# Body condition of returning Atlantic salmon *Salmo salar* L. correlates with scale δ13C and δ15N content deposited at the last marine foraging location

Rory Feeney1, Clive N. Trueman2, Patrick G. Gargan1, William K. Roche1 and Samuel Shephard1

1Inland Fisheries Ireland, 3044 Lake Drive, Citywest Business Campus, Dublin D24 Y265, Ireland

2Ocean and Earth Science, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK

**Corresponding author:**

Rory Feeney,

Inland Fisheries Ireland, 3044 Lake Drive, Citywest Business Campus, Dublin D24 Y265, Ireland.

[Rory.Feeney@fisheriesireland.ie](mailto:Rory.Feeney@fisheriesireland.ie)

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## Abstract

Patterns of feeding and growth of Atlantic salmon *Salmo salar* L. in the marine environment are critical to understanding how observed declines in recruitment may reflect warming or other oceanic drivers. The isotopic composition of scales can provide insight into differences in marine feeding location and possibly temperature regime. We used archived scale samples to measure δ13C and δ15N deposited in the scales of one sea‑winter (1SW) salmon during their last season of growth at sea before they returned to five Irish rivers. δ13C values were related statistically to observed salmon body condition (Fulton’s K), and fish with higher δ13C values tended to show significantly better condition. In contrast, δ15N values were negatively related with body condition. There was no important effect on condition of length at smolt migration, while the effect of duration of marine residence varied among rivers. It is likely that δ13C values partly reflect ambient ocean temperature and recent marine feeding environment before return migration, such that the observed relationship between higher δ13C values and increased body condition may express an advantage for adult fish feeding in warmer, potentially closer, waters. If greater body condition influences fitness, then a changing temperature regime in the Northeast Atlantic may drive shifts in salmon survival and reproduction. This study provides evidence that there is spatial and trophic variation at sea between salmon from rivers of origin that are located relatively close to each other, with potential consequences for body condition and, consequently, fitness and life history; this suggests that salmon populations from geographically proximate rivers within regions may exhibit differential responses to ocean-scale climatic changes across the Northeast Atlantic.

## Keywords

*Salmo salar*, marine feeding, δ13C, δ15N, smolt length, growth at sea, ocean temperature, body condition

# Introduction

The Atlantic salmon (*Salmo salar* L., henceforth ‘salmon’) has a remarkable life history. Juveniles spend one to four years in their natal stream, then transform into smolts and migrate to the ocean, usually in spring. At sea, post‑smolts spread outwards from the coast and follow warmer currents in the North Atlantic, where they forage in the upper surface layers of the ocean (Holm et al. 2000), feeding primarily on small fish and zooplankton (Haugland et al. 2006; Jacobsen & Hansen 2001). Salmon from Ireland are considered part of the southern European complex of salmon populations, which migrate northwards to waters north of the Faroe Islands, into the Norwegian Sea and along the coast of Greenland (Gilbey et al. 2017; Hansen & Jacobsen 2003; International Council for the Exploration of the Sea 2008; Olafsson et al. 2016). Some salmon spend only one winter at sea (1SW) before maturing and returning to spawn in their natal river system the following summer, whereas multi sea‍–‍winter (MSW) salmon spend more than one winter at sea before returning as older, larger fish.

The migration of post‑smolts and their growth into 1SW salmon are vital aspects of salmon population dynamics. Acoustic telemetry of smolts from rivers in the northeast of Ireland has provided evidence that they progress offshore and northwards quickly after entering the sea, using local current conditions to aid their migration (Barry et al. 2020). Modelling of post‑smolt migration from the west of Ireland indicates that their trajectories northwards are influenced by ocean currents, sea surface temperature (SST) or a combination of both (Booker et al. 2008). Simulations of migration in the Northeast Atlantic showed that ocean currents can guide post‑smolts towards oceanic feeding areas, whereas interannual variations in surface currents may alter routes to areas with different prey and environmental conditions (Mork et al. 2012). Since the 1970s, declining marine survival of salmon together with an increasing proportion of fish maturing at 1SW has been a coherent trend across geographically proximate populations from the southern European complex that probably share similar migration routes. This coherence suggests that salmon population dynamics are being driven by large‑scale changes in the North Atlantic marine environment (Friedland et al. 2014; Olmos et al. 2019).

The relationship between ocean temperature and different aspects of salmon migration, growth, survival and recruitment during their time at sea is complex. The migration behaviour of post‑smolts may drive them to seek optimal temperature ranges for growth (Friedland et al. 2003), and there is evidence that spatiotemporal variation in increasing SST is related to reduced growth and survival of post‑smolt salmon at sea, possibly due to climate forcing of the marine food web on which they forage (Friedland et al. 2009). The mechanisms driving the relationship between 1SW salmon recruitment and SST are not clear: the marine survival of Irish 1SW salmon has been negatively correlated to positive North Atlantic Oscillation index and increasing SST (Peyronnet et al. 2008), but synchronous population declines in salmon cohorts that fed in regions of the North Atlantic undergoing differing trends in SST indicate that ocean warming may not be the primary cause of marine mortality. Poorer condition in 1SW salmon has been linked with anomalous warming trends in the subarctic North Atlantic (Todd et al. 2008), and phenological change in Scottish rivers, with 1SW salmon staying at sea for longer in years of poorer adult condition, possibly reflecting an influence of ocean temperature on prey abundance (Todd et al. 2012). Survival of 1SW salmon may also reflect interactions between ambient ocean conditions and infestation with sea lice from coastal salmon farms (Shephard & Gargan 2021). Furthermore, infestation of 1SW salmon with sea lice can decrease their body condition, with negative consequences for their fecundity, sexual maturation and survival at sea, thereby potentially mediating changes in population dynamics (Susdorf et al. 2018).

The ecology of dispersed, highly migratory oceanic animals is difficult to study through direct observation. Stable isotope analysis can provide indirect information regarding ‘trophic geography’: the spatial aspects of migration and foraging (Bird et al. 2018). Fish absorb structural nutrients, such as carbon, nitrogen and other elements, from their environment and diet, incorporating them into biomineralised tissues, such as scales, otoliths and bones, which grow incrementally over their lifetime. Models of spatiotemporal variation in the isotopic composition of these structural nutrients in the environment (i.e., ‘isoscapes’) can be used to investigate the movements of fish across known geochemical gradients in ocean basins (Bird et al. 2018; McMahon et al. 2013; St. John Glew et al. 2019; Trueman & St. John Glew 2019). Using isotope ratios in archived fish tissues to study the ocean-scale movements of marine fish has key advantages: it circumvents the expense and disadvantages of tagging, it is minimally invasive and relatively non‑destructive when scales are used, and it allows for retrospective identification of marine feeding grounds (St. John Glew et al. 2019; Trueman et al. 2012a).

The isotopic composition of carbon in marine food webs is influenced by the extent of fractionation of C isotopes during photosynthetic fixation in primary producers. In turn, this is influenced by the isotopic composition of dissolved inorganic carbonate, phytoplankton taxonomy and growth rates, all of which co-vary with SST (Goericke & Fry 1994; MacKenzie et al. 2011; Magozzi et al. 2017; Trueman et al. 2012b). Warmer temperatures are typically associated with lower concentrations of dissolved CO2 and faster cell growth, leading to higher δ13C values in plankton, while cooler temperatures show the opposite (Goericke & Fry 1994; Magozzi et al. 2017; Rau et al. 1996; Trueman et al. 2012a). Predictable spatial variations in δ13C values at the base of marine food chains can be used to generate spatial information about marine pelagic predators (McMahon et al. 2013); for instance, predictive models of global variations in phytoplankton δ13C values have been used to reconstruct variations in spatial foraging strategies in sharks globally (Bird et al. 2018). At high latitudes in the Atlantic Ocean, to which salmon migrate for marine feeding, patterns of planktonic δ13C at the base of the marine food web strongly reflect gradients in SST (Magozzi et al. 2017), and this spatial covariance of δ13C with SST has been used to investigate the distribution of salmon at sea on the basis of scale δ13C values (Almodóvar et al. 2020; MacKenzie et al. 2011).

The input of nitrogen into marine food webs is primarily by assimilation of dissolved inorganic nitrogen sources, e.g. nitrate, and through direct fixation of N2 into N biomass by marine micro‑organisms. Other sources comprise terrestrial runoff into river systems and atmospheric precipitation, which are poorly constrained, more variable inputs (Sigman et al. 2009). Furthermore, cycling of N species from surface waters through the water column to the deep ocean and sediments is complex, with involving multiple interacting processes of assimilation, remineralisation and denitrification with associated isotopic expressions (Sigman et al. 2009; Somes et al. 2010), and uncertainties around these processes can make it challenging to interpret N isotope biogeochemistry in the North Atlantic (Somes et al. 2010). In offshore regions, spatial variation in δ15N values of dissolved organic nitrogen, and in food chains, broadly covaries with the source of nitrogen entering food webs and the degree of marine denitrification (e.g. Somes et al., 2010, Ryabenko, 2013, Trueman and St John Glew, 2019). Once constrained in animal tissues, δ15N values increase in consumers’ tissues compared with their prey, whereas δ13C values are relatively conserved, thereby providing insight into the diet of animals and their trophic level in food chains (DeNiro & Epstein 1978; Peterson & Fry 1987; Zanden & Rasmussen 1999). Stable isotope analyses of δ15N and δ13C values in salmon have been used to gain insights to the trophic ecology and marine feeding conditions of salmon at sea (Dempson et al. 2010; Sinnatamby et al. 2009).

Although stable isotope analyses have been used extensively to test whether salmon sampled in different natal rivers returned from common feeding grounds (Espinasse et al. 2020; MacKenzie et al. 2011; Soto et al. 2018; Trueman et al. 2012b), relatively few studies have tested whether variations in the likely last feeding location at sea correspond to biological parameters (e.g., body condition) that may influence fitness. Salmon show complex migratory behaviours with potentially equally complex dynamic responses to marine climate change (Trueman et al. 2012b). Understanding relationships between salmon growth and distributions at sea has increasing resonance in the context of critical declines in salmon marine survival and ocean warming.

In this study, we use δ13C values in scale samples to investigate whether differences in the δ13C value at the final marine feeding grounds covaried with body condition of returning 1SW Irish salmon, which reported national data indicate represents an estimated 9.6% of the modelled global salmon spawning stock over the last five years (International Council for the Exploration of the Sea 2020). We discuss the possibility that variations between individuals in scale δ13C values are indicative of marine feeding success and related to ocean temperature, with higher values reflecting warmer conditions. We also consider complementary information from δ15N values in scale samples.

# Methods

## Scale collection

The National Salmon Scale Archive curated by Inland Fisheries Ireland (IFI) holds thousands of scale samples collected by IFI staff, salmon anglers and commercial fishermen over several decades from river systems and estuaries around Ireland. For the current study, samples of 3 to 6 scales were selected from individual 1SW salmon (*n* = 281) that were captured between May and September inclusive as they returned to five rivers in Ireland in 2011: Erriff (*n* = 12), Moy (*n* = 79), Corrib (*n* = 80), Munster Blackwater (*n* = 34) and Nore (*n* = 76). The rivers may be grouped into two areas by geographical proximity: the Nore and Blackwater are situated approximately 120 km apart on the southeast coast, whereas the Corrib, Erriff and Moy rivers are located between 400 to 600 km away on the west coast (Figure 1). The scale archive records the reported length and weight of each sampled salmon, and this data was used to calculate body condition.

## Scale preparation and imaging

The scale samples were treated with a physical cleaning protocol (MacKenzie 2010): they were soaked briefly in distilled water, then scraped gently on both sides with a clean scalpel on a glass slide and rinsed again to remove any adhering dirt, lipids or skin, thereby exposing the scale biomineralised external layer and collagenous basal plate. Using a calibrated TIF image of a representative scale for each fish, a distance calliper was drawn with Image Pro Plus 6.3 from the focus to the edge along the anterior scale axis, and radii were measured to the end of smolt growth at transition to sea and to the end of the first winter band in marine growth, thus partitioning smolt length and growth as mature 1SW salmon prior to return to river. Smolt length was back‑calculated using the Dahl‑Lea method, which assumes an isometric relationship between scale radius and body length, and which is suitable for calculating marine growth in salmon scales (Hanson et al. 2019; Heidarsson et al. 2006).

After imaging, scales were dissected under a binocular microscope to physically remove any residual matter and to excise the marine growth after the end of the 1SW winter band at sea and prior to return to river, and this excised sample was used for stable isotope analysis (see section 2.3). Scales have a lamellar structure and grow incrementally by underplating of older layers of collagen across the basal plate with newer layers, which means that vertical sections through the scale contain newer layers of collagen laid down over older ones over the fish’s lifetime; therefore, only the last season of growth towards the outermost scale edge with the newest layers of collagen should be sampled for isotopic analysis that requires a temporally defined period (Hutchinson & Trueman 2006; Trueman et al. 2012a).

Although scale C and N content derives mostly from collagen in the basal plate, there is also carbonate within the carbonated bioapatite that forms the calcified external layer of scales, as well as other non-collagenous proteins; however, the proportion of scale carbon contributed by these additional sources is small relative to collagen (Hutchinson & Trueman 2006), and it has been shown that acid treatment to remove mineral carbon forms does not have a significant effect on either C or N isotope values (Sinnatamby et al. 2007). Therefore, due to the very small size of the scale samples (typically *circa* 0.5 mg composed of the post‑winter 1SW growth band excised from 3–5 scales), the scales were subject to the physical cleaning procedure outlined above but not to further chemical treatment to purify scale proteins before isotope analysis (see section 2.3).

## Isotope analysis

Bulk C and N content and the stable isotope ratios of carbon and nitrogen, expressed as δ13C and δ15N values (Figure 2), were determined by elemental analysis–isotope ratio mass spectrometry (EA-IRMS); the equipment used comprised an Elementar PYRO Cube Elemental Analyser interfaced with an Isoprime VisION continuous flow isotope ratio mass spectrometer. The dissected scale samples were weighed to approximately 0.6 mg and packaged into clean tin capsules on a Sartorius ME5 micro balance. The samples were then combusted at 920°C with addition of pure oxygen. The resulting gases NOx and CO2 were subsequently reduced to N2 and CO2 in the reduction column which was held at 600°C. The N2 was analysed whilst the CO2 was held in a desorption trap, and then the trap was heated to 110°C to release the CO2 for analysis.

Acetanilide and sulphanilamide were used as elemental standards for C and N, and USGS40 and USGS41 L‑glutamic acid was used as a calibration standard for the normalisation of the isotope ratios. Protein standards that are certified reference materials together with in-house replication control standards were also used to ensure quality control and comparability with previously analysed scale samples. Long term analytical precision determined through repeat analyses of laboratory internal standards in the University of Southampton stable isotope facility is lower than 0.2 per mille (standard deviation) for both δ13C and δ15N values.

There are strong relationships between lipid content and C:N ratio in aquatic animals (Post et al. 2007; Schmidt et al. 2003; Sweeting et al. 2005), driven by the high proportion of C content and little or no N content in most classes of lipids, and C:N ratio can be used to correct for the presence of lipid contamination of samples (Post et al. 2007). The C:N ratio of pure collagen can be expected to fall within a defined range, which is an important means to identify deterioration or contamination of samples in which the isotope composition has been systematically skewed (Guiry & Szpak 2020); however, it must be noted that although our samples were likely composed largely of collagen, other, non collagenous proteins with higher C:N ratios than collagen will be present, elevating the bulk C:N ratio beyond that expected from pure collagen. Collagen can be isolated by gelatinization, filtration and lyophilisation, but such treatments can result in sample loss which is problematic for the small sample sizes considred here. Scale samples were therefore not subject to purification by chemical treatment or filtration; therefore, , their C:N ratios are higher than expected for pure collagen. Lipid contamination can further complicate interpretation of protein δ13C values. For aquatic animals, it has been shown that it is not necessary to account for lipid in samples in muscle tissues from aquatic animals when lipid content of samples is low, with C:N ratio < 3.5 (Post et al. 2007). In our total sample, δ13C values covary negatively with C:N ratios when the atomic C:N ratio increases beyond 3.5 (supplementary material, Figure 1); therefore, to safeguard against the possibility of lipid contamination, scale samples with atomic C:N ratio ≥ 3.5 were excluded from statistical modelling, reducing the total dataset to *n* = 263 for statistical modelling (see section 2.4).

## Statistical methods

Marine feeding success of salmon returning to five Irish rivers in 2011 was characterised using body condition (Fulton’s K = 100 × weight/length3). This response was modelled in a Bayesian statistical framework that implemented integrated nested Laplace approximations (INLA) using the R package ‘INLA’ (Rue et al. 2017).

Back‑calculated smolt length was included as a continuous covariate, while river was included as a categorical fixed effect. A separate random walk smoother (*ƒ*) was used for each river to model the temporal trend in condition of salmon returning to that river across the observed range of return dates (run days), with the trend for day *i* modelled as the trend for day *i-1* plus some error. Run day *i=1 …, n* for each river was counted from the date of the first returning fish caught across all five rivers in 2011. This river‑specific smoother was assumed to describe time at sea, given that smolt migration occurs at a similar time across all rivers.

Five candidate models were defined (Table 1) to test possible interactions between covariates, as well as simpler scenarios. Body condition (K) was assumed to have normally distributed (Gaussian) errors. The deviance information criterion (DIC) was used to select the best-fitting model(s) for each response. The full model for body condition of salmon *i* in relation to δ13C was specified as:

Condition*i* ~ *N*(*µi, σ2*)

*E*(Condition*i*) = *µi* and var(Condition*i*) = *σ2*

*µi* = *β1* + River*i* × δ13C*i* + Smolt length*i* × δ13C*i* + *ƒ*(Return day*i*)

The full model for body condition of salmon *i* in relation to δ15N was specified as:

Condition*i* ~ *N*(*µi, σ2*)

*E*(Condition*i*) = *µi* and var(Condition*i*) = *σ2*

*µi* = *β1* + River*i* × δ15N*i* + Smolt length*i* × δ15N*i* + *ƒ*(Return day*i*)

Model validation used residual plots to check the assumptions of linearity and homogeneity of residuals. The predicted effects of return day and values for δ13C and δ15N in recently deposited scale material were plotted to express the form and relative importance of these drivers of salmon feeding success (Figure 3, Figure 4).

# Results

This study confirmed that there were differences in smolt length, body condition and scale isotope composition among rivers (Table 2; Figure 1; Figure 2). Scale reading showed that mean smolt length was least in the Moy (11.6 cm) and greatest in the Erriff (13.7 cm). The greatest observed body condition (Fulton’s K) at return was observed in the Corrib and Nore 1SW salmon, whereas the lowest body condition was observed in the Blackwater 1SW salmon (Table 2).

Tested statistical models suggested that the observed range of δ13C values in scale protein was associated with a strong positive effect on body condition of returning salmon. The effect of run day varied among rivers, with greater body condition evident in later returning fish on Moy, Erriff and Corrib rivers but in earlier returning fish on the Blackwater and Nore rivers (Figure 3). For each river, the relationship between body condition and run day was consistent over the observed range of δ13C values (Figure 3). There was no statistically important relationship between smolt length and body condition (Table 3).

In contrast to the results for δ13C values, the statistical models tested showed that the observed range of δ15N values in the scale protein had a negative association with body condition of returning salmon (Figure 4). The effect of run day varied among rivers but had a similar relationship to the δ13C model, with greater body condition evident in later returning fish on Moy, Erriff and Corrib systems, but in earlier returning fish on the Blackwater and Nore rivers. Again, the relationship between body condition and run day was consistent over the observed range of δ15N values (Figure 4) and there was no statistically important relationship between smolt length and body condition (Table 4).

Comparison of the means and standard deviations for scale δ13C and δ15N values in 1SW salmon from the study rivers in Figure 5 shows that there is partitioning between the southeast coast (Blackwater and Nore rivers) and the west coast (Moy, Erriff and Corrib rivers). For the southeast coast, this separation between the Blackwater and the Nore rivers is relatively small for both isotopes, whereas for the west coast, the separation between the rivers shows more spread for both δ13C and δ15N values.

# Discussion

Salmon returning to five Irish rivers showed a range of isotope values in their scales protein, possibly indicating differences in thermal environment (δ13C) source nutrients and prey composition (δ15N) at the last marine foraging location (supplementary material: Figure S2, Figure S3). Body condition of returning salmon was positively related to observed scale δ13C values. Condition of returning salmon can have impacts on survival, fitness and population demographics, which suggests that the variation among salmon populations documented in this study provides evidence that the marine environment experienced by salmon towards the end of return migration can have an influence on salmon fitness and recruitment. Overall, we infer that Irish 1SW salmon from different rivers exhibit spatial variation between populations in their marine feeding location and have greater body condition when they migrate back to their natal rivers from relatively warmer, possibly more southerly or less distant, marine feeding grounds.

Assuming that most of the variance in observed salmon scale δ13C values reflects spatial variations in the isotopic composition of primary producers (Espinasse et al. 2020; MacKenzie et al. 2011), these results imply spatial variation at sea of salmon between rivers of origin that are relatively close to each other geographically. Previous work on the marine isotope ecology of Irish salmon populations has generally analysed spatial variation at sea at greater spatial scales, such as between rivers in North America and northern Europe (Sinnatamby et al. 2009) and between Irish salmon and North American populations (Dempson et al. 2010). Time series of δ13C and δ15N values from scale archives from different river populations on the south versus the northeast coast of Great Britain have also been used to suggest potentially contrasting areas of feeding based on assumed temporal covariance between isotopic compositions and environmental drivers (MacKenzie et al. 2011; Soto et al. 2018; Trueman et al. 2012b). Compared with these previous studies, the spatial scale of this analysis suggests that variation in distribution at sea between salmon populations occurs on an intra‑regional scale. Marine distributions may vary between salmon populations even when they originate from rivers that are located relatively close to each other, which consequentially produces differences between catchments in the growth and quality of their 1SW salmon stocks.

There is a large degree of similarity in the marine feeding environment used by salmon from the rivers studied, as shown by the standard deviations around mean isotope values for each river in Figure 5; nevertheless, rivers on the southeast coast are clearly grouped together and separated from rivers on the west coast. Salmon from rivers on the southeast coast showed higher δ13C values, presumably indicating that they are more likely to return from warmer marine thermal habitat, compared with salmon from rivers on the west coast. In terms of δ15N values, the rivers on the southeast coast were again closely grouped together, presumably indicating they share similar trophic ecology. In contrast, the west coast rivers exhibit more dissimilarity in both δ13C and δ15N values, possibly indicating that their foraging ecology before return to river spans a greater range of thermal habitat and prey composition. Albeit small, the observed degree of separation in mean isotope values between river populations, especially on the west coast, may indicate that variation in the thermal habitat and trophic ecology of salmon at sea prior to return migration may make an important contribution to differences between geographically proximate rivers.

Statistical modelling (Figure 3) identified a positive relationship between body condition at return and δ13C values assimilated during marine feeding in 1SW salmon that was consistent across study rivers. We identify three potential explanations for this relationship:

1. Salmon diets vary among individuals, and condition is mediated by diets dominated by prey items with relatively positive δ13C values.
2. Salmon condition is enhanced by warmer temperatures that are also associated with higher δ13C values.
3. Salmon condition is improved when less energy is expended during return migration (i.e., with shorter migration distances when fish return from warmer areas associated with higher δ13C values.).

For the first explanation, fish feeding at higher trophic levels (i.e., with more piscivorous diets) would be expected to show elevated δ13C and especially δ15N values; however, we saw no corresponding positive relationship between condition and δ15N values (Figure 4; supplementary material: Figure S3). The other two explanations are linked: both attribute variance in δ13C values primarily to spatial differences in δ13C values in phytoplankton that are themselves closely linked to sea surface temperature, as described in some previous work in which salmon scale δ13C values were used to identify marine feeding locations (Almodóvar et al. 2020; Espinasse et al. 2020; MacKenzie et al. 2011). In explanation (2) warming leads to improvement in condition, potentially via faster growth, whereas in (3) associations between temperature and condition are secondary, mediated by migration distance. The lack of a positive relationship between observed scale δ15N and δ13C values (supplementary material: Figure S4) may indicate that for these fish, the observed scale δ13C values were not dependent on trophic level; thus, differences in δ13C are less likely to reflect body mass and dietary intake of individuals and more likely to reflect variation in geographic distribution due to spatial variation in planktonic fraction of δ13C in the marine food chain (MacKenzie et al. 2011). This would support the proposed explanations that the observed positive correlation of body condition with δ13C values was mediated by higher rates of growth in warmer waters, less energy expenditure required for migration from more southerly waters, or both.

The δ15N data (Table 2, Figure 4) may imply differences in the trophic level at which salmon from the studied rivers feed. Food availability in marine feeding grounds, especially of pelagic juvenile fish as prey for salmon post‑smolts, has been identified as an important bottom‑up control of growth and body condition in salmon (Jensen et al. 2012; Jonsson et al. 2016). The lower median δ15N values for the Blackwater, Nore and Moy populations may indicate that they are feeding on a shorter food chain or consume relatively more prey from a low trophic level. The higher median δ15N value and greater interquartile range observed for the Erriff may indicate that salmon from this system may be more piscivorous and have a greater degree of omnivory (Bearhop et al. 2004). These differences in trophic ecology may contribute to observed contrasting relationships in body condition between rivers, particularly between the Erriff and the other rivers studied; however, it must be noted that the modelled sample size is small for the Erriff (*n* = 12). Furthermore, variation in salmon scale δ15N values may also reflect spatial variation along isoscapes of baseline δ15N in marine food webs as well as trophic level (Satterfield & Finney 2002), and there is insufficient data in this study to parse the relative contribution of trophic level versus spatial variation in δ15N levels in food webs to body condition. Nonetheless, it may be inferred that the observed differences in scale δ15N values between 1SW salmon populations on their return to rivers arise from spatiotemporal variation in their foraging ecology at sea during return migration.

We observe a contrasting effect of return date on condition across the different rivers in the model: salmon returning to rivers on the west coast of Ireland showed higher condition in later returning fish, whereas those returning to rivers on the southeast coast showed higher condition in early returning fish. The timing of return migration in salmon has a strong genetically inherited component (Stewart et al. 2002), and run timing in 1SW salmon has been shown to depend on body condition achieved in response to ocean climate, with salmon staying longer at sea in years in which their condition is poor (Todd et al. 2012). In timing their return migration from the sea, salmon must trade off the reproductive fitness advantages of achieving larger size at marine feeding areas against the probability of marine mortality and the energetic costs of return migration from marine feeding areas back to their natal river systems; selection may also act to produce divergence in timing of return migration from the ocean among salmon populations as they adapt to seasonal environmental conditions in their natal river systems (Quinn et al. 2016). Furthermore, there is evidence that individual variation in marine diet and foraging strategy is associated with genomic regions that influence life-history variation and population divergence (Aykanat et al. 2020). Body condition may potentially drive salmon population dynamics and population resilience to environmental challenges by mediating impacts on traits such as fecundity, sexual maturation and survival at sea (Susdorf et al. 2018). In this context, differences in the relationship between run timing and body condition among rivers observed in our study may possibly arise from divergence between rivers in life‑history adaptations: how long 1SW salmon remain at sea involves a trade‑off between return when optimal condition is reached for maturation by individuals versus return at optimal timing that a population has adapted to for its natal river. Such variation in the response of body condition to marine thermal and feeding conditions as identified by δ13C and δ15N isotope analysis can be expected to have an impact on salmon fitness.

Smolt size also varied between rivers but did not show an important effect on body condition, which may indicate that salmon can compensate for smaller size at smolt migration to sea in their growth and that their ultimate body condition may be more strongly related to ambient temperature, as well as factors such as prey composition, during marine foraging. The growth of salmon during their first year at sea from post‑smolts to 1SW adults has been shown to be positively correlated with increased NAO index, which is indicative of warmer, milder conditions in the Northeast Atlantic (Jonsson & Jonsson 2004b), and spatial and annual variation in growth of salmon from rivers in Norway has been shown to be correlated with SST across their range in the Norwegian Sea (Jensen et al. 2011). Smolt size is thought to be important for survival of salmon at sea, and modelling has linked smolt size with return rate of 1SW salmon (Gregory et al. 2019). Growth during the post‑smolt period has been linked to survival of Irish 1SW salmon (Peyronnet et al. 2007), and growth in warmer waters potentially enables salmon post‑smolts to grow faster, thereby lessening the risk of predation, which is a critical factor in survival of post‑smolts to grow into 1SW salmon (Friedland et al. 2009; Jonsson & Jonsson 2004a). Whether growth in warmer waters represents an optimal scenario for 1SW salmon must be interpreted with caution, however. Some studies have linked deleterious effects of elevated SST on condition of returning salmon and recruitment, usually attributed to climate forcing impacts on marine food webs (Jonsson et al. 2013; Otero et al. 2012; Peyronnet et al. 2008; Todd et al. 2008). On the other hand, warmer ocean temperature conditions have been associated with greater growth of salmon in the Northwest Atlantic, and this relationship may indicate that ocean climate has a direct physiological effect on growth and indirect effects through its impacts on the pelagic ecosystem on which salmon prey (Friedland & Todd 2012). Our result on the relationship between smolt length and body condition may indicate that, while smolt size may influence individual survival until the first winter at sea, smolt size does not subsequently have a significant influence on the ultimate condition of 1SW salmon that survive to return to rivers. It must be noted that our study sampled only 1SW salmon at their return to river and therefore represents only those survivors that successfully fed at sea and completed return migration after their first winter at sea; data are lacking on growth of the proportion of the cohort that remained at sea to mature as MSW fish as well as on growth of post‑smolts that failed to survive.

The capacity of salmon to direct and optimise their migration trajectories is an open question (Thorstad et al. 2012), but increasingly, evidence indicates that oceanic currents and SST have a major influence. Modelling studies indicate that rheotaxis guides salmon post‑smolts from Ireland’s west coast towards the Northeast Atlantic and Norwegian Sea (Booker et al. 2008; Mork et al. 2012), whereas post‑smolts from Scotland appear to follow preferred routes that are not necessarily aligned with current direction (Newton et al. 2021; Ounsley et al. 2019); this suggests that salmon adapt their migratory behaviour to local coastal currents. Tagging has shown that salmon are very mobile in their migration from coastal waters to marine feeding areas and back again (Guðjónsson et al. 2015) and that the movements of salmon in pelagic waters are highly variable among individuals, thereby exposing them to varying environmental conditions and potentially affecting their growth and survival (Strøm et al. 2018). Archival telemetry tagging has indicated that individual salmon may even shift their routes to find favourable thermal habitat in response to annual variation in ocean temperature in the Northeast Atlantic (Strøm et al. 2020). Changes in migration routes by salmon to find suitable thermal habitat and prey availability would have an impact on growth of salmon (Friedland & Todd 2012; McCarthy et al. 2008), and spatiotemporal variation in marine growth patterns of 1SW salmon have been interpreted as evidence of reallocation of shifts in migration patterns that differ between rivers in North American salmon (Hubley et al. 2008). Salmon clearly have the potential to shift migration to seek out feeding grounds where they can optimise their growth in their first year at sea, thereby avoiding predation mortality and achieving greater body condition. The results indicating spatial variation in scale δ13C values found in this study may provide further evidence of such shifts in migration patterns among river populations to exploit overlapping but spatially variable thermal habitat and marine feeding grounds, and thus may help explain why geographically proximate rivers have 1SW salmon stocks that differ in the body condition that they achieve on return migration.

Recently, pop‑up satellite tagging has shown that adult salmon from Ireland migrating back to sea after returning to rivers to spawn swim towards preferred feeding grounds along oceanographic fronts south of Greenland, showing an oceanic distribution that overlapped more with a geographically proximate southern population (Spain) than with more distant northern populations (Denmark & Norway) (Rikardsen et al. 2021). Spatial partitioning of salmon stocks at sea has also been indicated by modelling of recaptures of tagged salmon, including 1SW Irish salmon, in relation to the Iceland‍–‍Faroe Front, where warmer, more saline North Atlantic water from the southwest meets cooler, less saline water from the northeast; geographic distribution is not random but depends on country of origin, with temporal differences in the distribution of 1SW and MSW stocks (Jacobsen et al. 2001; Jacobsen et al. 2012); Irish 1SW salmon tended to overwinter in warmer waters along the southwest of the front in the early winter, before presumably leaving on their homeward migration in the late winter (Jacobsen et al. 2012), and there is a tendency for Irish 1SW salmon to be smaller, to have spent less time at sea and to shift in a more westerly distribution as the winter progresses (Ó'Maoiléidigh et al. 2018). Irish 1SW salmon have been captured further west around Greenland, but these fish are generally presumed to spend further winters at sea to mature as MSW fish before return migration. These movements of 1SW salmon in wintering feeding areas leads to spatiotemporal differences between stocks that may involve trade‑offs between food availability, competition with other fish species and thermal habitat (Jacobsen et al. 2012). The isotopic evidence of variation in geographic distribution at sea between rivers found in this study suggests that timing of arrival at important marine feeding grounds along North Atlantic currents, spatiotemporal variation in prey distribution encountered there and movement into warmer thermal habitat in advance of return migration are all likely to be contributory factors to the modelled differences in body condition among the 1SW salmon populations returning to rivers.

Climate driven changes in Northeast Atlantic pelagic ecosystems have caused bottom-up changes in salmon abundance through changes in plankton distribution, thereby altering marine feeding conditions (Beaugrand & Reid 2003, 2012). Although little is known about top‑down control of salmon populations at sea, geographical variation in predation by marine mammals and piscivorous fish has recently been shown to be more highly correlated with population declines of southern European salmon (Strøm et al. 2019); moreover, warming trends in SST have been linked to increased abundance and diversity of pelagic piscivorous fish in the migration corridors of salmon post‑smolts and declines in their recruitment (Friedland et al. 2012). The variation in geographic distribution at sea into a range of marine thermal habitats documented in this study suggests that salmon populations from different Irish rivers will encounter different bottom‑up (marine feeding) and, potentially, top‑down (predation) impacts related to SST, indicating that they will exhibit differential responses to ocean‑scale climatic changes across the Northeast Atlantic.

The marine thermal habitat used by salmon from different rivers in Ireland and its consequential impacts on growth and body condition are not homogenous. The results of this study demonstrate that scale δ13C values in 1SW salmon deposited at the last marine feeding location prior to return to natal rivers are positively correlated to body condition, which affects fecundity and reproductive success, thereby potentially influencing fitness and population dynamics. Scale isotope values showed that marine feeding location varied among salmon from different study rivers, and the observed among‑river differences in δ13C and δ15N values suggest that realized body condition may be influenced by SST and prey composition in the marine feeding grounds. If condition is related to survival and recruitment success, then changing ocean conditions may drive shifts in the population dynamics of Atlantic salmon. These results also provide insight into the geographic diversity that underlies salmon migration to marine feeding areas and its implications for marine feeding success and body condition at return. Recent marine feeding environment prior to return migration may explain observed differences between rivers in the condition of 1SW grilse stocks that are exploited by anglers and commercial fisheries. Conservation and management of salmon stocks from individual rivers will be better informed by an understanding of the oceanic climatic changes that have impacts on their marine feeding success.

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# Authors' contributions

This study was conceived and designed by SS, PG, WR, and CT. RF processed the scale samples. CT conceived and supervised the isotope analysis. SS conceived the modelling framework and carried out the statistical analyses. RF prepared the manuscript. All authors contributed to interpreting the results and reviewing the manuscript.

# Significance statement

Our work uses stable isotope analysis to show that salmon populations from geographically proximate rivers experience different thermal habitats and feeding conditions at sea prior to their return to rivers and that this consequently influences body condition. Our results provide insight into the geographic diversity that underlies salmon migration, its implications for marine feeding success and subsequent fitness, as well as the response of an iconic fish species to oceanic climatic change.

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# Tables

Table 1. Candidate statistical models for body condition as a metric of marine feeding success for *Salmo salar* returning to five Irish rivers in 2011.

|  |  |  |
| --- | --- | --- |
| **Model** | **Covariates δ13C models** | **Covariates δ15N models** |
| 1 | River*i* × δ13C*i* + Smolt length*i* × δ13C*i* + ƒ(Return day*i*) | River*i* × δ15N*i* + Smolt length*i* × δ15N*i* + ƒ(Return day*i*) |
| 2 | River*i* × δ13C*i* + Smolt length*i* + ƒ(Return day*i*) | River*i* × δ15N*i* + Smolt length*i* + ƒ(Return day*i*) |
| 3 | River*i* + δ13C*i* × Smolt length*i* + ƒ(Return day*i*) | River*i* + δ15N*i* × Smolt length*i* + ƒ(Return day*i*) |
| 4 | River*i* + δ13C*i* + Smolt length*i* + ƒ(Return day*i*) | River*i* + δ15N*i* + Smolt length*i* + ƒ(Return day*i*) |
| 5 | River*i* + Smolt length*i* + ƒ(Return day*i*) | River*i* + Smolt length*i* + ƒ(Return day*i*) |

Table 2. Mean values and standard deviations (sd) obtained for *Salmo salar* smolt length (cm), return condition (Fulton’s K), scale δ13C value and scale δ15N values.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **River** | **Sample size** | **Smolt length (cm)** | **Body condition (K)** | **δ13C** | **δ15N** |
|  |  | **mean (sd)** | **mean (sd)** | **mean (sd)** | **mean (sd)** |
| Moy | 79 | 11.6 (2.3) | 1.04 (0.11) | -16.56 (0.46) | 9.69 (0.81) |
| Erriff | 11 | 13.7 (3.0) | 1.05 (0.10) | -16.41 (0.38) | 10.68 (1.18) |
| Corrib | 79 | 13.4 (3.2) | 1.10 (0.13) | -16.39 (0.52) | 10.03 (0.92) |
| Blackwater | 34 | 11.8 (2.3) | 1.01 (0.13) | -16.21 (0.49) | 9.23 (1.17) |
| Nore | 76 | 12.4 (2.5) | 1.10 (0.24) | -16.16 (0.37) | 9.39 (1.08) |

Table 3. Posterior means, standard deviations (sd) and 95% credible intervals for parameters of the selected statistical model of body condition (Fulton’s K) in relation to δ13C for *Salmo salar* returning to five Irish rivers in 2011. Statistically important covariates are emboldened.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Mean** | **sd** | **2.5%q** | **97.5%q** |
| (Intercept) | 1.953 | 0.372 | 1.223 | 2.683 |
| Corrib | 0.084 | 0.067 | -0.049 | 0.216 |
| Erriff | 0.042 | 0.084 | -0.125 | 0.207 |
| Moy | 0.003 | 0.071 | -0.137 | 0.141 |
| Nore | 0.093 | 0.070 | -0.046 | 0.230 |
| δ13C | 0.056 | 0.022 | **0.013** | **0.099** |
| Smolt length | -0.001 | 0.004 | -0.008 | 0.006 |

Table 4. Posterior means, standard deviations (sd) and 95% credible intervals for parameters of the selected statistical model of body condition (Fulton’s K) in relation to δ15N for *Salmo salar* returning to five Irish rivers in 2011.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Mean** | **sd** | **2.5%q** | **97.5%q** |
| (Intercept) | 1.3965 | 0.1266 | 1.148 | 1.645 |
| Corrib | 0.09 | 0.0665 | -0.041 | 0.22 |
| Erriff | 0.0676 | 0.0836 | -0.097 | 0.232 |
| Moy | -0.0035 | 0.0698 | -0.141 | 0.133 |
| Nore | 0.1012 | 0.0693 | -0.035 | 0.237 |
| δ15N | -0.0382 | 0.0104 | -0.059 | -0.018 |
| Smolt length | -0.0002 | 0.0037 | -0.007 | 0.007 |

# Figures



Figure 1. Top inset: Location of the five study rivers around Ireland. Bottom inset: Boxplot of back‑calculated *Salmo salar* smolt length (cm) by river. Main map: Study rivers in relation to the North Atlantic Ocean and Norwegian Sea; mean sea surface temperature (SST) in °C displayed for the probable period of scale growth sampled. Map produced using Ordnance Survey Ireland license MP 007508, Optimum Interpolation SST (Reynolds et al. 2002), GEBCO bathymetry (azimuthal equidistant projection).



Figure 2. Boxplots of δ13C (‰) and δ15N (‰) values in scales from 1SW *Salmo salar* returning to the five study rivers in 2011 that were included in the statistical modelling.



Figure 3. Predicted body condition (Fulton’s K) associated with δ13C (‰) in scales from 1SW *Salmo salar* for the marine period from the winter annulus to the return to river. The Moy, Corrib and Erriff rivers are on the west coast, whereas the Blackwater and Nore rivers are on the south coast. Separate lines are shown for two values of return date (‘Run day’), counted from the date of the first returning fish in the five study rivers in 2011.



Figure 4. Predicted body condition (Fulton’s K) associated with δ15N (‰) values in scales from 1SW *Salmo salar* for the marine period from the winter annulus to the return to river. The Moy, Corrib and Erriff rivers are on the west coast, whereas the Blackwater and Nore rivers are on the south coast. Separate lines are shown for two values of return date (‘Run day’), counted from the date of the first returning fish in the five study rivers in 2011.



Figure 5. Bivariate scatterplot of mean values for scale δ13C (‰) and δ15N (‰) for 1SW *Salmo salar* returning to the five study rivers in 2011 that were included in the statistical modelling (*n* = 263). The triangular points show rivers on the west coast, whereas the square points show the rivers on the southeast coast. The error bars show the standard deviation for each river.

# Electronic supplementary material

Chart, scatter chart

Description automatically generated

Figure S1. Scatterplot of scale value for δ13C (‰) plotted against atomic C:N ratio for 1SW *Salmo salar* returning to the five study rivers in 2011. The violet linear regression with 95% confidence interval shows the relationship of between scale δ13C and atomic C:N ratio for all samples analysed for stable isotope content (*n* = 281); the green linear regression with 95% confidence interval shows the relationship of between scale δ13C and atomic C:N ratio for the samples that were retained for modelling (*n* = 263). Samples with an atomic C:N ratio ≥ 3.5 were excluded from modelling.



Figure S2. Scatterplot of body condition (Fulton’s K) plotted against scale δ13C value (‰) for 1SW *Salmo salar* returning to the five study rivers in 2011 that were included in the statistical modelling (*n* = 263), fitted with locally estimated scatterplot smoothing (LOESS) shown as a blue line.



Figure S3. Scatterplot of body condition (Fulton’s K) plotted against scale δ15N value (‰) for 1SW *Salmo salar* returning to the five study rivers in 2011 that were included in the statistical modelling (*n* = 263), fitted with locally estimated scatterplot smoothing (LOESS) shown as a blue line.



Figure S4. Scatterplot of scale values for δ15N (‰) and δ13C (‰) for 1SW *Salmo salar* returning to the five study rivers in 2011 that were included in the statistical modelling (*n* = 263), fitted with linear regression (*m* = -0.8549, *c* = -4.2811, r2 = 0.1391) shown as a grey line with 95% confidence bands.