of Alaska pink salmon. *Royal Society Open Science*, **11**(7), 240455.
- McCarthy, JL, Friedland, KD, & Hansen, LP. 2008. Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. *Journal of Fish Biology*, **72**(7), 1572–1588.
- McCormick, Stephen D. 2024. physiology of smolting. *The 50th Anniversary Issue of Fish Physiology: Physiological Applications*, 1.
- McCormick, Stephen D, Hansen, Lars P, Quinn, Thomas P, & Saunders, Richard L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 77–92.
- McCormick, Stephen D, Lerner, DARREN T, Monette, MICHELLE Y, Nieves-Puigdoller, K, Kelly, JOHN T, & Björnsson, BJÖRN THRANDUR. 2009. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. *Pages 195–214 of: American Fisheries Society Symposium*, vol. 69.
- McGinnity, P, Stone, C, Taggart, JB, Cooke, D, Cotter, D, Hynes, R, McCamley, C, Cross, T, & Ferguson, A. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science*, **54**(6), 998–1008.
- Metcalfe, Neil B, Huntingford, Felicity A, & Thorpe, John E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Animal Behaviour*, **35**(3), 901–911.
- Mills, K., Pershing, A., Sheehan, T., & Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, **19**(10), 3046–3061.

- Milner, NJ, Elliott, JM, Armstrong, JD, Gardiner, R, Welton, JS, & Ladle, M. 2003. The natural control of salmon and trout populations in streams. *Fisheries research*, **62**(2), 111–125.
- Mink, Nicolaas. 2013. *Salmon: a global history*. Reaktion Books.
- Minkoff, David, Putman, Nathan F, Atema, Jelle, & Ardren, William R. 2020. Nonanadromous and anadromous Atlantic salmon differ in orientation responses to magnetic displacements. *Canadian Journal of Fisheries and Aquatic Sciences*, **77**(11), 1846–1852.
- Moore, A, Freake, SM, & Thomas, IM. 1990. Magnetic particles in the lateral line of the Atlantic salmon (*Salmo salar* L.). *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **329**(1252), 11–15.
- Moore, Jonathan W, McClure, Michelle, Rogers, Lauren A, & Schindler, Daniel E. 2010. Synchronization and portfolio performance of threatened salmon. *Conservation Letters*, **3**(5), 340–348.
- Moore, Jonathan W, Ulaski, Marta E, Wilson, Kyle L, Martin, Tara G, Kuiper, Spencer Dakin, Peacock, Stephanie J, Braun, Douglas C, Naman, Sean M, Pitman, Kara J, Reid, Andrea J, *et al.* 2025. A safe operating space for salmon watersheds under rapid climate change. *Fish and Fisheries*.
- Moriarty, PE, Byron, CJ, Pershing, AJ, Stockwell, JD, & Xue, H. 2016. Predicting migratory paths of post-smolt Atlantic salmon (*Salmo salar*). *Marine Biology*, **163**(4), 1–11.
- Mork, Kjell Arne, Gilbey, John, Hansen, Lars Petter, Jensen, Arne J, Jacobsen, Jan Arge, Holm, Marianne, Holst, Jens Christian, Ó Maoiléidigh, Niall, Vikebø, Frode, McGinnity, Philip, *et al.* 2012. Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES Journal of Marine Science*, **69**(9), 1616–1624.
- Morrongiello, John R, Bond, Nicholas R, Crook, David A, & Wong, Bob BM. 2012. Spatial variation in egg size and egg number reflects trade-offs and bet-hedging in a freshwater fish. *Journal of Animal Ecology*, **81**(4), 806–817.
- Muff, S., Nilsen, E., O’Hara, R., & Nater, C. 2022. Rewriting results sections in the language of evidence. *Trends in ecology & evolution*, **37**(3), 203–210.
- Murray, Alexander G, & Moriarty, Meadhbh. 2021. A simple modelling tool for assessing interaction with host and local infestation of sea lice from salmonid farms on wild salmonids based on processes operating at multiple scales in space and time. *Ecological Modelling*, **443**, 109459.
- Murray, Rory O’Hara. 2017. Modelling Scottish shelf seas. *Ocean Challenge*, **22**(1).
- Myers, George S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia*, **1949**(2), 89–97.

- Nelson, Thomas Reid, Michel, Cyril J, Gary, Meagan P, Lehman, Brendan M, Demetras, Nicholas J, Hammen, Jeremy J, & Horn, Michael J. 2021. Effects of Artificial Lighting at Night on Predator Density and Salmonid Predation: ARTIFICIAL LIGHTING IMPACTS SALMONID PREDATION. *Transactions of the American Fisheries Society*, **150**(2), 147–159.
- Nevoux, Marie, Forcada, Jaume, Barbraud, Christophe, Croxall, John, & Weimerskirch, Henri. 2010. Bet-hedging response to environmental variability, an intraspecific comparison. *Ecology*, **91**(8), 2416–2427.
- Newton, Matthew, Barry, James, Dodd, Jennifer A, Lucas, MC, Boylan, P, & Adams, Colin E. 2016. Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. *Journal of Fish Biology*, **89**(3), 1641–1650.
- Newton, Matthew, Barry, James, Lothian, Angus, Main, Robert, Honkanen, Hannele, Mckelvey, Simon, Thompson, Paul, Davies, Ian, Brockie, Nick, Stephen, Alastair, *et al.* 2021. Counter-intuitive active directional swimming behaviour by Atlantic salmon during seaward migration in the coastal zone. *ICES Journal of Marine Science*.
- Newton, Matthew, Main, Robert, Gardiner, Ross, Kynoch, Robert, Gilbey, John, Cauwelier, Eef, Watret, Robert, Stainer, Paul, Bridcut, Emily, Archer, Jonathan A, *et al.* 2026. Distribution of Atlantic salmon (*Salmo salar*) from epipelagic trawling surveys and genetic analysis in Scotland. *ICES Journal of Marine Science*, **83**(2), fsag007.
- Nieto, A. 2015. *European Red List of marine fishes*. Publications Office of the European Union.
- Nilsen, Cecilie, Vollset, Knut Wiik, Velle, Gaute, Barlaup, Bjørn T, Normann, Eirik Straume, Stöger, Elisabeth, & Lennox, Robert J. 2022a. Atlantic salmon of wild and hatchery origin have different migration patterns. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Nilsen, Cecilie, Vollset, Knut Wiik, Velle, Gaute, Barlaup, Bjørn T, Normann, Eirik Straume, Stöger, Elisabeth, & Lennox, Robert J. 2022b. Atlantic salmon of wild and hatchery origin have different migration patterns. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Nye, Janet A, Baker, Matthew R, Bell, Richard, Kenny, Andrew, Kilbourne, K Halimeda, Friedland, Kevin D, Martino, Edward, Stachura, Megan M, Van Houtan, Kyle S, & Wood, Robert. 2014. Ecosystem effects of the Atlantic multidecadal oscillation. *Journal of Marine Systems*, **133**, 103–116.
- Økland, F, Thorstad, EB, Finstad, B, Sivertsgård, R, Plantalech, N, Jepsen, Niels, & McKinley, RS. 2006. Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration. *Fisheries Management and Ecology*, **13**(4), 271–274.
- Olafsson, K. 2016. Origin of Atlantic salmon (*Salmo salar*) at sea in Icelandic waters. *ICES Journal of Marine Science*, **73**(6), 1525–1532.

- Olin, Agnes B, Banas, Neil S, Johns, David G, Heath, Michael R, Wright, Peter J, & Nager, Ruedi G. 2022. Spatio-temporal variation in the zooplankton prey of lesser sandeels: species and community trait patterns from the Continuous Plankton Recorder. *ICES Journal of Marine Science*.
- Olmos, Maxime, Massiot-Granier, Félix, Prévost, Etienne, Chaput, Gérald, Bradbury, Ian R, Nevoux, Marie, & Rivot, Etienne. 2019. Evidence for spatial coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic. *Fish and Fisheries*, **20**(2), 322–342.
- Olmos, Maxime, Payne, Mark R, Nevoux, Marie, Prévost, Etienne, Chaput, Gérald, Du Pontavice, Hubert, Guitton, Jérôme, Sheehan, Timothy, Mills, Katherine, & Rivot, Etienne. 2020. Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Global Change Biology*, **26**(3), 1319–1337.
- Oppedal, Frode, Barrett, Luke T, Fraser, Thomas WK, Vågseth, Tone, Zhang, Guosong, Andersen, Oliver G, Jacson, Lea, Dieng, Marie-Aida, & Vindas, Marco A. 2025. The behavioral and neurobiological response to sound stress in salmon. *Brain Behavior and Evolution*, **100**(1), 11–28.
- OSPAR. 2008. *Case reports for the OSPAR List of Threatened and/or Declining Species and Habitats*. OSPAR Commission.
- Otero, Jaime, L'Abée-Lund, Jan Henning, Castro-Santos, Ted, Leonardsson, Kjell, Storvik, Geir O, Jonsson, Bror, Dempson, Brian, Russell, Ian C, Jensen, Arne J, Baglinière, Jean-Luc, *et al.* 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global change biology*, **20**(1), 61–75.
- Ounsley, James P, Gallego, Alejandro, Morris, David J, & Armstrong, John D. 2020. Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—a modelling study. *ICES Journal of Marine Science*, **77**(1), 315–325.
- Pacariz, S. 2016. Nutrient-driven poleward expansion of the Northeast Atlantic mackerel (*Scomber scombrus*) stock: A new hypothesis. *Elementa*, **4**.
- Pardo, Sebastián A, Bolstad, Geir H, Dempson, J Brian, April, Julien, Jones, Ross A, Raab, Dustin, & Hutchings, Jeffrey A. 2021. Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*.
- Parrish, Donna L, Behnke, Robert J, Gephard, Stephen R, McCormick, Stephen D, & Reeves, Gordon H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian journal of fisheries and aquatic sciences*, **55**(S1), 281–287.

- Petrik, Colleen M, Luo, Jessica Y, Heneghan, RF, Everett, Jason D, Harrison, Cheryl Shannon, & Richardson, AJ. 2022. Assessment and constraint of mesozooplankton in CMIP6 Earth system models. *Global Biogeochemical Cycles*, **36**(11), e2022GB007367.
- Peyronnet, A, Friedland, KD, & Ó Maoileidigh, N. 2008. Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. *Journal of Fish Biology*, **73**(4), 945–962.
- Peyronnet, Arnaud, Friedland, KD, Maoileidigh, NÓ, Manning, M, & Poole, WR. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology*, **71**(3), 684–700.
- Piou, Cyril, & Prévost, Etienne. 2012. A demo-genetic individual-based model for Atlantic salmon populations: Model structure, parameterization and sensitivity. *Ecological modelling*, **231**, 37–52.
- Piou, Cyril, & Prévost, Etienne. 2013. Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. *Global Change Biology*, **19**(3), 711–723.
- Plantalech Manel-La, N. 2009. Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration. *Fisheries Management and Ecology*, **16**(2), 147–154.
- Plantalech Manel-la, N, Chittenden, CM, Økland, F, Thorstad, EB, Davidsen, JG, Sivertsgård, R, McKinley, RS, & Finstad, B. 2011. Does river of origin influence the early marine migratory performance of *Salmo salar*? *Journal of Fish Biology*, **78**(2), 624–634.
- Power, Michael, Thorstad, Eva B, Forseth, Torbjørn, & Fiske, Peder. 2023. Temporal shifts in the marine feeding of individual Atlantic salmon inferred from scale isotope ratios. *Ecology and Evolution*, **13**(11), e10656.
- Priede, Imants George, Solbé, JF de LG, Nott, JE, O’Grady, KT, & Cragg-Hine, D. 1988. Behaviour of adult Atlantic salmon, *Salmo salar* L., in the estuary of the River Ribble in relation to variations in dissolved oxygen and tidal flow. *Journal of Fish Biology*, **33**, 133–139.
- Putman, Nathan F, Scanlan, Michelle M, Billman, Eric J, O’Neil, Joseph P, Couture, Ryan B, Quinn, Thomas P, Lohmann, Kenneth J, & Noakes, David LG. 2014. An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Current Biology*, **24**(4), 446–450.
- Pyper, Brian J, & Peterman, Randall M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(9), 2127–2140.
- Queiroz, N. 2019. Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, **572**(7770), 461–466.

- Quinn, Thomas P. 1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *Journal of Comparative Physiology*, **137**(3), 243–248.
- Rao, C Radhakrishna. 1982. Diversity: Its measurement, decomposition, apportionment and analysis. *Sankhyā: The Indian Journal of Statistics, Series A*, 1–22.
- Reed, Thomas E, Wynne, Robert, Coughlan, Jamie, Gargan, Patrick, Kaufmann, Joshka, Phillips, Karl P, Rinaldo, Adrian, Poole, Russell, & McGinnity, Philip. 2025. A common garden experiment in the wild reveals heritable differences in migration tendencies among brown trout populations. *Journal of Fish Biology*.
- Reilly, James R, & Reilly, Robert J. 2009. Bet-hedging and the orientation of juvenile passerines in fall migration. *Journal of Animal Ecology*, **78**(5), 990–1001.
- Reitan, Ole, Hvidsten, Nils Arne, & Hansen, Lars P. 1987. Bird predation on hatchery reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. *Fauna norvegica*, **8**, 35–38.
- Renkawitz, Mark D, Sheehan, Timothy F, & Goulette, Graham S. 2012. Swimming depth, behavior, and survival of Atlantic salmon postsmolts in Penobscot Bay, Maine. *Transactions of the American Fisheries Society*, **141**(5), 1219–1229.
- Richardson, AJ, Walne, AW, John, AWG, Jonas, TD, Lindley, JA, Sims, DW, Stevens, D, & Witt, M. 2006. Using continuous plankton recorder data. *Progress in Oceanography*, **68**(1), 27–74.
- Rikardsen, AH, Haugland, M, Bjørn, PA, Finstad, B, Knudsen, R, Dempson, JB, Holst, JC, Hvidsten, NA, & Holm, M. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of Fish Biology*, **64**(6), 1655–1679.
- Rikardsen, Audun H, & Dempson, J Brian. 2011. Dietary life-support: the food and feeding of Atlantic salmon at sea. *Atlantic salmon ecology*, 115–143.
- Riley, WD, Bendall, B, Ives, MJ, Edmonds, NJ, & Maxwell, DL. 2012. Street lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture*, **330**, 74–81.
- Rinaldo, Adrian, de Eyto, Elvira, Reed, Thomas, Gjelland, Karl Øystein, & McGinnity, Philip. 2023. Global warming is projected to lead to increased freshwater growth potential and changes in pace of life in Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, **104**(3), 647–661.
- Robertson, Iain A. 2001. *Salmon Conservation in Scotland: A History of Legislative Tradition and Private Action*. <https://cei.org/wp-content/uploads/2013/04/Iain-A.-Robertson-Salmon-Conservation-in-Scotland-A-History-of-Legislative-Tradition-and-Private-Action.pdf>. (last accessed March 2026).

- Rodger, Jessica R, Lilly, Jessie, Honkanen, Hannele M, Del Villar, Diego, Kennedy, Richard, Maoiléidigh, Niall Ó, Boylan, Patrick, Rosell, Robert, Morris, David J, O'Neill, Ross, *et al.* 2025. Inshore and offshore marine migration pathways of Atlantic salmon post-smolts from multiple rivers in Scotland, England, Northern Ireland, and Ireland. *Journal of Fish Biology*, **106**(5), 1422–1439.
- Rose, G. 2005. On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science*, **62**(7), 1360–1374.
- Ross, PS, Kennedy, CJ, Shelley, LK, Tierney, KB, Patterson, DA, Fairchild, WL, & Macdonald, RW. 2013. The trouble with salmon: relating pollutant exposure to toxic effect in species with transformational life histories and lengthy migrations. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(8), 1252–1264.
- Russell, Ian C, Aprahamian, Miran W, Barry, Jon, Davidson, Ian C, Fiske, Peder, Ibbotson, Anton T, Kennedy, Richard J, Maclean, Julian C, Moore, Andrew, Otero, Jaime, *et al.* 2012. The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, **69**(9), 1563–1573.
- Ryman, Nils, & Laikre, Linda. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology*, **5**(3), 325–329.
- Sabal, M. 2023. Warm oceans exacerbate Chinook salmon bycatch in the Pacific hake fishery driven by thermal and diel depth-use behaviours. *Fish and Fisheries*, **24**(6), 910–923.
- Samhuri, Jameal F, & Levin, Phillip S. 2012. Linking land-and sea-based activities to risk in coastal ecosystems. *Biological Conservation*, **145**(1), 118–129.
- Sarafanov, Artem. 2009. On the effect of the North Atlantic Oscillation on temperature and salinity of the subpolar North Atlantic intermediate and deep waters. *ICES Journal of Marine Science*, **66**(7), 1448–1454.
- Säterberg, Torbjörn, Jacobson, Philip, Ovegård, Maria, Rask, Jörgen, Östergren, Johan, Jepsen, Niels, & Florin, Ann-Britt. 2023. Species-and origin-specific susceptibility to bird predation among juvenile salmonids. *Ecosphere*, **14**(12), e4724.
- Satterthwaite, William H, & Carlson, Stephanie M. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **72**(12), 1860–1875.
- Satterthwaite, William H, Carlson, Stephanie M, Allen-Moran, Shanae D, Vincenzi, Simone, Bograd, Steven J, & Wells, Brian K. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Marine Ecology Progress Series*, **511**, 237–248.

- Sayer, C. 2024. *Salmo salar* (Europe assessment). *The IUCN Red List of Threatened Species* 2024. <https://dx.doi.org/10.2305/IUCN.UK.2024-2.RLTS.T19855A212864916.en>.
- Schabetsberger, Robert, Miller, Michael J, Olmo, Giorgio Dall, Kaiser, Roland, Økland, Finn, Watanabe, Shun, Aarestrup, Kim, & Tsukamoto, Katsumi. 2016. Hydrographic features of anguillid spawning areas: potential signposts for migrating eels. *Marine Ecology Progress Series*, **554**, 141–155.
- Schindler, Daniel E, Hilborn, Ray, Chasco, Brandon, Boatright, Christopher P, Quinn, Thomas P, Rogers, Lauren A, & Webster, Michael S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, **465**(7298), 609–612.
- Schindler, Daniel E, Armstrong, Jonathan B, & Reed, Thomas E. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, **13**(5), 257–263.
- Schreck, Carl B, Stahl, Thomas P, Davis, Lawrence E, Roby, Daniel D, & Clemens, Benjamin J. 2006. Mortality estimates of juvenile spring–summer Chinook salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? *Transactions of the American Fisheries Society*, **135**(2), 457–475.
- Schulz-Mirbach, Tanja, Ladich, Friedrich, Plath, Martin, & Heß, Martin. 2019. Enigmatic ear stones: what we know about the functional role and evolution of fish otoliths. *Biological Reviews*, **94**(2), 457–482.
- Sharpe, William F. 1963. A simplified model for portfolio analysis. *Management science*, **9**(2), 277–293.
- Sharpe, William F. 1964. Capital asset prices: A theory of market equilibrium under conditions of risk. *The journal of finance*, **19**(3), 425–442.
- Sharples, Ruth Jemma, Arrizabalaga, B, & Hammond, Philip Steven. 2009. Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Marine Ecology Progress Series*, **390**, 265–276.
- Sheehan, Peter MF, Berx, Barbara, Gallego, Alejandro, Hall, Rob A, Heywood, Karen J, & Hughes, Sarah L. 2017. Thermohaline forcing and interannual variability of northwestern inflows into the northern North Sea. *Continental Shelf Research*, **138**, 120–131.
- Shelton, RGJ, Turrell, WR, Macdonald, A, McLaren, IS, & Nicoll, NT. 1997. Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. *Fisheries Research*, **31**(1-2), 159–162.
- Simons, Andrew M. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B: Biological Sciences*, **278**(1712), 1601–1609.

- Simpson, John H, & Sharples, Jonathan. 2012. *Introduction to the physical and biological oceanography of shelf seas*. Cambridge University Press.
- Skóra, Michał E, Jones, J Iwan, Youngson, Alan F, Robertson, Sean, Wells, Alan, Lauridsen, Rasmus B, & Copp, Gordon H. 2023. Evidence of potential establishment of pink salmon *Oncorhynchus gorbuscha* in Scotland. *Journal of Fish Biology*.
- Smith, I Philip, Booker, Douglas J, & Wells, Neil C. 2009. Bioenergetic modelling of the marine phase of Atlantic salmon (*Salmo salar* L.). *Marine Environmental Research*, **67**(4-5), 246–258.
- Sobocinski, Kathryn L, Greene, Correigh M, Anderson, Joseph H, Kendall, Neala W, Schmidt, Michael W, Zimmerman, Mara S, Kemp, Iris M, Kim, Su, & Ruff, Casey P. 2021. A hypothesis-driven statistical approach for identifying ecosystem indicators of coho and Chinook salmon marine survival. *Ecological Indicators*, **124**, 107403.
- Solomon, DJ, & Sambrook, HT. 2004. Effects of hot dry summers on the loss of Atlantic salmon, *Salmo salar*, from estuaries in South West England. *Fisheries Management and Ecology*, **11**(5), 353–363.
- Sortland, Lene Klubben, Lennox, Robert J, Velle, Gaute, Vollset, Knut Wiik, & Kambestad, Marius. 2023. Impacts of predation by Eurasian otters on Atlantic salmon in two Norwegian rivers. *Freshwater Biology*, **68**(7), 1176–1193.
- Stabell, Ole B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biological Reviews*, **59**(3), 333–388.
- Starrfelt, Jostein, & Kokko, Hanna. 2012. Bet-hedging—a triple trade-off between means, variances and correlations. *Biological Reviews*, **87**(3), 742–755.
- Stich, Daniel S, Zydlewski, Gayle B, Kocik, John F, & Zydlewski, Joseph D. 2015. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Marine and Coastal Fisheries*, **7**(1), 68–86.
- Stock, B. 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences*, **77**(1), 143–163.
- Strøm, John Fredrik, Thorstad, Eva Bonsak, Hedger, Richard David, & Rikardsen, Audun Håvard. 2018. Revealing the full ocean migration of individual Atlantic salmon. *Animal Biotelemetry*, **6**(1), 1–16.
- Sturrock, Anna M, Wikert, JD, Heyne, Timothy, Mesick, Carl, Hubbard, Alan E, Hinkelman, Travis M, Weber, Peter K, Whitman, George E, Glessner, Justin J, & Johnson, Rachel C. 2015. Reconstructing the migratory behavior and long-term survivorship of juvenile Chinook salmon under contrasting hydrologic regimes. *PLoS One*, **10**(5), e0122380.

- Sturrock, Anna M, Carlson, Stephanie M, Wikert, John D, Heyne, Tim, Nusslé, Sébastien, Merz, Joseph E, Sturrock, Hugh JW, & Johnson, Rachel C. 2020. Unnatural selection of salmon life histories in a modified riverscape. *Global Change Biology*, **26**(3), 1235–1247.
- Tabor, Roger A, Brown, Gayle S, & Luiting, Victoria T. 2004. The effect of light intensity on sockeye salmon fry migratory behavior and predation by cottids in the Cedar River, Washington. *North American Journal of Fisheries Management*, **24**(1), 128–145.
- Taylor, Eric B. 1991. A review of local adaptation in Salmonidac, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**(1-3), 185–207.
- Taylor, PB. 1986. Experimental evidence for geomagnetic orientation in juvenile salmon, *Oncorhynchus tshawytscha* Walbaum. *Journal of Fish Biology*, **28**(5), 607–623.
- Tétard, Stéphane, Maire, Anthony, Lemaire, Marine, De Oliveira, Eric, Martin, Patrick, & Courret, Dominique. 2019. Behaviour of Atlantic salmon smolts approaching a bypass under light and dark conditions: importance of fish development. *Ecological Engineering*, **131**, 39–52.
- Thorpe, John E, Mangel, Marc, Metcalfe, Neil B, & Huntingford, Felicity A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology*, **12**(5), 581–599.
- Thorstad, E., Whoriskey, F., Rikardsen, A., & Aarestrup, K. 2011. Aquatic nomads: the life and migrations of the Atlantic salmon. *Atlantic salmon ecology*, **1**(6), 1–32.
- 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. *Journal of fish biology*, **81**(2), 500–542.
- Thorstad, Eva B, Rikardsen, Audun H, Alp, Ahmet, & Økland, Finn. 2013. The use of electronic tags in fish research—an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences*, **13**(5), 881–896.
- Thorstad, Eva B, Bliss, Doug, Breau, Cindy, Damon-Randall, Kim, Sundt-Hansen, Line E, Hatfield, Emma MC, Horsburgh, Grant, Hansen, Heidi, Maoiléidigh, Niall Ó, Sheehan, Timothy, *et al.* 2021. Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **31**(9), 2654–2665.
- Thorstad, Eva B, Frøiland, Eirik, Fagard, Pierre, Kvaal, Marianne, & Lehne, Camilla Kvitberg. 2025. Assessing the extraordinary measures used to counteract invasion of pink salmon into the North Atlantic. *Management of Biological Invasions*, **16**(2), 465–487.
- Todd, Christopher D, Hughes, Sarah L, Marshall, C Tara, MacLEAN, JULIAN C, Lonergan, Michael E, & Biuw, E Martin. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global change biology*, **14**(5), 958–970.

- Todd, Christopher D, Hanson, Nora N, Boehme, Lars, Revie, Crawford W, & Marques, Ana R. 2021. Variation in the post-smolt growth pattern of wild one sea-winter salmon (*Salmo salar* L.), and its linkage to surface warming in the eastern North Atlantic Ocean. *Journal of Fish Biology*, **98**(1), 6–16.
- Tréhin, Cécile, Rivot, Etienne, Lamireau, Ludivine, Meslier, Lisa, Besnard, Anne-Laure, Gregory, Stephen D, & Nevoux, Marie. 2021. Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **78**(6), 659–669.
- Tréhin, C. 2024. A multi-population approach supports common patterns in marine growth and maturation decision in Atlantic salmon (*Salmo salar* L.) from Southern Europe. *Journal of Fish Biology*, **104**(1), 125–138.
- Turrell, B. 1997. *Observations made from FRV Scotia during 1997 investigations of salmon post-smolt at the northwest European shelf edge*. Tech. rept. Technical report. Aberdeen: Marine Laboratory Aberdeen.
- Tyldesley, EJ, Banas, NS, Wakelin, S, Johns, DG, Jardine, JE, Searle, K, Daunt, F, Bull, C, Krivtsov, V, Heath, MR, & Speirs, DC. 2026. Projected declines in zooplankton energy supporting Northeast Atlantic ecosystems. *Nature Communications Earth and Environment*.
- Tyldesley, Emma, Banas, Neil S, Diack, Graeme, Kennedy, Richard, Gillson, Jonathan, Johns, David G, & Bull, Colin. 2024. Patterns of declining zooplankton energy in the northeast Atlantic as an indicator for marine survival of Atlantic salmon. *ICES Journal of Marine Science*, **81**(6), 1164–1184.
- Tyldesley, Emma, Banas, Neil, Kennedy, Richard, Diack, Graeme, & Bull, Colin. 2025. River–sea thermal differential experienced by salmon post-smolts is not a proximal driver of marine survival. *Journal of Fish Biology*.
- Urban, P. 2024. eDNA based bycatch assessment in pelagic fish catches. *Scientific Reports*, **14**(1), 2976.
- Utne, K R, Thomas, K, Jacobsen, J A, Fall, J, Maoiléidigh, N Ó, Broms, C T, & Melle, W. 2020. *Salmon post-smolt, mackerel and herring stomach content*.
- Utne, Kjell Rong, & Mousing, Erik Askov. 2025. Regional differences in salmon post-smolt migration routes can explain variation in individual growth at sea. *Ecological Modelling*, **500**, 110955.
- Utne, Kjell Rong, Thomas, Katie, Jacobsen, Jan Arge, Fall, Johanna, Maoiléidigh, Niall Ó, Broms, Cecilie Thorsen, & Melle, Webjørn. 2021a. Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, **78**(3), 255–268.

- Utne, Kjell Rong, Pauli, Beatriz Diaz, Haugland, Monika, Jacobsen, Jan Arge, Maoileidigh, Niall, Melle, Webjørn, Broms, Cecilie Thorsen, Nøttestad, Leif, Holm, Marianne, Thomas, Katie, *et al.* 2021b. Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES Journal of Marine Science*, **78**(8), 2844–2857.
- Utne, Kjell Rong, Skagseth, Øystein, Wennevik, Vidar, Broms, Cecilie Thorsen, Melle, Webjørn, & Thorstad, Eva B. 2022. Impacts of a changing ecosystem on the feeding and feeding conditions for Atlantic salmon during the first months at sea. *Frontiers in Marine Science*, **9**, 824614.
- van Deurs, Mikael, Christensen, Asbjørn, & Rindorf, Anna. 2013. Patchy zooplankton grazing and high energy conversion efficiency: ecological implications of sandeel behavior and strategy. *Marine Ecology Progress Series*, **487**, 123–133.
- van Zyll De Jong, Michael C, Cowx, Ian G, & Scruton, David A. 1997. An evaluation of instream habitat restoration techniques on salmonid populations in a Newfoundland stream. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, **13**(6), 603–614.
- Vargas-Chacoff, Luis, Regish, Amy M, Weinstock, Andrew, & McCormick, Stephen D. 2018. Effects of elevated temperature on osmoregulation and stress responses in Atlantic salmon *Salmo salar* smolts in fresh water and seawater. *Journal of Fish Biology*, **93**(3), 550–559.
- Vega, Catherine Pérez, Jechow, Andreas, Campbell, James A, Zielinska-Dabkowska, Karolina M, & Hölker, Franz. 2024. Light pollution from illuminated bridges as a potential barrier for migrating fish—Linking measurements with a proposal for a conceptual model. *Basic and Applied Ecology*, **74**, 1–12.
- Verspoor, Eric, Stradmeyer, Lee, & Nielsen, Jennifer L. 2007. *The Atlantic salmon: genetics, conservation and management*. John Wiley & Sons.
- Veselov, AE, Kazakov, RV, Sysoyeva, MI, & Bahmet, IN. 1998. Ontogenesis of rheotactic and optomotor responses of juvenile Atlantic salmon. *Aquaculture*, **168**(1-4), 17–26.
- Vollset, Knut Wiik, Lennox, Robert J, Lamberg, Anders, Skaala, Øystein, Sandvik, Anne Dagrund, Sægrov, Harald, Kvingedal, Eli, Kristensen, Torstein, Jensen, Arne Johan, Haraldstad, Tormod, *et al.* 2021. Predicting the nationwide outmigration timing of Atlantic salmon (*Salmo salar*) smolts along 12 degrees of latitude in Norway. *Diversity and Distributions*, **27**(8), 1383–1392.
- Vollset, Knut Wiik, Urdal, Kurt, Utne, Kjell, Thorstad, Eva B, Sægrov, Harald, Raunsgard, Astrid, Skagseth, Øystein, Lennox, Robert J, Østborg, Gunnel M, Ugedal, Ola, *et al.* 2022. Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, **8**(9), eabk2542.
- Wakelin, SL, Woodworth, PL, Flather, RA, & Williams, JA. 2003. Sea-level dependence on the NAO over the NW European Continental Shelf. *Geophysical Research Letters*, **30**(7).

- Waters, C, Cotter, D, O'Neill, R, Drumm, A, Cooney, J, Bond, N, Rogan, G, & Maoiléidigh, N Ó'. 2024. The use of predator tags to explain reversal movement patterns in Atlantic salmon smolts (*Salmo salar* L.). *Journal of Fish Biology*.
- Watts, Glenn, Battarbee, Richard W, Bloomfield, John P, Crossman, Jill, Daccache, Andre, Durance, Isabelle, Elliott, J Alex, Garner, Grace, Hannaford, Jamie, Hannah, David M, *et al.* 2015. Climate change and water in the UK—past changes and future prospects. *Progress in Physical Geography*, **39**(1), 6–28.
- Wilcove, David S, & Wikelski, Martin. 2008. Going, going, gone: is animal migration disappearing. *PLoS biology*, **6**(7), e188.
- Wilson, Samantha M, Buehrens, Thomas W, Fisher, Jennifer L, Wilson, Kyle L, & Moore, Jonathan W. 2021. Phenological mismatch, carryover effects, and marine survival in a wild steelhead trout *Oncorhynchus mykiss* population. *Progress in Oceanography*, **193**, 102533.
- Witherell, D., Ackley, D., & Coon, C. 2002. An overview of salmon bycatch in Alaska groundfish fisheries. *Alaska Fishery Research Bulletin*, **9**(1), 53–64.
- Xu, Weidong, Miller, Peter I, Quartly, Graham D, & Pingree, Robin D. 2015. Seasonality and interannual variability of the European Slope Current from 20 years of altimeter data compared with in situ measurements. *Remote Sensing of Environment*, **162**, 196–207.
- Yackulic, Charles B, Blake, Stephen, Deem, Sharon, Kock, Michael, & Uriarte, María. 2011. One size does not fit all: flexible models are required to understand animal movement across scales. *Journal of Animal Ecology*, **80**(5), 1088–1096.
- Yasui, Yukio. 2022. Evolutionary bet-hedging reconsidered: What is the mean–variance trade-off of fitness? *Ecological Research*, **37**(3), 406–420.
- Yin, Y., Heather, B., & Hugues, B. 2024. A roadmap for generating annual bycatch estimates from sparse at-sea observer data. *ICES Journal of Marine Science*, **81**(9), 1850–1867.
- Youngson, AF, & Verspoor, E. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 153–160.