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Stable isotopes reveal linkages between ocean climate, plankton community dynamics, and survival of two populations of Atlantic salmon (*Salmo salar*)

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An 18-year record of stable isotopes from Atlantic salmon (*Salmo salar*) migrating to two different regions of the North Atlantic reveals climate-driven subdecadal variations. Time-series of carbon isotopes in one salmon stock, thought to feed in the Faroes/Iceland Basin area, show Subpolar Gyre (SPG) modal variability, which is not seen in fish feeding in the Norwegian Sea. At times of weak SPG circulation, when waters in the Iceland Basin are relatively warm, carbon isotope values are somewhat negative, suggesting possible changes in phytoplankton community structure. The fluctuations in plankton community dynamics suggested by the stable isotope values are coincident with fluctuations in the estimates of marine mortality in one sea-winter fish feeding in the Norwegian Sea, but not in those feeding in the Iceland Basin. Marine mortality in salmon feeding in the Iceland Basin is therefore likely to be more strongly influenced by factors other than bottom–up control. Time-series analysis of stable isotopes in consumer tissues provides information on the interaction between climate and ecosystem dynamics on the scale of individual stocks and cohorts.

Keywords: ecosystem, NE Atlantic, salmon, time-series.

Introduction

The North Atlantic Ocean is known to have been warming over the past century (Beaugrand and Reid, 2003; Curry *et al.*, 2003). However, superimposed on the long-term warming trends in the North Atlantic are shorter term climatic variations controlled by, for example, the North Atlantic Oscillation (NAO) and the North Atlantic Subpolar Gyre (SPG; Friedland *et al.*, 1993; Hakkinen and Rhines, 2004). The inherent variability in the climate of the North Atlantic affects ecosystem structures and dynamics, and many studies have shown coincidence of climate forcing and organism abundance measures at all levels within marine ecosystems (Friedland *et al.*, 1998; Beaugrand and Reid, 2003; Beare *et al.*, 2004; Behrenfeld *et al.*, 2006; Todd *et al.*, 2008). Despite this extensive literature, evidence for the mechanisms driving climate impacts on higher trophic levels is more difficult to obtain (Zohary *et al.*, 1994; Friedland *et al.*, 2000, 2003). Here, we use stable isotopes to track climatic influences on primary production through the foodweb to a marine pelagic predator (Atlantic salmon, *Salmo salar*).

The Atlantic salmon is an anadromous fish that usually feeds for between 1 and 4 years at sea before returning to natal rivers to spawn. Fish returning to natal rivers after spending one winter at sea are known as one sea-winter (1SW) fish, and fish returning after two winters at sea are known as 2SW fish. In addition, fish spending more than one winter in the marine environment are known as multi-sea-winter (MSW) fish. Atlantic salmon are found in European rivers ranging from northern Russia to northern Spain and migrate to feed in the Subarctic waters of the North Atlantic (Verspoor *et al.*, 1999). The current understanding of marine location in salmon is derived largely from tagging fish in home waters and recovering tagged fish in high-seas fisheries (Reddin *et al.*, 1988; Crozier *et al.*, 2004; ICES, 2009b; Dadswell *et al.*, 2010). Based on such data, European fish from rivers north of 62°N are believed to migrate to feeding grounds off the Faroe Islands and in the Norwegian and Barents Seas, and fish originating in European rivers below 62°N are thought to feed farther west, with some MSW returning fish feeding in the Labrador Sea west of Greenland (Schell *et al.*, 1989; Hansen and Jacobsen, 2003; Cherel and Hobson, 2007; Friedland *et al.*, 2009).

It is assumed generally that salmon originating from different natal rivers mix during marine feeding, but specifying feeding areas in wide-ranging pelagic species is challenging, as is analysing the environmental conditions they experience.

The abundance of populations of wild Atlantic salmon have been decreasing throughout most of their natural range over recent decades (Friedland *et al.*, 2003, 2009; Jonsson and Jonsson, 2004), with most of the decline attributed to increased mortality during the marine phase of life (Jonsson and Jonsson, 2004; Friedland *et al.*, 2005, 2009; Peyronnet *et al.*, 2007). Declines have been most severe in the southern parts of the range, with links made to increasing temperatures (Todd *et al.*, 2008).

The most marked decreases in overall numbers of salmon returning to their natal streams to spawn were recorded in the late 1970s and the late 1980s to early 1990s, the latter coinciding with a period of long-term increase in sea surface temperature (SST; Beaugrand and Reid, 2003; Peyronnet *et al.*, 2008; Todd *et al.*, 2008), a sudden change in the strength of the SPG circulation (Friedland *et al.*, 1993), and a presumably related regime shift in many components of the North Atlantic ecosystem (Carscadden *et al.*, 2001; Hátún *et al.*, 2009). This change involved a decrease in zooplankton abundance overall, particularly in larger, cooler-water euphausiids and copepods, but a general increase in phytoplankton biomass and abundance of smaller, warm-water euphausiids and copepods (Carscadden *et al.*, 2001; Beaugrand *et al.*, 2003; Beaugrand and Reid, 2003). The shift in plankton types from larger, cooler-water to smaller, warmer-water species has in turn been linked to changes in the abundance, distribution, and recruitment success of predatory pelagic species such as blue whiting, cod, herring, Atlantic salmon, and pilot whales (Carscadden *et al.*, 2001; Beaugrand *et al.*, 2003; Beaugrand and Reid, 2003; Hátún *et al.*, 2009).

Responses to changing SSTs vary between differing salmon populations and ages within those populations, with temperature correlating positively with post-smolt and 2SW growth, but negatively with 1SW growth in Scottish fish (Friedland *et al.*, 2005). Friedland *et al.* (2005) also found that the sign of correlations between growth and SST could vary by month in salmon from the Margaree River, Canada, with negative correlations in May, but positive correlations in June. Although many North American salmon populations have shown apparent deleterious effects of warming winter and spring SSTs linked to winter NAO (Reddin and Shearer, 1987; Friedland *et al.*, 2003), the abundance of returning European 1SW salmon has been linked positively to warmer SSTs in May (Friedland *et al.*, 1993, 1998, 2000; Todd *et al.*, 2008), although a negative impact of warmer temperatures has been reported in 2SW salmon returning to Scotland (Friedland *et al.*, 2005).

It has been suggested that ocean climate and salmon returns are linked indirectly via bottom–up ecosystem control, with the availability of prey under differing temperature regimes implicated as the causal mechanism (Beaugrand and Reid, 2003; Friedland *et al.*, 2005; Todd *et al.*, 2008). There is, however, also an argument for growth-mediated survival (i.e. top–down control) at the post-smolt stage, where smaller fish may be under predation risk (Friedland *et al.*, 2000, 2005, 2009; Peyronnet *et al.*, 2007). Under warmer conditions at sea, the combination of metabolic rate increase and reduced prey availability has been linked both to fewer returns and to those returning fish exhibiting poorer condition, and lower relative fecundity, weight, and lipid reserves (Jonsson and Jonsson, 2004; Todd *et al.*, 2008). These effects, however, may differ by population, age class, and stock (Jonsson and Jonsson, 2004; Friedland *et al.*, 2005).

There is a natural tendency to seek ocean-scale explanatory variables, such as the NAO, in the decline in Atlantic salmon, but the accumulated weight of evidence and the variability in numbers of returning fish, even to rivers that are relatively close, suggest that mortality may be controlled at more localized geographic scales. The various and contrasting responses to changing marine temperatures discussed above suggest segregation in feeding locations between North American and European salmon populations, between European 1SW and 2SW age classes, and between different river stocks from the same country, as discussed by MacKenzie *et al.* (2011).

In this study, we use an independent measure of salmon biology derived from the stable isotope composition of scale collagen and relate the measurements to climatic conditions experienced by the fish. The isotopic composition of a consumer's tissues varies with that of its food, and it gives a direct measure of the isotopic composition in assimilated diet. Time-series of variations in consumer isotopes therefore provide a direct record of variations in diet that may be compared with records of climate forcing. The carbon isotope composition (expressed as δ^{13}C values) of pelagic animal tissues depends strongly on the photosynthetic fractionation of carbon isotopes by phytoplankton at the bottom of the marine foodweb (Schell *et al.*, 1989; Zohary *et al.*, 1994; Lee *et al.*, 2005; Phillips *et al.*, 2009). Carbon isotope fractionation during photosynthesis (E_p) varies inversely with the ratio of plankton cell growth rate to dissolved carbonate concentration (Laws *et al.*, 1995; Rau *et al.*, 1996), and this relationship is influenced further by light and nutrient availability (Burkhardt *et al.*, 1999; Cassar *et al.*, 2006).

Phytoplankton taxonomy and cell geometry also influence the isotope composition of bulk production, because large cells, and diatoms in particular, are typically enriched in ^{13}C compared with other phytoplankton groups (Lara *et al.*, 2010). Dissolved carbonate concentrations, cell growth rates, and phytoplankton size distributions are directly and indirectly linked to temperature, and vary spatially and temporally across marine systems (Hofmann *et al.*, 2000; Barnes *et al.*, 2009; Graham *et al.*, 2010), leading to spatio-temporal variations in the δ^{13}C values of phytoplankton in the North Atlantic more than 6‰ (Barnes *et al.*, 2009; Graham *et al.*, 2010). The trophic fractionation of carbon isotopes is, in contrast, around 0–2‰ (Vander Zanden and Rasmussen, 1999; Newsome *et al.*, 2010). The carbon isotope composition of pelagic consumers of similar size, therefore, varies largely in relation to plankton conditions in the feeding location (Schell *et al.*, 1989; Cherel and Hobson, 2007; Phillips *et al.*, 2009; Graham *et al.*, 2010; Newsome *et al.*, 2010).

The nitrogen isotope composition (expressed as δ^{15}N values) of pelagic animal tissues is more strongly dependent on the trophic level of the animal than that of carbon (Vander Zanden and Rasmussen, 1999; Newsome *et al.*, 2010). Nevertheless, nitrogen isotopic fractionation associated with the uptake of dissolved nitrate by marine phytoplankton can also vary by up to 5‰, based on the availability of nitrate ions (Waser *et al.*, 2000; Lara *et al.*, 2010) and the extent of microbial N_2 fixation. Proximity to coastal areas can also play a strong role in determining nitrogen isotope composition in phytoplankton, because terrestrial sources of nitrates tend to be comparatively enriched in ^{15}N (Jennings and Warr, 2003; Jennings *et al.*, 2008). Variations in predator δ^{15}N values may, therefore, contain both trophic and baseline (primary production) components (Jennings and Warr, 2003; Mendes *et al.*, 2007; Graham *et al.*, 2010).

Here, we measure temporal variations in the stable isotope composition of salmon scale collagen from two subpopulations from the UK. By comparing time-series of stable isotopes with available climatic and population data, we can test whether climate forcing influences on primary production can be detected in tissues of higher trophic level predators and also whether these influences coincide with the measures of population abundance.

Methods

Sample collection

Time-series of scales taken from Atlantic salmon returning to distinct freshwater populations are routinely stored for studies of age and growth (Davidson and Hazlewood, 2005). These scales are grown incrementally, with bioapatite circuli laid down at regular intervals, and collagen layers underplating the circuli in an irregular "plywood" formation (Hutchinson and Trueman, 2006). The circuli can be read, much like growth rings in trees, to gain information about the life history of the salmon. As scale archives are collected and maintained in archives spanning years to decades, the collagen in the scale tissues can be analysed to extract carbon and nitrogen isotope records of the conditions of primary production and/or trophic level through time (Satterfield and Finney, 2002; Sinnatamby *et al.*, 2009; MacKenzie *et al.*, 2011). The scale collections analysed here are drawn from two separate UK locations (Figure 1), the River Frome (RF; Centre for Ecology and Hydrology, CEH, RF archive) in Dorset and the northeast English coast (Centre for Environment, Fisheries and Aquaculture Science, Cefas, North Sea Driftnet archive). Scales are associated with body-mass data for all samples from the RF, but in the northeast coast (NEC) archive, many samples did not have body-mass information available. For both archives, we determined δ^{13}C and δ^{15}N values of scales from ~10 1SW and 10 MSW fish for each available year between 1985 and 2002 in the North Sea driftnet archive and between 1979 and 2002 for the RF archive.

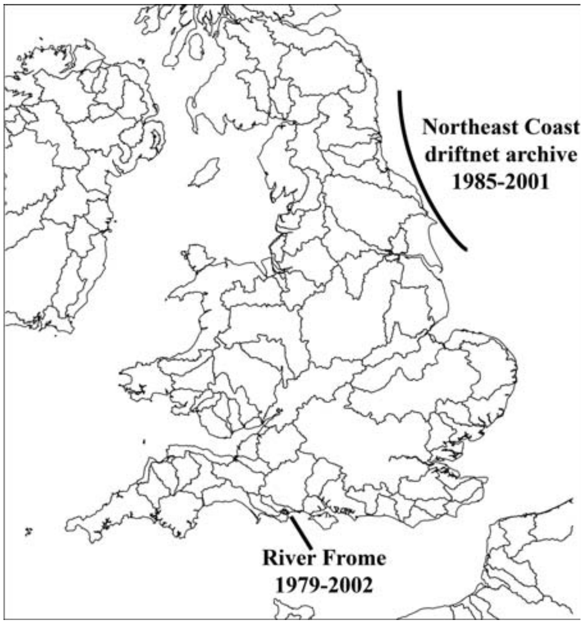


Figure 1. Location of the natal rivers for the two populations of Atlantic salmon sampled in this study.

Measurement of stable isotope values

Scales are incremental tissues growing allometrically with body size increase. Scale collagen is deposited only during seasonal growth and is not turned over metabolically (Hutchinson and Trueman, 2006). Occasionally scales are resorbed, but this is easily identified, and any scales showing resorption are not used for analyses. We therefore target collagen formed during spring–summer growth. Scales were briefly (ca. 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. The last summer of growth at sea (indicated by widely spaced circuli) was excised to obtain a temporally distinct sample (Hutchinson and Trueman, 2006). In 1SW fish, the summer section from the edge of the scale was sampled, but in MSW fish, summer immediately before the final winter at sea was sampled. Because of the three-dimensional nature of growth of collagen in scales (Hutchinson and Trueman, 2006), both 1SW and, to a lesser extent, 2SW samples will include a minor contribution of collagen laid down during the return migration. Samples were weighed to ~0.60 mg, and the isotope ratios were determined by elemental analysis isotope ratio mass spectrometry (EA–IRMS), using L-glutamic acid as an in-house calibration standard. Measurement precision, assessed as 2× the standard deviation of 16 replicate analyses of USGS40 glutamic acid for δ^{15}N and δ^{13}C, is 0.7 and 0.1‰, respectively. Full details of the preparation and analytical methods are given in MacKenzie *et al.* (2011).

Abundance data

The RF is an ICES (International Council for the Exploration of the Sea) North East Atlantic Commission Index River, in which the salmon stock has been well monitored historically, with an electronic resistivity fish counter in operation since 1970, providing the longest dataset for salmon migration in the UK (Welton *et al.*, 1999).

The NEC scale collection comes from an archive of samples taken while a driftnet fishery was in operation along that coast, harvesting a mixed-stock complex of salmon from the River Coquet, through the Tyne, Wear, Tees, as far as the Yorkshire Esk to the south, and from adjacent Scottish rivers to the north (see Figure 1). Unlike the Frome, none of the rivers thought to be represented by this archive are ICES North East Atlantic Commission (NEAC) Index Rivers, so they are not as well monitored and researched for their salmon populations (ICES, 2002). As a result, the best index of abundance for this mixed salmon population is thought to be the ICES pre-fishery abundance (PFA) model for England and Wales (ICES, 2009a).

Gyre index

Climate in the Northeast Atlantic is strongly influenced by exchanges of subtropical and Subarctic water masses associated with the strength of the SPG, an anticlockwise rotating body of relatively cold water of low salinity in the central northern North Atlantic (Hakkinen and Rhines, 2004; Hátún *et al.*, 2005). When circulation in the SPG is particularly intense, relatively cold water extends eastwards in the Iceland Basin and Faroes/Rockall areas and impinges upon the continental shelf, restricting the northward flow of warmer waters. During times of relatively low-intensity circulation, the centre of the gyre moves west, allowing the area of mixed warm and cold water to expand into the Iceland Basin (Hátún *et al.*, 2005). An index of the strength of the SPG based on a principal component analysis of sea surface heights captures much of the variation in measured salinity and water transport (Hátún *et al.*, 2005). This index has been extended back in time based on Oceanic General Circulation Model (OGCM) data and is termed the Gyre index (GI). Values for the GI were kindly provided by H. Hatún (pers. comm., 2011).

NAO index

The NAO refers to changes in pressure between a region of low pressure over Iceland and a region of high pressure over the Azores, with the difference recorded as the NAO Index (NAOI). The positive phase of the NAOI, where the pressure difference is greater, is associated with stronger westerly winds across the North Atlantic, leading to warmer, wetter winters in Europe. Negative phases of NAOI result in weaker westerlies, with Europe experiencing cooler, drier winters (Hurrell *et al.*, 2003). Values of the winter NAOI (wNAOI) were taken from NOAA (http://www.cgd.ucar.edu/cas/jhurrell/indices.html, accessed July, 2011).

Results

Influence of mass on δ^{15}N values

Significant, positive relationships exist between body mass and δ^{15}N values for both RF and NEC fish (RF salmon, $n = 309$, $r^2 = 0.41$, $p < 0.001$; NEC salmon, $n = 169$ $r^2 = 0.17$, $p < 0.001$; Figure 2a and b). These relationships suggest that trophic level influences δ^{15}N values (Jennings *et al.*, 2008). However, there is a large degree of scatter around these lines. The influence of mass on δ^{15}N values was removed by correcting measured values using the best-fit relationships shown in Figure 2. In NEC fish, correction for mass could be applied only where body-mass data were available, limiting the confidence in these data. No significant relationship was found between mass and δ^{13}C values for either population, indicating that the effect of variations in baseline (phytoplankton) isotopic composition masks any trophic level effect in salmon δ^{13}C values. Both δ^{13}C values and mass-corrected δ^{15}N values record isotopic variations in phytoplankton physiology or taxonomic composition, so potentially record the influence of climate variables on marine ecosystems.

Throughout the 18 years of concurrent sampling, salmon returning to the RF maintain consistently different δ^{13}C values from those returning to the NEC (ANOVA, with geographic origin as sole co-factor; $n = 523$, d.f. = 1, $F = 116.9$, $p < 0.001$). In addition, both year and sea age significantly influence δ^{13}C values (year, $n = 523$, d.f. = 17, $F = 9.1$, $p < 0.001$; sea age d.f. = 1, $F = 16$, $p < 0.001$), with a significant interaction between all factors (MacKenzie *et al.*, 2011). These data strongly suggest that, in each year sampled, returning salmon from different natal origins fed in distinct locations.

Time-series of carbon isotopes

The isotopic composition of carbon in the atmosphere and hence the oceans decreased steadily during the 18 years of sampling, owing to the contribution of burning fossil fuels depleted in ^{13}C (the Suess effect; Gruber *et al.*, 1999). The long-term reduction in δ^{13}C values of dissolved organic carbon in the global ocean is estimated at ca. 0.018‰ year^{-1} for the period 1980–1995, and this value is likely to be higher in the North Atlantic south of Iceland, but lower in Subarctic waters of the Norwegian Sea (Schöne *et al.*, 2011). However, whereas records of dissolved inorganic carbon isotopes preserved in marine carbonates show the Suess effect clearly (Schöne *et al.*, 2011), the effect is masked in organic tissues because of the large shorter term variations in isotopic fractionation during photosynthesis. A linear model fitted to all dataseries yields a negative slope ranging from −0.06 to −0.003‰ year^{-1}, but never is the slope significant. Hence, the 18-year time-series analysed here is probably too short to identify clear Suess effects. As there is no clear Suess effect demonstrated in the time-series, we have not attempted to impose an arbitrary correction based on non-significant linear trends. The marginal decrease in δ^{13}C values through the 18-year time-series has no significant impact on the large cyclic fluctuations that are the subject of the following investigations.

The time-series of δ^{13}C values from different age classes show subdecadal variability, but with differing amplitudes; δ^{13}C values in 1SW and MSW fish from the RF vary by ca. 0.5‰ and ca. 0.3‰, respectively (Figure 3a), whereas 1SW and MSW fish from the NEC archive are more variable with a total range of ca. 1.5‰ (Figure 3b). In both the RF and NEC samples, temporal fluctuations in δ^{13}C values of 1SW and MSW fish match closely (Figure 3c and d), despite having different absolute δ^{13}C values in any single year. This suggests that, although these age classes are likely not feeding in the same exact feeding areas at sea, the two feeding areas are most probably subject to the same climatic influences and are likely to be associated spatially. The time-series of δ^{13}C values from the two different areas of natal origin do not coincide (Figure 4), suggesting that salmon from different natal populations are more spatially distinct in marine feeding areas than 1SW and MSW returning salmon from the same natal population.

The apparent cyclicity in the δ^{13}C data and the strong links between the age classes for each population, but weaker links between the populations, suggest that the age classes are feeding in population-specific regions, separate from each other. Within each region, these fish are likely subject to differing controls on their isotope compositions, which are largely climate-driven for carbon and have a climatic component to the nitrogen values (Waser *et al.*, 2000; Lara *et al.*, 2010).

Comparison of isotope time-series with climate data

There is a strong relationship between the GI and carbon isotope values in the RF population for both 1SW and MSW returns (Figure 5a and b). Peak correlation is with 1SW fish when the δ^{13}C values are lagged by 1 year with respect to the GI (Figure 5c), suggesting rapid trophic cycling of a planktonic response to gyre-induced temperature variations. In contrast, there is no correspondence between δ^{13}C values and the GI in NEC salmon (not shown), implying a relatively minor influence of SPG modal variability on plankton physiology or species composition in the central and mid-Norwegian Sea. No relationship was found between isotope data and the wNAOI in either population.

To assess the extent of temporal covariance between the GI and δ^{13}C values in RF-origin salmon, we applied a linear model to both time-series. We do not expect the GI to have a direct influence on δ^{13}C values, so the intention here is to test whether the two time-series share a common pattern of temporal variation that may imply the existence of a common, but unmeasured,

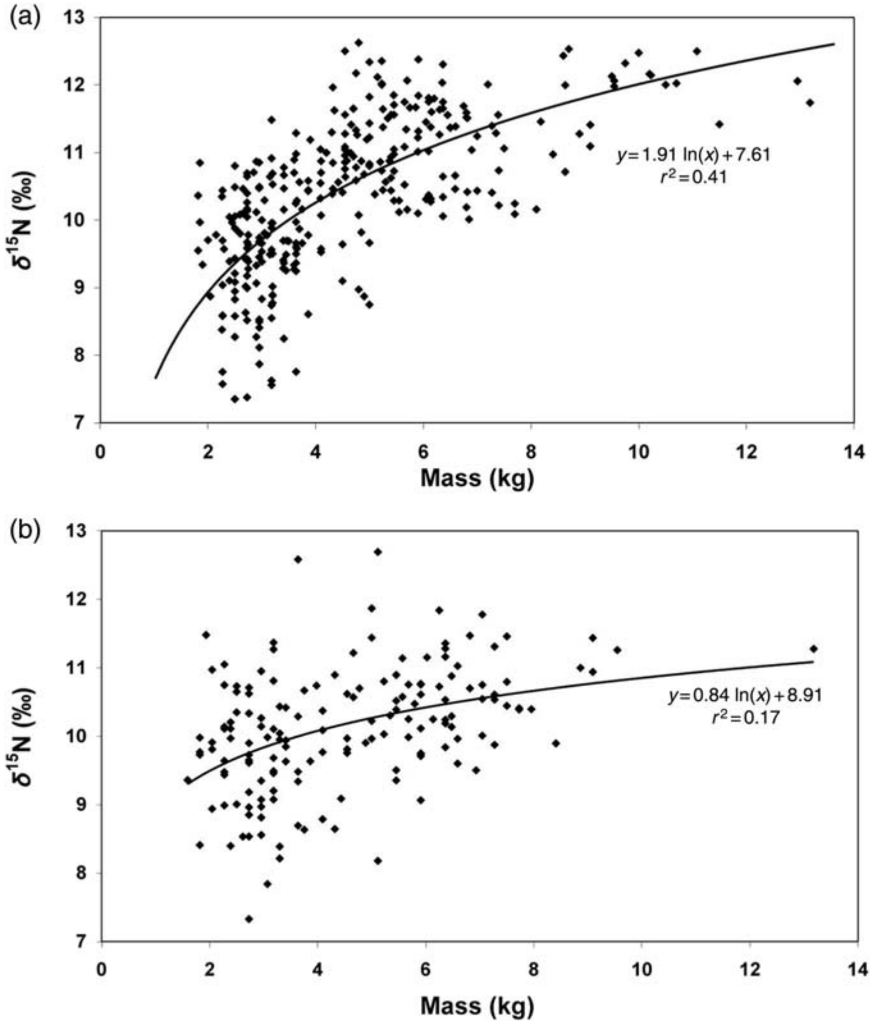


Figure 2. Scatterplots of relationships between mass and δ^{15}N values for (a) RF salmon and (b) NEC salmon. Fish with no record of mass were excluded from the analyses (RF: missing 1SW $n = 3$, missing MSW $n = 11$; NEC: missing 1SW $n = 56$, missing MSW $n = 64$).

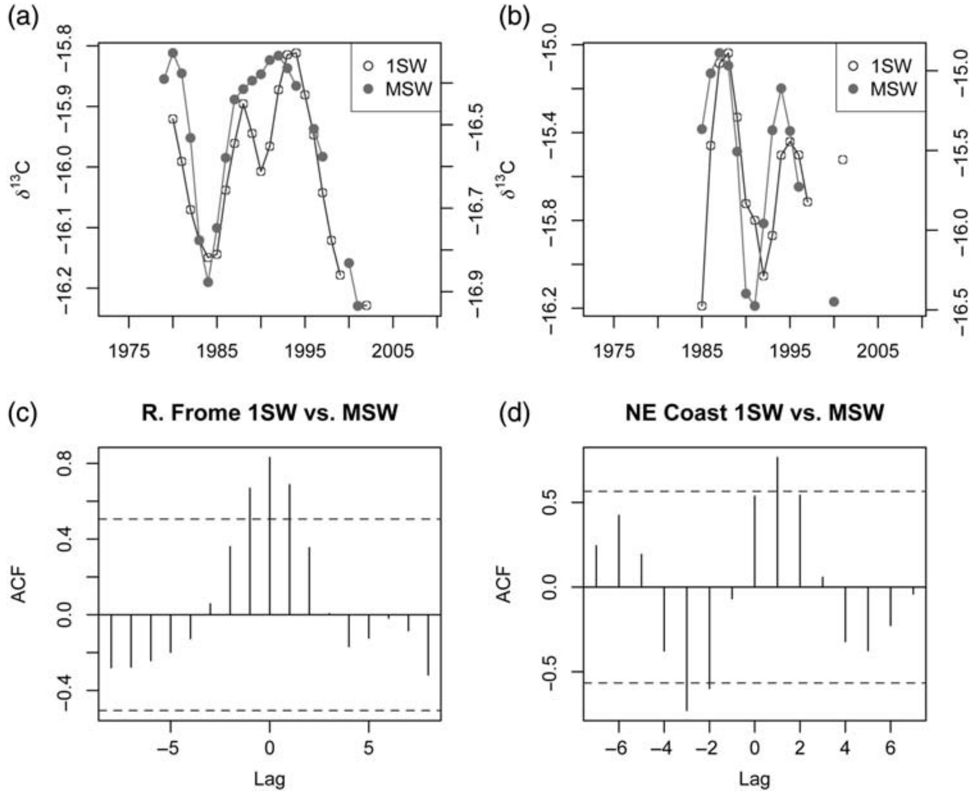
variable. It is hence inappropriate to detrend the two time-series, but the effect of autocorrelation must be considered when assigning significance values to any regression coefficient measured. Here we adopt the modified Chelton approach of Pyper and Peterman (1998) to adjust the degrees of freedom associated with the linear correlation. The resulting linear correlation (Figure 6) implies that variations in the GI explain ~60% of the variation in scale δ^{13}C values; the relationship is statistically significant despite the autocorrelation present in both time-series, with an adjusted p-value of 0.03.

Relationships between isotope composition and return rates

In contrast to the isotope data, estimates of the numbers of salmon returning to the RF and the PFA models display strong and significant negative trends through time. We therefore removed a linear (or, for the RF returns, second-order polynomial) trend from the population datasets before comparing them with the isotope data. There was no significant relationship between δ^{13}C values and returning numbers to the RF (Figure 7a and b). Detrended PFA model returns peaked in the early 1980s and mid-1990s, corresponding closely to positive excursions in δ^{13}C values measured in 1SW and, to a lesser extent, MSW fish returning to the NEC (Figure 7c and d). The linear correlation between detrended PFA model returns and δ^{13}C values measured in 1SW fish returning to the NEC fails a test of significance when adjusted for autocorrelation (adjusted p-value 0.08), but the extent of correspondence between the two time-series ($r^2 = 0.3$), and particularly the correspondence in extreme years, implies a degree of temporal coincidence between the oceanic conditions promoting relatively positive δ^{13}C values in phytoplankton and the relatively large numbers of returning salmon.

Discussion

The two natal origin populations of salmon sampled in this study differ in terms of their absolute δ^{13}C values and the temporal series of their δ^{13}C values. As δ^{13}C values in consumer protein primarily reflect variations at the base of the food chain, the results indicate that the primary production supporting the food chains sampled by these fish were influenced by differing climatic histories and hence that the fish feed in different regions of the North Atlantic (MacKenzie *et al.*, 2011). This statement is supported by



R. Frome 1SW vs. MSW

NE Coast 1SW vs. MSW

Figure 3. Time-series of carbon stable isotope compositions of scale collagen from 1SW and MSW salmon returning to (a) the RF and (b) the NEC of the UK. The left axis gives the isotope composition of 1SW fish and the right axis the isotope composition of MSW fish. Cross-correlations of carbon isotope time-series for 1SW and MSW fish are shown in (c) and (d) for RF and NEC fish, respectively.

contrasting temporal abundance trends seen in Norwegian and Scottish populations and by the greater similarity in marine growth patterns for salmon from natal populations local to each other than for more distant populations (Vøllestad *et al.*, 2009; Jensen *et al.*, 2011). These trends suggest a strong regional component to marine feeding and survival. The temporal δ^{13}C records sampled by the RF population show a strong SPG modal variation. The SPG closely controls temperature variations and plankton community dynamics in the Faroes shelf/Iceland Basin/Rockall Plateau area, and it is likely that the RF fish are feeding there. Tag-recapture datasets suggest that fish from Scottish natal rivers feed either north of the Faroe Islands or in the Norwegian Sea. The lack of correlation between the NEC population and the SPG is consistent with tagging datasets, suggesting that these fish feed in an ecosystem where the SPG does not exert the strongest control on SST.

The SPG exerts a strong influence on the dynamics of phyto- and zooplankton, influences the location (and abundance) of higher trophic level organisms through bottom–up controls on prey availability and location (Hátún *et al.*, 2009), and is likely to influence bulk plankton δ^{13}C values indirectly through SST.

As discussed above, isotopic fractionation during photosynthesis is influenced by cell growth rates and dissolved CO_2 content, both of which are influenced by temperature. Plankton cell size has a significant influence on δ^{13}C values (Laws *et al.*, 1995; Popp *et al.*, 1999). Diatoms are generally enriched in ^{13}C, in part because of different enzymatic pathways (Cassar and Laws, 2007; Lara *et al.*, 2010) and partly through kinetic effects (Popp *et al.*, 1999).

Picophytoplankton may be responsible for >40% of all primary production in open ocean environments especially in warmer more oligotrophic environments (Morán *et al.*, 2010). Isotopic fractionation associated with picoplankton groups is relatively poorly known, but size-fractionated analyses of phytoplankton δ^{13}C values indicates that the smallest fractions typically contain the most negative δ^{13}C values (Rau *et al.*, 1990). SST also has a profound effect on phytoplankton cell size, size structure, and taxonomic composition (Leterme *et al.*, 2005; Morán *et al.*, 2010). Hence, the strong SPG modal variability in δ^{13}C values for the RF population implies a temperature effect on either growth rates and CO_2 contents, or cell size and taxonomy.

The correlation between SPG index and δ^{13}C values is positive, indicating that years with warm SST (low GI) correspond to relatively negative δ^{13}C values. The concentrations of dissolved CO_2 decrease with increasing temperature, so the observed negative relationship between SST and δ^{13}C values implies either a reduction in phytoplankton growth rates with increasing SST (Laws *et al.*, 1995; Cassar *et al.*, 2006) or changes in phytoplankton community composition. Weaker SPG circulation (and warmer SSTs) are linked to increased primary production in the Faroes/Iceland Basin (Hátún *et al.*, 2009), implying an increase rather than a decrease in growth rates with SST. Within the Northeast Atlantic, diatoms and dinoflagellate abundances both increase with increasing SST, but the slope of the relationship is greater for dinoflagellates, suggesting a decreasing proportional abundance of diatoms with increasing SST (Leterme *et al.*, 2005). Similarly, Morán *et al.* (2010) demonstrate a strong relationship between increasing SST and increasing proportion of picophytoplankton, so it is likely

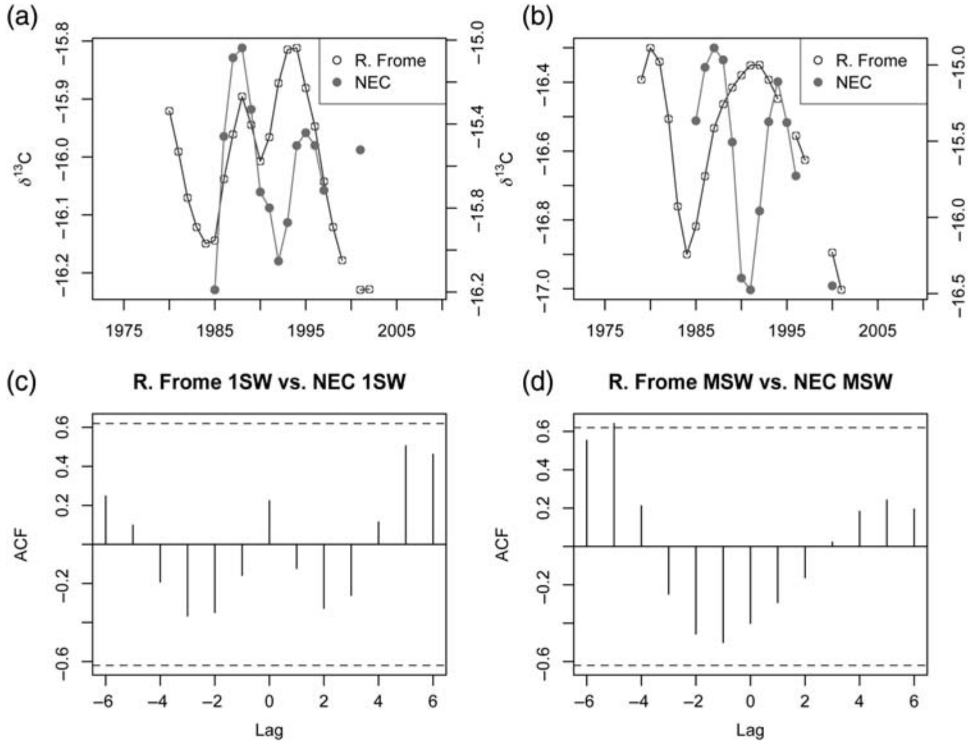


Figure 4. Comparison of time-series of carbon isotope compositions between (a) 1SW and (b) MSW salmon returning to the RF (open symbols) and the UK's NEC (filled symbols). The left axis gives the isotope composition of Rive Frome fish and the right axis the isotope composition of NEC fish. Cross-correlations of carbon isotope time-series between RF and NEC returning fish are shown in (c) and (d) for 1SW and MSW fish, respectively.

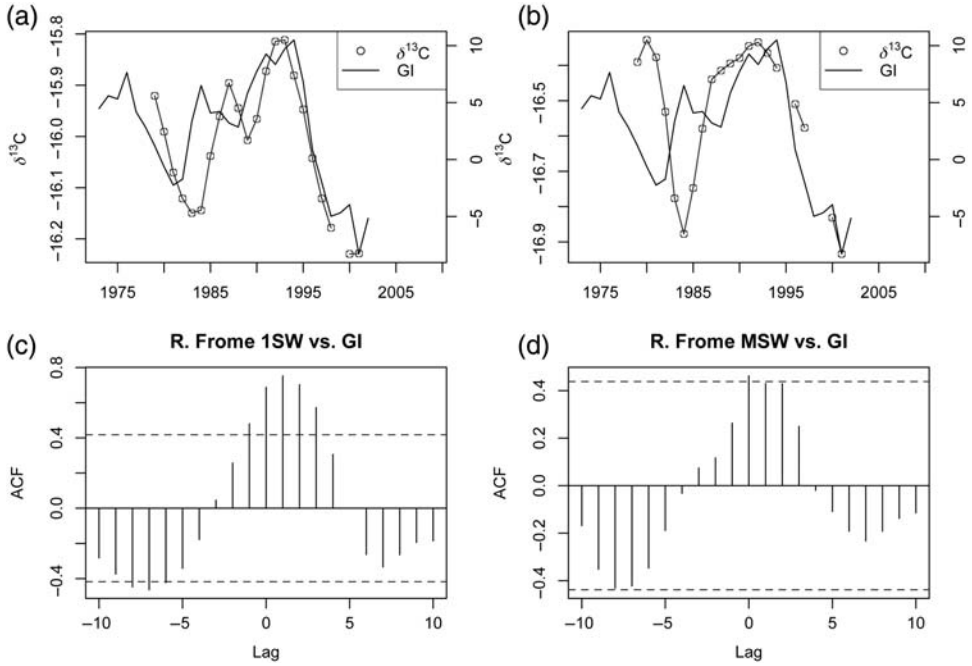


Figure 5. Correspondence between time-series of carbon isotope values in scale collagen in (a) 1SW and (b) MSW salmon returning to the RF and the GI of Hátún *et al.* (2005). The left axis gives the isotope composition of RF fish and the right axis the GI. Cross-correlation plots (c) and (d) indicate maximum covariance at a lag of 1 year.

that increasing SST influences bulk organic $\delta^{13}C$ values by increasing the proportion of small cells with increased isotopic discrimination and lower $\delta^{13}C$ values.

Salmon returning to the NEC of the UK likely feed in the Norwegian Sea (Todd *et al.*, 2008; Friedland *et al.*, 2009). $\delta^{13}C$ values for the NEC population also correlate closely with SST in the Norwegian Sea (MacKenzie *et al.*, 2011), with warmer SST corresponding to lower $\delta^{13}C$ values, as in the RF population. Carbon isotope data therefore imply similar, close coupling between SST and phytoplankton community composition in the Iceland Basin/Rockall area and in the central Norwegian Sea.

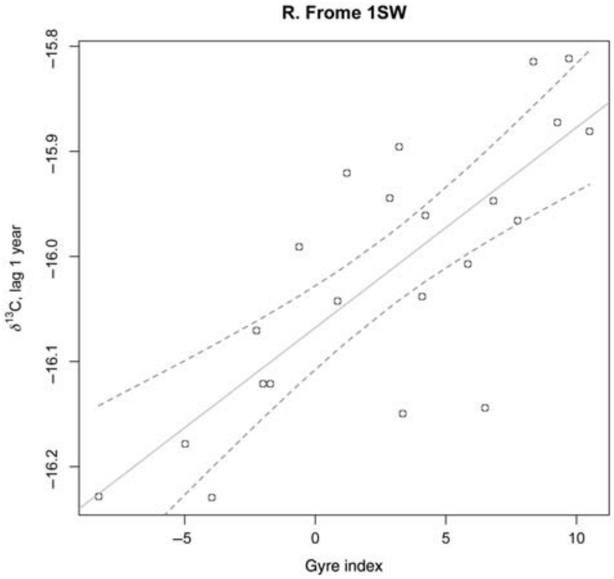


Figure 6. Linear correlation between carbon isotope values in scale collagen in salmon returning as 1SW fish to the RF and the GI of Hátún *et al.* (2005). Dotted lines indicate 95% confidence intervals.

The strong SPG modal variability in $\delta^{13}C$ values for the RF population reveals that that population is influenced by SPG modal variation (Figure 6), but the inferred effect of the SPG on phytoplankton community dynamics has a relatively weak influence on either return rates measured directly in the RF or on estimated PFA of English- and Welsh-origin salmon (Figure 7). Time-series of $\delta^{13}C$ values in 1SW fish returning to the NEC do, however, coincide with peak (modelled) PFA in the late 1980s and early-mid 1990s, suggesting that controls on plankton community dynamics in the Norwegian Sea either directly influenced mortality rates or were correlated with other environmental variables or biological responses that influenced return rates. The influence of any environmental effect on widely, but patchily, distributed animals such as salmon at high trophic levels is likely to vary between geographically segregated populations, and the isotope data suggest that the level of marine mortality of salmon feeding in the Norwegian Sea is more strongly influenced by climate-driven bottom–up effects than that of salmon feeding in the Iceland Basin. As RF salmon do show clear evidence for climate-related variation in plankton communities, effects other than bottom–up control must regulate population numbers. It needs to be stressed, however, that river-count data on salmon are a crude measure of open-ocean marine mortality, because they do not account for variations in the size of the out-migrating

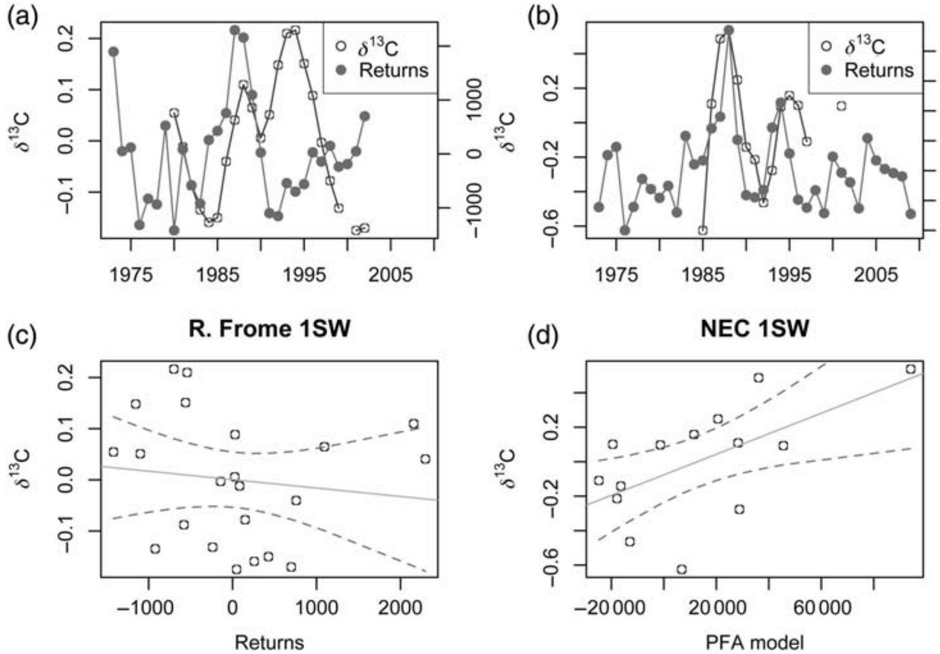


Figure 7. Correspondence between time-series of carbon isotope values in scale collagen in 1SW salmon returning to (a) the RF and (b) the UK's NEC. The numbers of salmon returning to the RF are derived from fish counts. No direct measures of abundance are available for the NEC subpopulation, so ICES PFA models for English and Welsh salmon were used as the best available estimates for changes in temporal abundance. In all plots, the left axis gives the isotope composition and the right axis the population abundance estimate. Linear models showing covariation between isotope data and population estimates are shown in (c) and (d) for the RF and NEC samples, respectively. Dotted lines on those panels indicate 95% confidence intervals.

population or the assumed heavy mortality on initial smoltification (transfer from fresh- to saltwater).

Conclusions

The stable isotope composition of collagen in the scales of Atlantic salmon varies systematically, with a subdecadal variability in $\delta^{13}C$ values likely reflecting a mixture of changes in phytoplankton community composition. Salmon are pelagic predators at a high trophic level, and the sampled tissue reflects the average isotopic composition of diet assimilated over a full season of feeding. The measured amplitude of isotopic variation will be attenuated therefore during transfer from primary production to consumer tissues, and it likely reflects relatively large subdecadal variation in the mean isotope composition of phytoplankton. Although the exact cause of the isotopic response is uncertain, one strong candidate is changes in the relative proportion of production corresponding to small (picoplankton) compared with large (diatom) cells.

Two populations of salmon returning to different natal rivers display contrasting isotope time-series, indicating migration to different sea areas to feed. Fish originating from the RF show carbon isotope time-series with a strong SPG modal variability, supporting arguments that they feed in a broad area around the Iceland Basin. Salmon originating along the NEC of the UK, in contrast, show no influence of the SPG on their isotope composition, indicating feeding in a region where SST does not correspond closely to the SPG. This is consistent with the presumed feeding area for NEC fish in the Norwegian Sea.

The stable isotope record of salmon scale collagen demonstrates large fluctuations in the physiology or community dynamics of phytoplankton in the salmon feeding areas. The temporal coincidence between changes in phytoplankton community dynamics and population mortality/abundance estimates varies between salmon populations and cohorts. This implies that the relative importance of specific ecological and environmental drivers in influencing population dynamics is a function of the migration route and feeding area used by individual stocks or stock complexes.

Archived consumer tissues provide a valuable retrospective measure of ecosystem response to changing climatic conditions, but more work is needed to interpret the finer details of stable isotope variation in marine environments.

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