



Original Article

Stable isotopes suggest the location of marine feeding grounds of South European Atlantic salmon in Greenland

Ana Almodóvar^{1*}, Graciela G. Nicola², Daniel Ayllón¹, Clive N. Trueman³, Ian Davidson⁴, Richard Kennedy⁵, and Benigno Elvira¹

¹Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid (UCM), Madrid E-28040, Spain

²Department of Environmental Sciences, University of Castilla-La Mancha (UCLM), Toledo E-45071, Spain

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

⁴Natural Resources Wales, Buckley CH7 3AJ, UK

⁵AFBI Aquatics Group, River Bush Salmon Station, 21 Church Street, Bushmills, Co. Antrim BT57 8QJ, Northern Ireland

*Corresponding author: tel: +34 91 3945135; e-mail: aalmodovar@bio.ucm.es

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Historical data on the oceanic distribution and migration routes of southernmost Atlantic salmon *Salmo salar* populations from Europe are almost non-existent, as no rigorous tagging initiatives have been conducted. Here, we used stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of historic scale collections to identify the potential marine feeding areas of the largest salmon population in the Iberian Peninsula. Data were compared with published datasets from Northern Ireland, Wales, south England, and northeast UK coast, which correspond to series between 15- and 33-year long within the time period from 1958 to 2009. Temporal covariation in sea surface temperature, primary productivity, and $\delta^{13}\text{C}$ values suggests that feeding areas of Iberian salmon are located around Greenland, both in the Labrador and the Irminger seas. Furthermore, $\delta^{13}\text{C}$ values of Atlantic salmon from Canadian rivers reported in the literature are similar to those found in individuals from Spanish rivers. Our results suggest that Iberian salmon follow a westerly migration route towards Greenland instead of following the easterly branch of the North Atlantic current into the Norwegian Sea. Characterization of feeding patterns and migration routes might help to understand the causes of ongoing population decline and establish targeted conservation programmes for threatened Iberian salmon.

Keywords: migration, North Atlantic, *Salmo salar*, scales, time series

Introduction

Atlantic salmon *Salmo salar* is culturally and economically relevant all over its native range; however, its populations have markedly declined in the last 50 years (Chaput, 2012; Almodóvar *et al.*, 2019). Reduced survival and growth during the marine phase, linked to strong climate-driven regime shifts in biophysical conditions at feeding grounds, seem to be the main drivers of such a decline (Beaugrand and Reid, 2003; Mills *et al.*, 2013; Friedland *et al.*, 2014; Almodóvar *et al.*, 2019). However, its distribution and migration patterns in the ocean remain relatively unknown. The lack of stock-specific data hinders decision-making regarding the regulation of fishing

pressure at feeding grounds and the establishment of preservation programmes for threatened stocks.

The case of the southernmost European Atlantic salmon populations is paradigmatic. Despite the reported ongoing decline (ICES, 2013; Nicola *et al.*, 2018; Almodóvar *et al.*, 2019), basic information of its life at sea is still scarce. Although systematic tagging studies have been carried out by countries around the North Atlantic from 1935 (Ó'Maoiléidigh *et al.*, 2018), historical data on the migration of salmon from Spanish rivers are almost non-existent, as no rigorous tagging programmes have been conducted over time. Likewise, the trophic ecology of Spanish salmon populations at sea is totally unknown as no dietary studies have ever

been performed. These knowledge gaps regarding marine feeding patterns are critical as the observed changes in the abundance, composition, and distribution of their marine prey species have been suggested as a main driver of ongoing Atlantic salmon decline (Beaugrand and Reid, 2003; Mills *et al.*, 2013; Almodóvar *et al.*, 2019).

The movements of Atlantic salmon at sea have been traditionally studied by tag-recapture methods. Results from 50-year historical monitoring (period 1960s to 2000s; Jacobsen *et al.*, 2012; Reddin *et al.*, 2012; Ó'Maoiléidigh *et al.*, 2018) suggest that European salmon populations from rivers north of 62°N (except the Baltic subpopulation, which stays in the Baltic Sea) migrate to areas around the Faroe Islands, and the Norwegian and Barents Seas (Jacobsen *et al.*, 2001, 2012). Likewise, the one-sea-winter (1SW) salmon from rivers south of 62°N begin their marine migration by swimming north into the Norwegian Sea (Holm *et al.*, 2000). However, most of multi-sea-winter (MSW) salmon from southern European stocks and from rivers in North America feed in the Labrador Sea (Idler *et al.*, 1981; Reddin *et al.*, 2012). The Greenland waters are the only area where North American and European salmon populations mix extensively. An alternative model of salmon marine migration proposes that all salmon perform continuous counter-clockwise transoceanic movements using surface currents of the North Atlantic Subpolar Gyre (Dadswell *et al.*, 2010), and the location of fish within the gyre depends on latitude of origin, fish age, and sea temperature. Hansen and Jacobsen (2003) and Jacobsen *et al.* (2001, 2012) observed that a significant proportion of salmon tagged throughout the distribution area was recovered in early and late winter in Faroe waters, which would be consistent with this model.

Neither migration model can totally be supported by current data, as the historical recovery rates of tags are too low. For example, almost 4 million salmon have been tagged in English and Welsh rivers since the 1950', but fewer than 3000 (<0.08%) have been recovered at sea, almost all of them at the two historic fishery areas west of Greenland and north of the Faroe Islands (MacKenzie *et al.*, 2012). Yet recent studies suggest that other less-studied areas, such as the seas south and east of Iceland, might be also important feeding areas for Atlantic salmon (e.g. Olafsson *et al.*, 2016). In addition, the distribution of tag recoveries at sea highly depends on the temporal and spatial distribution of fishing effort, rather than on the true distribution of salmon. Fortunately, alternative methods have emerged to identify the location of marine animals, such as stable isotope analysis. Recently, the use of stable isotopes in trophic ecology (Boecklen *et al.*, 2011), and in the study of marine animals' movements (Trueman and Moore, 2007; Trueman *et al.*, 2012; McMahan *et al.*, 2013; Trueman and St John Glew, 2019), has allowed a better understanding of the biology of species such as the Atlantic salmon during its marine phase (e.g. Sinnatamby *et al.*, 2009; Dempson *et al.*, 2010; MacKenzie *et al.*, 2011; Torniaainen *et al.*, 2014; Dixon *et al.*, 2017).

The composition of carbon and nitrogen isotopes in fish tissues ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) overall depends on variations in the isotopic composition at the base of the food web (i.e. primary producers) and on trophic discrimination processes within organisms. Both growth rates of phytoplankton cells and dissolved carbonate concentrations are intrinsically related to temperature and vary spatially and temporally across ocean basins, leading to spatial and temporal variations in the $\delta^{13}\text{C}$ values of plankton in the North Atlantic in excess of 6‰ (McMahon *et al.*, 2013). In contrast,

fractionation of carbon isotopes associated with an increase in trophic level is about 0–2‰ (McMahon *et al.*, 2013). Thus, the carbon isotope composition of pelagic predators of similar sizes varies largely according to feeding location. Nitrogen fractionates more than carbon during dietary assimilation, with a trophic increase ranging from 2.6‰ to 3.4‰, and a mean of about 3‰ (Owens, 1987; McCutchan *et al.*, 2003; Vanderklift and Ponsard, 2003). The $\delta^{15}\text{N}$ stable isotope ratios of primary producers at the base of food webs are also known to vary spatially and to influence organisms at higher trophic levels (Jennings and Warr, 2003; Choy *et al.*, 2015). Salmon scales, which have been routinely archived during decades for many systems and thus can be used as comparative material, are appropriate tissues for retrospective analyses because (i) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of scale and muscle tissues are related in a consistent way and (ii) isotope values determined from a single scale are representative of the composition of the whole fish (Satterfield and Finney, 2002).

The aim of the present study was to use stable isotope analyses to characterize marine feeding of Atlantic salmon returning to Iberian rivers, specifically regarding their trophic ecology and location of feeding areas. We hypothesized that Spanish populations of Atlantic salmon would present similar trophic patterns and migrate to similar feeding areas as Southern European populations (England and Wales, Ireland, France), which are thought to mainly migrate to the southern part of the Norwegian Sea as 1SW salmon, and then to west Greenland as MSW salmon. As an alternative hypothesis, 1SW and MSW salmon from Spanish rivers would follow the easterly branch of the North Atlantic current into the Norwegian Sea, as has been proposed for populations from the northeast United Kingdom (MacKenzie *et al.*, 2011, 2012). We tested our predictions by comparing the spatial and temporal variations of stable isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of scale collagen of 1SW and MSW salmon from the largest Spanish salmon population (River Sella) with published datasets from geographically distinct populations from Northern Ireland (River Bush), Wales (River Dee), south England (River Frome), and rivers from the northeast UK coast (England and Scotland) during the period 1958–2009.

Methods

Sample collection

Atlantic salmon is an anadromous species, which spawn in its natal rivers after spending either one (1SW) or more winters (MSW) at sea. We analysed time series (from 1958 to 2004) of scales taken from Atlantic salmon returning to the Spanish River Sella (43°N 5°W; Figure 1). For comparative purposes, we used published isotope data from scale collections from United Kingdom coming from River Bush in Northern Ireland (55°N 6°W, time series 1958–2007), River Dee in Wales (53°N 3°W, time series 1983–2009), River Frome in south England (50°N 2°W, time series 1970–2002), and rivers from the northeast UK coast (55°N 1°W, time series 1985–2001; Figure 1). The International Council for the Exploration of the Sea (ICES) has assigned all these sampled populations to the Southern European stock of Atlantic salmon (ICES, 2013). Published data were taken from MacKenzie *et al.* (2011, 2012) and DEFRA (2013).

Each scale was associated to the length (mm), mass (g), and age (1SW or MSW) of the captured individual. The collagen in the scale tissue was analysed to extract carbon and nitrogen isotope records of the conditions of primary production and trophic

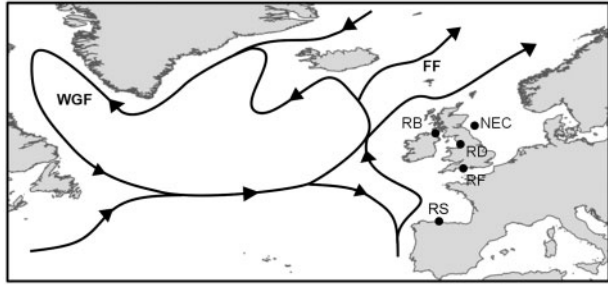


Figure 1. Circulation scheme of main surface currents in the North Atlantic based on [Daniault et al. \(2016\)](#). Location of River Sella (RS) in Spain and comparative populations from the British Isles: rivers Bush (RB), Dee (RD), Frome (RF), and northeast UK coast (NEC). West Greenland (WGF) and Faroe (FF) fisheries are indicated in bold.

level through time. We determined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of scales from approximately $n=10$ ISW and $n=10$ MSW salmon for each available year and river, which is the usual sample size in this type of studies (e.g. [Sinnatamby et al., 2009](#); [Soto et al., 2018](#)).

Measurement of stable isotope values

Scales grow allometrically with fish size. Scale collagen is deposited only during growth and is not turned over metabolically ([Hutchinson and Trueman, 2006](#)). We, therefore, target collagen formed during spring–summer growth. First, scales were briefly (2–5 min) soaked in deionized water, cleaned manually with forceps and a scalpel to remove adherents such as lipids and guanine, and dissected under a transmitted light microscope.

Scales were dissected to sample the portion corresponding to the period of marine growth between the last winter at sea until return to home waters for ISW salmon, and the last full period of growth between the first and second winters at sea for MSW individuals. This dissection is a critical step when sampling fish scales for isotopic analysis, to avoid mixing collagen of different ages in unknown proportions ([Hutchinson and Trueman, 2006](#)).

Samples were weighed to ≈ 0.60 mg, and the isotope ratios were determined by continuous-flow isotope ratio mass spectrometry (EA-IRMS), using L-glutamic acid as an in-house calibration standard. Measurement precision, assessed as $2\times$ the standard deviation of 16 replicate analyses of USG40 glutamic acid for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, is 0.1‰ and 0.7‰ , respectively. Full details of the preparation and analytical methods are given in [MacKenzie et al. \(2011\)](#).

The $\delta^{13}\text{C}$ values were corrected to account for the Suess effect, which denotes the decrease in $^{14}\text{C}/\text{C}$ ratio in atmospheric CO_2 caused by the combustion of fossil fuel ([Keeling, 1979](#)). Human fossil fuel burning over the past 150 years have caused an exponentially accelerating decrease in $\delta^{13}\text{C}$ in the biosphere since the industrial revolution, caused by the fact that carbon introduced into the biosphere by the burning of fossil fuels has a lower $\delta^{13}\text{C}$ than background carbon. The reported mean annual depletion of $\delta^{13}\text{C}$ in the Atlantic Ocean due to Suess effect is 0.02‰ year^{-1} ([Gruber et al., 1999](#); [Körtzinger et al., 2003](#)). The corrected $\delta^{13}\text{C}$ value for a given year ($\delta^{13}\text{C}_{\text{corr}}$) was calculated considering the mean $\delta^{13}\text{C}$ value of that year, the time elapsed until the end of the study (years), and the annual rate of $\delta^{13}\text{C}$ depletion (‰ yr^{-1}).

Statistical analyses

We first compared the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between ISW and MSW salmon from River Sella using two-way ANOVAs, with sea age and year as factors, including their interaction. We subsequently compared the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each sea-age group among samples from the River Sella and the UK rivers using two-way ANOVAs with geographic origin and year as factors, including their interaction. Since $\delta^{15}\text{N}$ values typically correlate with salmon mass (e.g. [MacKenzie et al., 2011, 2012](#); [Trueman et al., 2012](#)), we also performed factorial ANCOVAs using body mass as covariate to control for its effect on $\delta^{15}\text{N}$ values. The assumption of normality of distributions (for each sea-age class and river) was verified through the Lilliefors test. The assumption of homogeneity of variances for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between compared pairs (i.e. between Sella and British rivers within each sea-age class, and between sea-age classes within River Sella) in the overlapping years of their time series was assessed through the Levene's test. The significance level for all statistical tests was set at 0.05.

Locating marine feeding grounds of River Sella salmon

We followed the approach of [MacKenzie et al. \(2011\)](#) to estimate potential marine feeding grounds of Atlantic salmon from River Sella. To do this, we analysed the temporal covariance between time series of scale carbon isotope values and 8-month summer (from March to October) median sea surface temperature (SST) in each grid square (see below) between $40\text{--}74^\circ\text{N}$ latitude and $66^\circ\text{W}\text{--}30^\circ\text{E}$ longitude. The $\delta^{13}\text{C}$ composition in marine algal primary producers co-varies with SST, as SST influences isotopic composition and concentration of dissolved CO_2 in seawater ([McMahon et al., 2013](#)). The scattered, low number of sampled years in the River Sella (see [Figure 2](#)) precluded a robust analysis of the temporal covariance between SST and $\delta^{13}\text{C}$ values. To overcome this limitation and given that there were not significant differences in $\delta^{13}\text{C}$ values between rivers Sella and Dee over the time series (see Results section), we pooled the MSW salmon data of these two rivers to perform the analysis (68 measurements from River Sella, 248 from River Dee). Therefore, spatial correlation between carbon isotope values and SST was assessed for the period 1983–2009. SST data were obtained from the NOAA Extended Reconstruction Sea Surface Temperature (ERSSTv4) dataset (<https://climatedataguide.ucar.edu/climate-data/sst-data-noaa-extended-reconstruction-ssts-version-4>, [Huang and National Center for Atmospheric Research Staff, 2017](#)). The ERSSTv4 dataset is based upon statistical interpolation on a $2^\circ \times 2^\circ$ spatial grid of the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) Release 2.5 SST data. This approach assumes that (i) SST is a good proxy for phytoplankton growth and global primary production and (ii) salmon return to the same area over the duration of the time series (see [MacKenzie et al. 2011](#) and [Espinasse et al. 2019](#) for discussion of both assumptions).

To reinforce this analysis, we additionally assessed the spatial and temporal correlation between $\delta^{13}\text{C}$ values of MSW salmon from River Dee and the values of Phytoplankton Colour Index (PCI), which was used as an indicator of primary production across the whole North Atlantic basin. The fractionation of stable carbon isotopes during photosynthesis by the phytoplankton community at the bottom of the food chain strongly determines the isotopic composition of carbon in tissues of pelagic predators

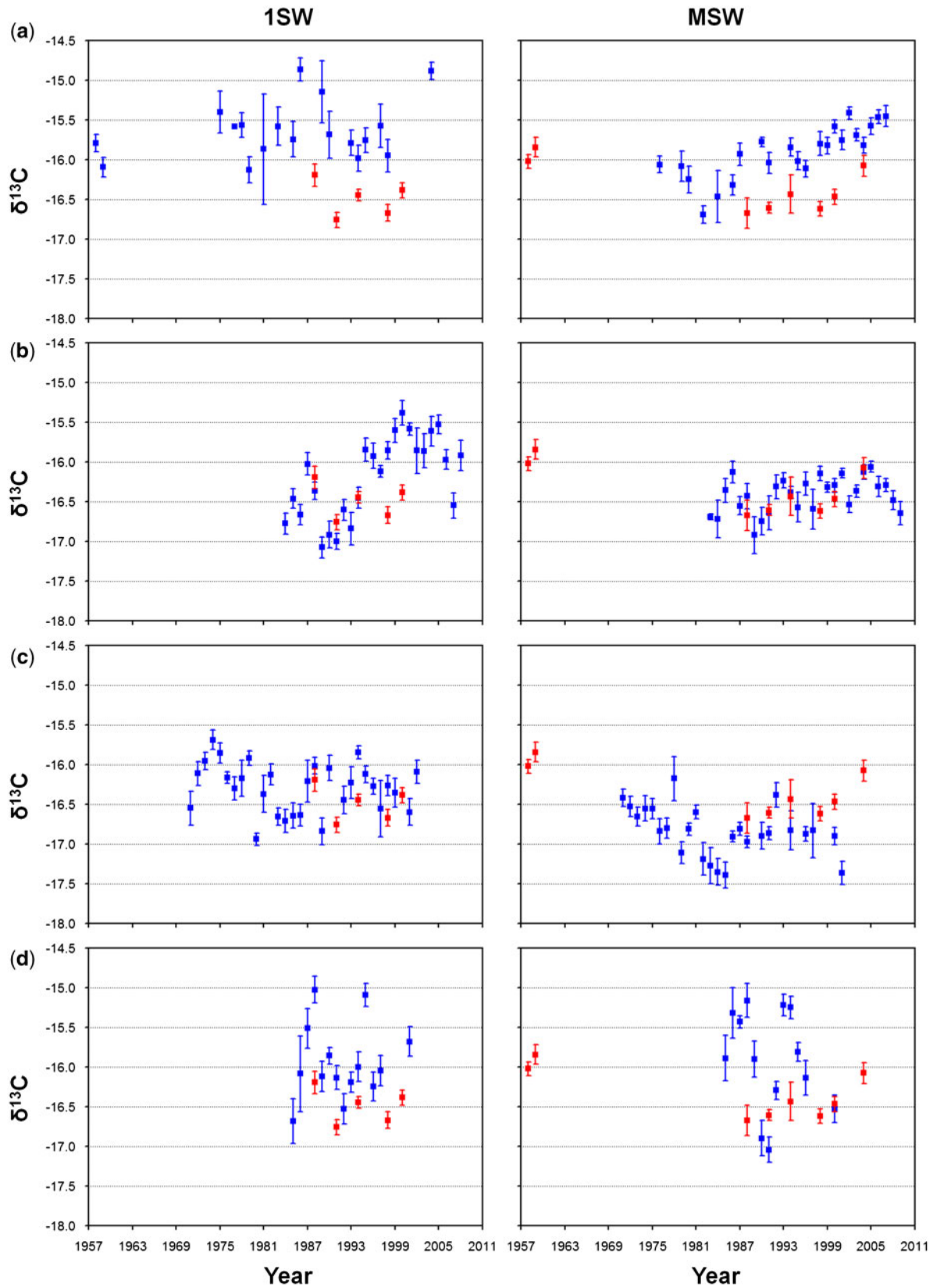


Figure 2. Time series of mean $\delta^{13}\text{C}$ values (‰ \pm s.e.) in 1SW and MSW salmon scale collagen from River Sella (red colour) and rivers Bush (a), Dee (b), Frome (c), and northeast UK coast (d) (blue colour).

(MacKenzie *et al.*, 2011), so both variables must be highly correlated over time. The PCI dataset (Johns, 2017) was obtained from the Continuous Plankton Recorder (CPR) survey operated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS; see Reid *et al.*, 2003 for details). The analysis was performed within a spatial domain encompassing 44° to 65°N and 55°W to 20°E (29 of the CPR standard areas). We calculated the 8-month summer mean for each area, excluding years with monthly data missing for more than 2 months. We used the regularized iterative principal component analysis algorithm implemented in the *missMDA* v1.11 R package (Husson and Josse, 2017) to impute the missing entries of the resulting dataset.

Results

Mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Atlantic salmon scales for all populations throughout the study ranged from -18.6‰ to -13.8‰ and $7.2\text{--}13.7\text{‰}$, respectively, in 1SW salmon, and from -18.7‰ to -13.9‰ and $7.9\text{--}13.7\text{‰}$ in MSW salmon (Table 1). Thus, the range of variation was similar in both age groups.

The $\delta^{13}\text{C}$ values in the scales of the River Sella were not correlated to body mass (correlation analysis, $n = 148$, $p = 0.46$). The $\delta^{13}\text{C}$ values did not differ between 1SW and MSW returning salmon over the study period ($p = 0.42$), the pattern being consistent across years (interaction term, $p = 0.22$). In contrast, the $\delta^{15}\text{N}$ values significantly increased with body mass (correlation analysis, $n = 148$, $r = 0.33$, $p < 0.001$). Therefore, there were significant differences in $\delta^{15}\text{N}$ values between sea-age groups ($F_{1,76} = 17.42$, $p < 0.0001$) and the differences were consistent across years (interaction term, $p = 0.66$).

The 1SW salmon from River Sella had significantly lower $\delta^{13}\text{C}$ values than those from UK rivers throughout the sampling period (Table 2, Figure 2). The $\delta^{13}\text{C}$ values for MSW salmon from River Sella did not show significant differences from those from River Dee and the similarity was maintained over time, but they were significantly different from the values presented by MSW salmon from the rest of studied UK rivers (Table 2, Figure 2). The fluctuations in carbon values in MSW scales from River Sella closely followed the same temporal pattern than those from river Dee (Figure 2); therefore, the mean, minimum, and maximum values of $\delta^{13}\text{C}$ as well as variance and standard deviation of the mean in the River Sella during the overlapping period 1988–2004 (mean = -16.4 , min = -18.3 , max = -15.0 , $SD = 0.53$, variance = 0.29) were nearly identical to those of the River Dee (mean = -16.4 , min = -18.5 , max = -15.4 , $SD = 0.45$, variance = 0.20). In consequence, we pooled the data from rivers to perform the next analysis.

Correlations between time series of $\delta^{13}\text{C}$ values of MSW salmon from both rivers Sella and Dee and SST varied spatially across the North Atlantic (Figure 3a). The spatial distribution of correlation degree was highly structured, the area of highest correlations, and thus most likely feeding areas, for MSW returning salmon being around Greenland, both in the Labrador Sea in the west and the Irminger Sea in the east. The strong correlation between PCI and scale $\delta^{13}\text{C}$ values in this area, especially south to Greenland (Figure 3b), is consistent with the proposed feeding grounds based on SST. This indicates a westerly migration route for MSW salmon from rivers Sella and Dee.

The $\delta^{15}\text{N}$ values also correlated positively with body mass in all UK rivers (Bush: $n = 484$, $r = 0.23$, $p < 0.001$; Dee: $n = 290$, $r = 0.49$, $p < 0.001$; Frome: $n = 256$, $r = 0.51$, $p < 0.001$; northeast UK coast: $n = 161$, $r = 0.42$, $p < 0.001$). The $\delta^{15}\text{N}$ values of 1SW

Table 1. Mean \pm SD (min, max) values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in 1SW and MSW scale samples of Atlantic salmon from Spanish River Sella and comparative populations from the British Isles.

River	Age	Mass (kg)	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Sella	1SW	2.478	39	-16.5 ± 0.3 ($-17.2, -15.8$)	10.7 ± 0.4 ($10.0, 11.7$)
Bush	1SW	2.194	171	-15.6 ± 0.7 ($-17.5, -14.0$)	10.44 ± 0.86 ($8.4, 13.7$)
Dee	1SW	2.820	249	-16.2 ± 0.7 ($-17.9, -14.5$)	9.1 ± 0.7 ($7.2, 11.8$)
Frome	1SW	3.132	249	-16.3 ± 0.6 ($-18.6, -14.5$)	9.9 ± 1.0 ($7.3, 12.6$)
Northeast UK coast	1SW	3.089	150	-15.9 ± 0.8 ($-18.1, -13.8$)	9.7 ± 1.1 ($7.0, 13.0$)
Sella	MSW	4.969	109	-16.2 ± 0.6 ($-18.2, -14.8$)	12.0 ± 0.9 ($9.3, 13.6$)
Bush	MSW	3.954	350	-15.8 ± 0.5 ($-17.6, -14.4$)	11.0 ± 0.8 ($9.0, 13.4$)
Dee	MSW	5.934	248	-16.4 ± 0.4 ($-18.5, -15.4$)	10.6 ± 0.7 ($7.9, 13.0$)
Frome	MSW	6.382	215	-16.8 ± 0.5 ($-18.7, -15.6$)	11.4 ± 0.8 ($8.9, 13.7$)
Northeast UK coast	MSW	6.354	139	-15.9 ± 0.8 ($-18.5, -13.9$)	10.5 ± 0.8 ($8.5, 12.6$)

Min–Max values are the minimum and maximum values of all sampled scales. Mean mass values and sample sizes (*n*) are also indicated.

salmon from River Sella were significantly higher than those of the study UK rivers, and such differences were consistent over time except for the comparison with River Bush (Table 2, Figure 4). The values of $\delta^{15}\text{N}$ of MSW salmon from River Sella were also significantly higher than those of UK rivers but for River Frome, which had similar values as River Sella (Table 2, Figure 4). These patterns were maintained over time except for the comparison again with River Bush (Table 2); in this case, significant differences emerged mainly from the sampling period from 2000 onwards (Figure 4). However, when we controlled for the effects of body mass on $\delta^{15}\text{N}$ values, samples from River Sella had significantly higher values than all UK rivers, including River Frome (Table 3, Figure 5).

Discussion

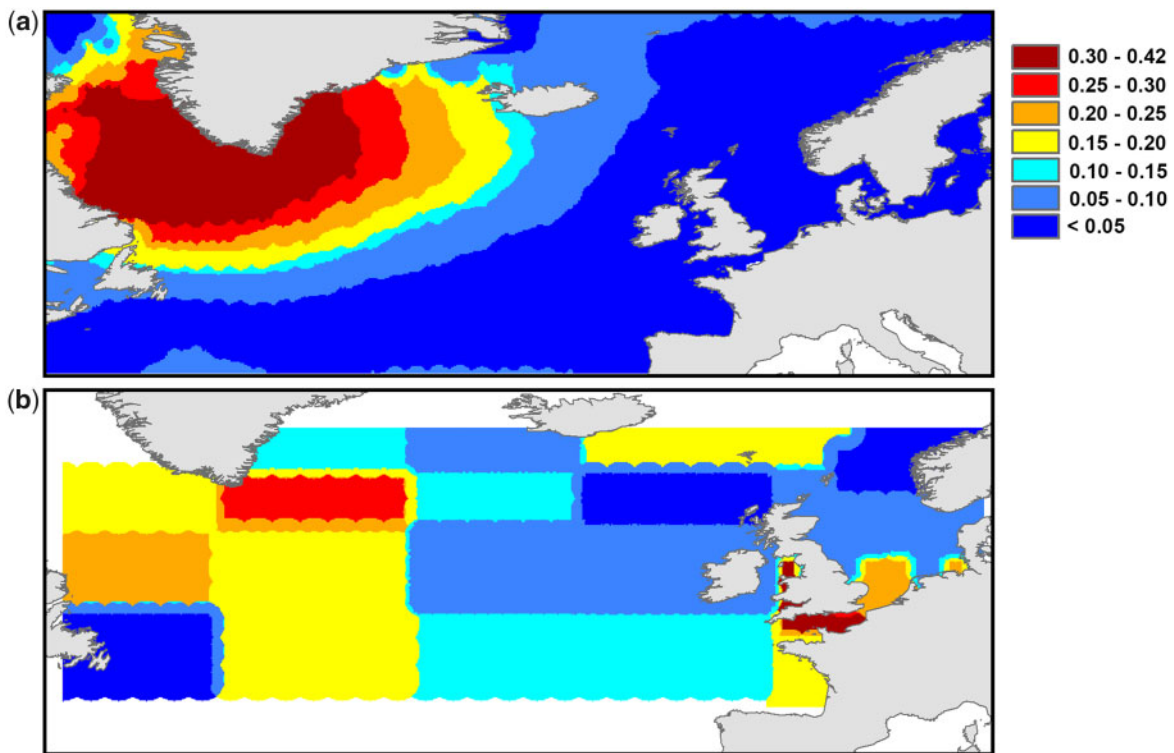
Potential feeding grounds of River Sella salmon

The temporal covariation in SST and $\delta^{13}\text{C}$ values suggested that salmon from River Sella forage in the western North Atlantic. Potential feeding areas for MSW returning salmon would be located around Greenland, both in the Labrador Sea in the west and the Irminger Sea in the east. The strong correlation found between time series of carbon composition in MSW salmon scales and primary productivity in these areas would support this hypothesis, as isotopic patterns in higher trophic level foragers typically mirror those observed in phytoplankton at the base of the food web (Graham *et al.*, 2010). Within these potential feeding areas, until now only three tag recoveries of Spanish salmon have been reported, two parrs and one smolt tagged in Spain in 2003–2006 and recaptured in Greenland in 2006–2007 (Ó'Maoiléidigh *et al.*, 2018). In addition, three adults tagged in Greenland were recaptured in Spain in 1969, 1971, and 1972, respectively (Ó'Maoiléidigh *et al.*, 2018). Historically, the highest number of

Table 2. Results from two-way ANOVA analyses with geographic origin and year as independent factors, including its interaction.

Sella versus the following	1SW				MSW			
	Bush	Dee	Frome	Northeast UK coast	Bush	Dee	Frome	Northeast UK coast
<i>n</i>	36	89	53	54	154	118	67	65
<i>df</i>	1,1,1	1,4,4	1,2,2	1,2,2	1,4,4	1,5,5	1,3,3	1,3,3
Carbon								
Origin	16.6***	13.7***	17.5***	31.4***	54.8***	2.7 ns	9.8**	17.2***
Year	0.4 ns	19.1***	6.8**	13.6***	2.8*	3.3**	0.6 ns	15.6***
OR × year	0.8 ns	12.3***	1.4 ns	2.5 ns	2.1 ns	0.9 ns	0.1 ns	15.6***
Nitrogen								
Origin	39.1***	228.6***	22.2***	45.4***	13.6***	60.3***	0.6 ns	14.0***
Year	2.2 ns	5.9***	2.4 ns	5.5**	2.8***	6.4***	2.7 ns	2.6 ns
OR × year	6.9*	2.3 ns	0.2 ns	0.9 ns	2.9*	1.4 ns	0.4 ns	2.4 ns

The *F*-value and its significance (ns: $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are shown for each tested effect, as well as the number of individuals (*n*) included in the analyses and the degrees of freedom (*df*) for each tested effect (geographic origin, year, interaction).

**Figure 3.** Proposed feeding areas for MSW Atlantic salmon from rivers Sella and Dee indicated by the strength of correlation between time series of $\delta^{13}\text{C}$ values and (a) sea surface temperature (SST) and (b) PCI. Colours indicate the degree of correlation (R^2).

salmon recaptured from the European Southern stock has been recorded also in the west off Greenland (Reddin *et al.*, 2012; Ó'Maoiléidigh *et al.*, 2018). Of course, we are cautious about our findings since covariation analyses were based, to a greater extent, on data from River Dee as the temporal overlap between series from rivers Sella and Dee was relatively low.

Our comparative analysis with UK populations suggests that MSW Spanish salmon share a common foraging area around Greenland with salmon from River Dee (Wales). The River Sella $\delta^{13}\text{C}$ values reported in our study are within the range of those

described in Hórreo *et al.* (2018) for rivers Sella and Cares during 2007–2009, hence salmon from Spanish rivers seems to be consistently using the same feeding areas over time. Although the feeding areas of MSW salmon from the River Frome (mostly around the Icelandic shelf; MacKenzie *et al.*, 2011, 2012) do not entirely coincide with the proposed foraging grounds for Sella and Dee salmon, the similarity of average $\delta^{13}\text{C}$ values over the entire time series among rivers Sella, Dee, and Frome points towards an overall westerly migration route for salmon from Spain and the west coast of Great Britain. In addition, the $\delta^{13}\text{C}$ values for MSW

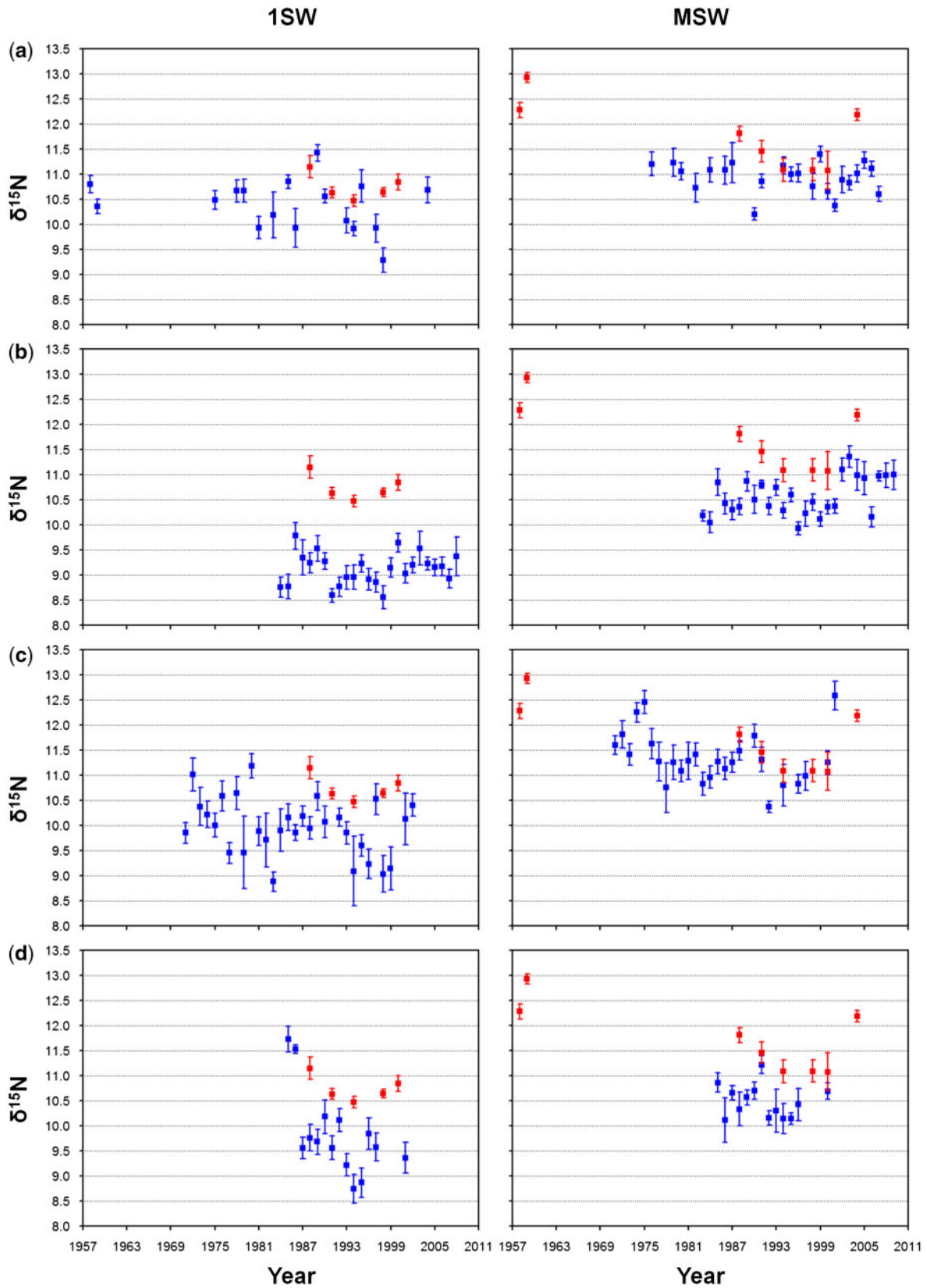


Figure 4. Time series of mean $\delta^{15}\text{N}$ values (‰ \pm s.e.) in 1SW and MSW salmon from River Sella (red colour) and rivers Bush (a), Dee (b), Frome (c), and northeast UK coast (d) (blue colour).

Table 3. Results from factorial ANCOVA analyses on $\delta^{15}\text{N}$ values, with body mass (kg) as covariate, and geographic origin and year as independent factors, including its interaction.

Sella versus the following	Bush	Dee	Frome	Northeast UK coast
<i>n</i>	222	215	126	81
<i>df</i>	1,1,4,4	1,1,5,5	1,1,4,4	1,1,2,2
Body mass	30.0***	96.1***	13.5***	12.6***
Origin	9.6**	264.2***	9.6**	29.7***
Year	8.5***	6.9***	10.1***	2.4 ns
Origin \times year	2.9*	1.5 ns	4.7**	1.3 ns

The *F*-value and its significance (ns: $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are shown for each tested effect, as well as the number of individuals (*n*) included in the analyses and the degrees of freedom (*df*) for each tested effect (body mass, geographic origin, year, interaction).

salmon from River Sella (Table 1) were very similar to those reported by Sinnatamby *et al.* (2009) for 1SW salmon from Newfoundland and Nova Scotia rivers (averages ranging from -15.8 to -16.2), Dixon *et al.* (2012) for 1SW (-16.3 ± 0.0) and MSW salmon (-16.1 ± 0.0) from rivers of Nova Scotia, eastern Newfoundland and western and northern Gulf of St. Lawrence, and Soto *et al.* (2018) for 1SW (-15.9 ± 0.3) and MSW salmon (-16.1 ± 0.4) from New Brunswick rivers. While some precaution is needed here as no statistical comparisons have been performed, such similarities in $\delta^{13}\text{C}$ with North American salmon stocks would give support to our hypothesis of a westerly migration route of Spanish populations of Atlantic salmon.

River Sella flows in an area influenced by the North Atlantic Current (NAC), a warm ocean current that continues the Gulf Stream northeast. This current divides into two parts to the north of Ireland along the European Continental Shelf edge; the northeasterly part becomes the Norwegian Current and flows into the Norwegian Sea, and the northwesterly part splits again to flow to the south of Iceland or towards Greenland (Figure 1). Spanish populations of Atlantic salmon are hypothesized to follow the western branch of the current to reach the feeding areas of west of Greenland. In fact, Ó'Maoiléidigh *et al.* (2018) recorded 100 recaptures of tagged salmon of Spanish origin in Irish marine salmon fisheries from 1993 to 2005, which would support the hypothesis that Spanish populations of Atlantic salmon follow the NAC.

Salmon returning to River Sella as 1SW and MSW showed a similar temporal trend in scale $\delta^{13}\text{C}$ values, which would suggest common feeding grounds around Greenland. Contrary to our results, previous works suggest some separation in feeding locations between 1SW and MSW salmon samples from Southern Europe. For example, MacKenzie *et al.* (2011, 2012) found differences in $\delta^{13}\text{C}$ values between 1SW and MSW Atlantic salmon returning to River Frome and to rivers from the northeast UK coast. These authors showed that 1SW salmon from rivers Frome and Dee likely occupied an area centred on the Faroe Islands and east Iceland, whereas MSW salmon from the River Frome fed in more westerly regions. Nevertheless, the mean $\delta^{13}\text{C}$ values of 1SW salmon from River Sella were closer to mean values reported by Sinnatamby *et al.* (2009), Dixon *et al.* (2012), and Soto *et al.* (2018) for 1SW salmon from Canadian rivers than to those from UK rivers. Furthermore, mean $\delta^{13}\text{C}$ values from River Sella were much higher than those from River Teno in Norway/Finland

(average -17.0 ± 0.4 , range between -18.1 and -16.0 ; Sinnatamby *et al.*, 2009).

Hence on the one hand, these comparisons together with the fact that salmon parrs of Spanish origin have been recaptured in Greenland (Ó'Maoiléidigh *et al.*, 2018) might give support to the idea of an early westerly migration of salmon from Spanish rivers. In this case, rheotaxis would be the main mechanism of migration, with salmon responding to local currents during the migratory process, which would allow to travel long distances. On the other hand, while almost 97% of salmon of European origin caught in the West Greenland fishery are non-mature 1SW salmon (ICES, 2018, table 5.2.1.4), most of them are thought to return to their home waters as 2SW, although such data are not available. While returning Spanish salmon have shown the fastest swimming speed within the southern European stocks [see figure 7.39 in Ó'Maoiléidigh *et al.* (2018)], likely link to more favourable current routes, it is not totally clear the viability, from a bioenergetic point of view, of such a long return migration to spawn after spending just one winter at sea. In addition, some caution is needed due to the low sample size of 1SW salmon scales from River Sella and the limited temporal overlap with data of both 1SW salmon from UK rivers and MSW from River Sella, which might impose some limits to the generalization of our results. Besides, the fact that tagged smolts of Spanish origin have been captured in the Faroes suggests that a fraction of the Spanish 1SW component likely mix with other 1SW salmon from the European Southern stock in the Iceland-Faroes-southern Norwegian Sea area [as suggested by MacKenzie *et al.* (2012) for 1SW of UK origin].

Trophic patterns of River Sella salmon

In the River Sella and the study UK rivers, the $\delta^{15}\text{N}$ values correlated positively with body size, which indicates changes in trophic level between 1SW and MSW salmon, the MSW feeding at higher trophic levels than the smaller 1SW. Similar results have been observed by MacKenzie *et al.* (2011, 2012) and Trueman *et al.* (2012) for Southern European stocks and Sinnatamby *et al.* (2009) and Dixon *et al.* (2012) for North American stocks. Pelagic marine ecosystems are strongly size-structured, with prey $\delta^{15}\text{N}$ values increasing systematically with size (Jennings *et al.*, 2008). In addition, the variance in $\delta^{15}\text{N}$ values in MSW from River Sella during the period 1958–2004 was higher than that of 1SW fish (see Table 1); this indicates a more opportunistic diet in MSW, as a larger variance in $\delta^{15}\text{N}$ is generally linked to omnivory (Dempson *et al.*, 2010; Dixon *et al.*, 2012). Such pattern observed in salmon from Spanish rivers disagrees with previous work of MacKenzie *et al.* (2012), which suggested that 1SW salmon returning to UK rivers would behave as an opportunistic pelagic predator, feeding both on invertebrates and fish, whereas MSW would feed more selectively, for example on key prey fish items such as capelin *Mallotus villosus*.

The observed variation in $\delta^{15}\text{N}$ among the River Sella and the study UK rivers was likely influenced by the feeding experiences of each population during the ocean phase. The $\delta^{15}\text{N}$ values from 1SW and MSW returning salmon from River Sella are very similar to those found by Dixon *et al.* (2012) in salmon captured in West Greenland but were higher than those from UK rivers. The following two hypotheses can be posed to explain the observed differences in $\delta^{15}\text{N}$ values between salmon from River Sella and UK rivers: (i) Salmon from Spanish rivers would feed at higher

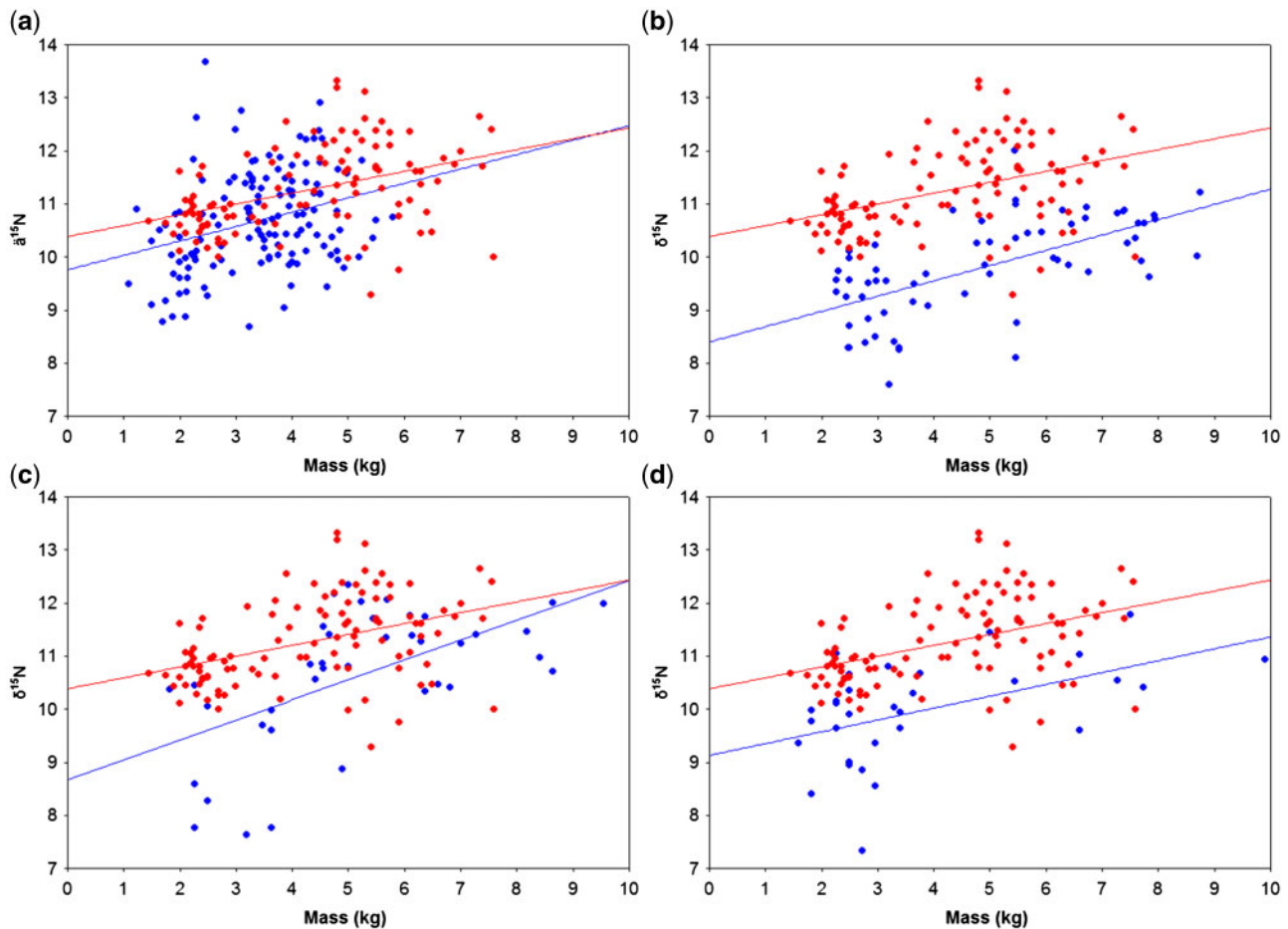


Figure 5. Relationships between mean $\delta^{15}\text{N}$ values (‰) and body mass (kg) of Atlantic salmon for River Sella (red colour) and rivers Bush (a), Dee (b), Frome (c), and northeast UK coast (d) (blue colour).

trophic levels than salmon from UK rivers (if baseline $\delta^{15}\text{N}$ values at feeding grounds are similar), or alternatively (ii) Spanish salmon would feed at similar trophic levels than UK salmon, but in waters with higher baseline $\delta^{15}\text{N}$ values. [McMahon *et al.* \(2013\)](#) reported relatively similar baseline $\delta^{15}\text{N}$ values in the Northwest and Northeast Atlantic Ocean, except for the northernmost waters of West Greenland, wherein baseline values are higher (see figure 1 in their paper). Regarding the first hypothesis (higher trophic feeding in Spanish salmon populations), there are observations that salmon feed proportionally more on invertebrates in the Northeast than in the Northwest Atlantic, where fishes are more important in the diet ([Dempson *et al.*, 2010](#)), which would be consistent with the observed trophic differences between salmon from River Sella, potentially foraging in the Northwest, and the populations from the northeast UK coast, which forage in the Northeast Atlantic. However, this first hypothesis would not explain the existing discrepancy between $\delta^{15}\text{N}$ values in scales from MSW fish returning to the rivers Sella and Dee, which might share common feeding areas according to our carbon isotope analyses. We suggest that this discrepancy would imply spatial segregation of salmon of Spanish and UK origin within West Greenland rather than differences in trophic level feeding (second hypothesis). The most recent analyses regarding the region of origin of catches at West Greenland show that salmon from Spanish rivers are found in the northernmost

NAFO Division 1B, waters predominantly used by North American salmon, while salmon of UK origin typically forage in southern waters (NAFO Divisions E and F; [ICES, 2018](#), table 5.2.2.7; [Ó'Maoiléidigh *et al.*, 2018](#)). Furthermore, the onset of salmon seaward migration is around 30 d earlier in Spain than in Wales ([Otero *et al.*, 2014](#)), so Spanish populations of Atlantic salmon might arrive earlier at Greenland and occupy more northerly waters, which present higher baseline $\delta^{15}\text{N}$ values ([McMahon *et al.*, 2013](#)).

The lack of a consistent visible trend in the $\delta^{15}\text{N}$ time series from River Sella and UK rivers implies that, in general, the mean trophic level of Atlantic salmon populations has not consistently changed in recent decades. Over the last 40 years, the Northwest Atlantic has experienced several oceanographic changes, including SST and salinity, that have altered the marine food web on which migrating Atlantic salmon rely ([Mills *et al.*, 2013](#); [Dixon *et al.*, 2017](#)). However, Atlantic salmon is an opportunistic generalist predator, which has a broad diet and demonstrates an ability to rapidly switch feeding to more abundant prey items, often at different trophic levels, as they become available ([Sinnatamby *et al.*, 2009](#); [Dixon *et al.* 2012, 2017](#)). Time series of $\delta^{15}\text{N}$ values in salmon scales are therefore confounded by both trophic level and location effects and are challenging to interpret.

This is the first time that potential marine feeding areas are proposed for 1SW and MSW Atlantic salmon from the Iberian

Peninsula. The long-term comparative analyses of stable isotopes with other populations from southern Europe supported the hypothesis of a westerly migration route by Spanish salmon towards Greenland instead of an easterly route to the Norwegian Sea. Climate-driven ecosystem changes in marine feeding grounds are potentially the main driver of ongoing salmon decline and those unfavourable conditions are likely to worsen in the next decades. Such changes in biophysical conditions have not been quantitatively and qualitatively homogeneous throughout the North Atlantic (Almodóvar *et al.* 2019), so basic knowledge regarding the trophic ecology and location of feeding habitats is essential for the management of populations, as they help identify potential local pressures at sea, thus contributing to more targeted conservation programmes.

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