



Ocean warming cannot explain synchronous declines in North American Atlantic salmon populations

David X. Soto^{1,2,*}, Clive N. Trueman³, Kurt M. Samways¹, Michael J. Dadswell⁴,
Richard A. Cunjak¹

¹Canadian Rivers Institute and Department of Biology, University of New Brunswick, Fredericton, NB E3B 5A3, Canada

²Department of Earth and Environmental Sciences, KU Leuven, 3001 Leuven, Belgium

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

⁴Biology Department, Acadia University, Wolfville, NS B4P 2R6, Canada

ABSTRACT: Atlantic salmon *Salmo salar* populations have suffered global, synchronous declines over the past decades. These declines are coincident with improvements in river habitats and reductions in high seas fisheries, implying higher rates of natural marine mortality that have been widely linked to increasing ocean temperatures in the North Atlantic. The mechanisms linking temperature to marine mortality in Atlantic salmon, however, are unclear. During the period 1980–2010, populations of *S. salar* returning to the St. John River, New Brunswick, Canada, after spending either 1 or multiple winters at sea have shown similar patterns of decline, coincident with recent ocean warming in the North Atlantic Ocean. Here we used stable isotope data from historic scale collections to investigate the relationship between foraging location, experienced ocean temperature and population trends for *S. salar* returning to the St. John River. We show that salmon spending either 1 or multiple winters at sea before returning to the St. John River consistently fed in different regions of the North Atlantic and experienced different ocean warming trends. However, both cohorts show synchronous progressive population declines over the study period. We therefore suggest that ocean warming cannot be the principal cause of increased marine mortality for salmon returning to the St. John River. Both cohorts experience similar conditions during the initial post-smolt period, and increased post-smolt mortality could underpin population declines. Our results support concentrating management and conservation efforts to reduce mortality in the post-smolt phase of salmon lifecycles.

KEY WORDS: Ocean warming · Ocean migration · *Salmo salar* · Sea surface temperature · Stable isotopes · Archived scale tissue

INTRODUCTION

Atlantic salmon *Salmo salar* are an important economic, cultural and ecological component of temperate, boreal and Arctic Atlantic ecosystems. Many European and North American populations of Atlantic salmon have declined significantly over the last few decades (Limburg & Waldman 2009, Chaput 2012, Jones et al. 2014). However, commercial fish-

ing in high seas areas has been reduced considerably during this period of time, and the freshwater environment has dramatically improved since the 1960s. Catches of high-seas fisheries, including those of west Greenland, the Faroe Islands, and the Norwegian Sea, declined from 2500 to 1500 t yr⁻¹ during the period 1968–1991 (Dadswell et al. 2010), and these fisheries were closed in 2002, 1991 and 1999, respectively. The synchronous salmon declines in both sides

*Corresponding author: david.soto@kuleuven.be

of the Atlantic, ~60–70% since the 1970s, strongly suggest that ocean basin-scale processes are driving increased marine mortality (Friedland et al. 2014). The North Atlantic Ocean has experienced a significant warming trend in the mid-1990s and the first part of the 2000s (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m601p203_supp.pdf; Straneo & Heimbach 2013, Robson et al. 2016). Salmon are a cold water species, and periods of warming are largely predicted to negatively impact marine survival at least for populations at the southern margins of the species' range (Trueman et al. 2012b, Mills et al. 2013, Piou & Prévost 2013, Friedland et al. 2014). After leaving freshwater, Atlantic salmon migrate rapidly to open-ocean feeding habitats where they feed for ≥ 1 yr before returning to natal rivers to spawn. Most anadromous Atlantic salmon populations migrate to the Atlantic Ocean and into the North Atlantic Sub-polar Gyre for feeding and growth before returning to natal rivers for spawning (Dadswell et al. 2010). Sub-optimal conditions during marine foraging, however, might contribute to poor growth and consequently to higher mortality rates (Bacon et al. 2009). Ocean conditions during the first year at sea (the post-smolt year) are thought to exert a particularly strong influence on growth and survival potential (Peyronnet et al. 2008, Friedland et al. 2014).

Changes in sea surface temperature (SST) in the oceanic feeding areas of Atlantic salmon are predicted to influence survival through direct effects on increased energy expenditure and metabolism and indirect effects such as migration timing, predation pressure, suboptimal food availability and growth (Hubley et al. 2008, Todd et al. 2008, Chaput 2012, Trueman et al. 2012b). Alternatively, changes in SST could potentially cause salmon to migrate to alternate regions in search of preferred thermal habitats (Rikardsen et al. 2008, Guðjónsson et al. 2015). Many authors have therefore recognized the likely contribution of marine environmental change to reductions in salmon abundances and growth on both sides of the Atlantic (Peyronnet et al. 2008, Todd et al. 2008, Bacon et al. 2009, Friedland et al. 2014, Renkawitz et al. 2015). This is important, as management efforts designed to minimize mortality in the more accessible coastal and shelf environments will have little benefit if population declines are largely caused by environmental change in open ocean habitats. However, tracking salmon distributions during open ocean feeding in the sub-Arctic waters of the North Atlantic has proven challenging (Dadswell et al. 2010), and we still have limited understanding of the

thermal and ecological conditions experienced by individual fish while feeding in the open ocean (MacKenzie et al. 2012, Hanson et al. 2013, Guðjónsson et al. 2015). It is therefore unclear whether and to what extent observed synchronous changes in marine mortality in Atlantic salmon populations are influenced by direct or indirect effects of warming in the open ocean feeding grounds.

Stable isotope analysis of collagen in archived salmon scales is well established as a tool for providing retrospective information on individual (and population) responses to environmental changes, primarily because the isotopic composition of scale collagen reflects the oceanic conditions experienced by the individual fish during marine feeding (Sinnatamby et al. 2009, MacKenzie et al. 2011, 2012, Trueman et al. 2012a). The isotopic composition of carbon ($\delta^{13}\text{C}$) in marine algal primary producers co-varies with SST, as SST influences the isotopic composition and concentration of dissolved CO_2 in seawater (Laws et al. 1995, Magozzi et al. 2017). Also, the growth rate of cells and taxonomic composition of algal populations can be factors influencing the fractionation of carbon isotopes during photosynthetic carbon fixation. Consequently, temporal variations in $\delta^{13}\text{C}$ values of salmon scales provide an indirect record of temporal trends in SST experienced by fish during marine feeding. Isotopic compositions of carbon in salmon scales therefore also discriminate between fish foraging in areas of contrasting SST, and the location of potential feeding areas can be inferred through comparisons of temporal trends in $\delta^{13}\text{C}$ in salmon tissues and SST measured through remote sensing across ocean basins (MacKenzie et al. 2011, Trueman et al. 2012b).

Here we used stable isotope analysis of salmon scales as outlined above to identify relative trends in experienced SST and to infer likely marine foraging areas used by salmon returning to the St. John River, New Brunswick (Canada). Annual returns of adult Atlantic salmon, either after spending 1 winter at sea (1SW) or multiple winters at sea (MSW), for the St. John River population have been steadily declining since the 1980s, with an increasing proportion of wild 1SW salmon declining over this period (Jones et al. 2014, DFO 2015, 2016, 2017) (Fig. 1; also see Fig. S2 in the Supplement), a trend that is seen across many Atlantic salmon populations. We tested the hypothesis that population trends of Atlantic salmon from the St. John River co-vary negatively with $\delta^{13}\text{C}$ values in scales of returning fish and, by inference, negatively with the SST experienced by individual fish in the specific marine foraging areas. Salmon populations

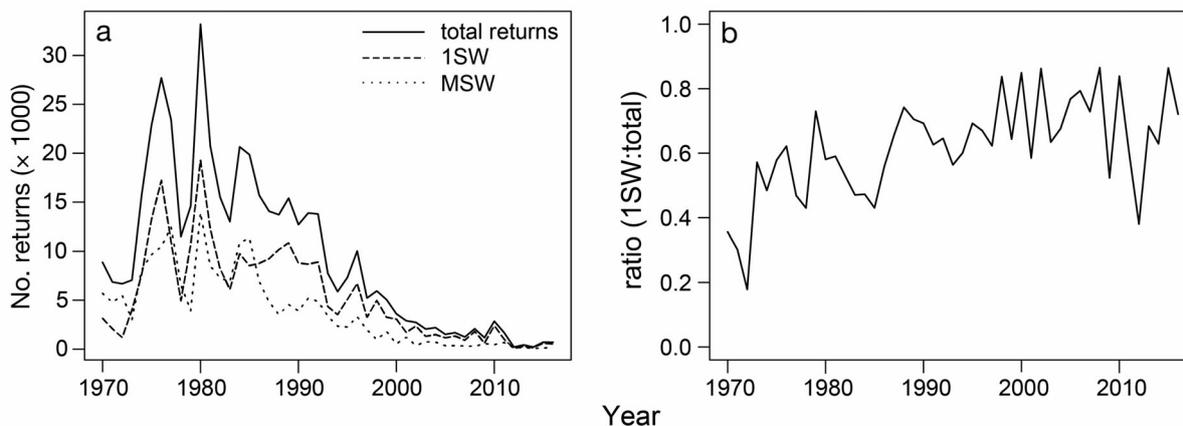


Fig. 1. Population trends of Atlantic salmon returning to the St. John River (New Brunswick, Canada) from the 1970s (after Jones et al. 2014, DFO 2015, 2016, 2017). (a) Number of salmon returns for fish that spent 1 winter at sea (1SW) or multiple winters at sea (MSW), as well as total returns. (b) Ratio between 1SW returns and total returns over the same time period

of distinct river origins and marine ages can follow distinctive migration routes (Dadswell et al. 2010); therefore, marine foraging areas were examined separately for 1SW and MSW salmon that return to freshwater.

MATERIALS AND METHODS

Sample collection

To evaluate temporal patterns in marine foraging, scale samples from adult Atlantic salmon of 1 population were obtained from Fisheries and Oceans Canada (DFO) archived collections from a long temporal series (1980–2011). We collected sufficient samples per sampling year and marine age, ca. 10 individuals for each of 1SW ($N = 325$) and MSW ($N = 307$). This archive collection includes samples from Atlantic salmon returning from the ocean and migrating to the upper reaches of the St. John River (Fredericton, New Brunswick, Canada; Fig. 2c), that are collected at the fish collection facilities at the Mactaquac Dam and an adult trap at the Mactaquac Biodiversity Facility, a federal Atlantic salmon mitigation facility. These facilities generally operate from early May until late October, and captured salmon are classified as 1SW or MSW by scale reading and as either wild or hatchery origin using a marked adipose clip (Jones et al. 2014).

From the archive, 5 to 10 scales ind.^{-1} were selected and cleaned by soaking in distilled water and gently scraping with a scalpel to remove any surface residue (MacKenzie et al. 2011). Before sampling scale tissue grown at sea for stable isotope analysis, a

digital image was taken from a representative scale for each individual to allow analyses of scale circuli spacing (see below).

Recent marine growth is represented at the outer regions of the scale of Atlantic salmon; widely spaced scale circuli identify summer growth at sea and narrowly spaced circuli show the winter portion. We sampled the most recent summer portion at the edge of the scale for 1SW samples, and the summer immediately before the final winter at sea for MSW samples (Hutchinson & Trueman 2006, MacKenzie et al. 2011). Therefore, the potential bias to the measured isotope values due to collagen laid down during other life stages was negligible or minimal, and $\delta^{13}\text{C}$ values of MSW fish collected in year X were correlated with variables of the previous year of growth $X - 1$. Critically, we did not sample conditions experienced during the post-smolt year in either 1SW or MSW returning fish. Portions of scale annuli from the last full season of at-sea summer growth were dissected under a microscope using a scalpel and stored dry until analysis. We pooled several scales for each individual to obtain enough material for stable isotope analysis, and we targeted ~ 0.4 mg for each sample isotope analysis. For each collection year, we sampled approximately 10 1SW and 10 MSW individuals. Scales that exhibited reabsorption were not used for analysis.

Stable isotope analysis

Stable isotope measurements in scale samples were conducted using continuous-flow isotope ratio mass spectrometry (CF-IRMS) at the Stable Isotopes

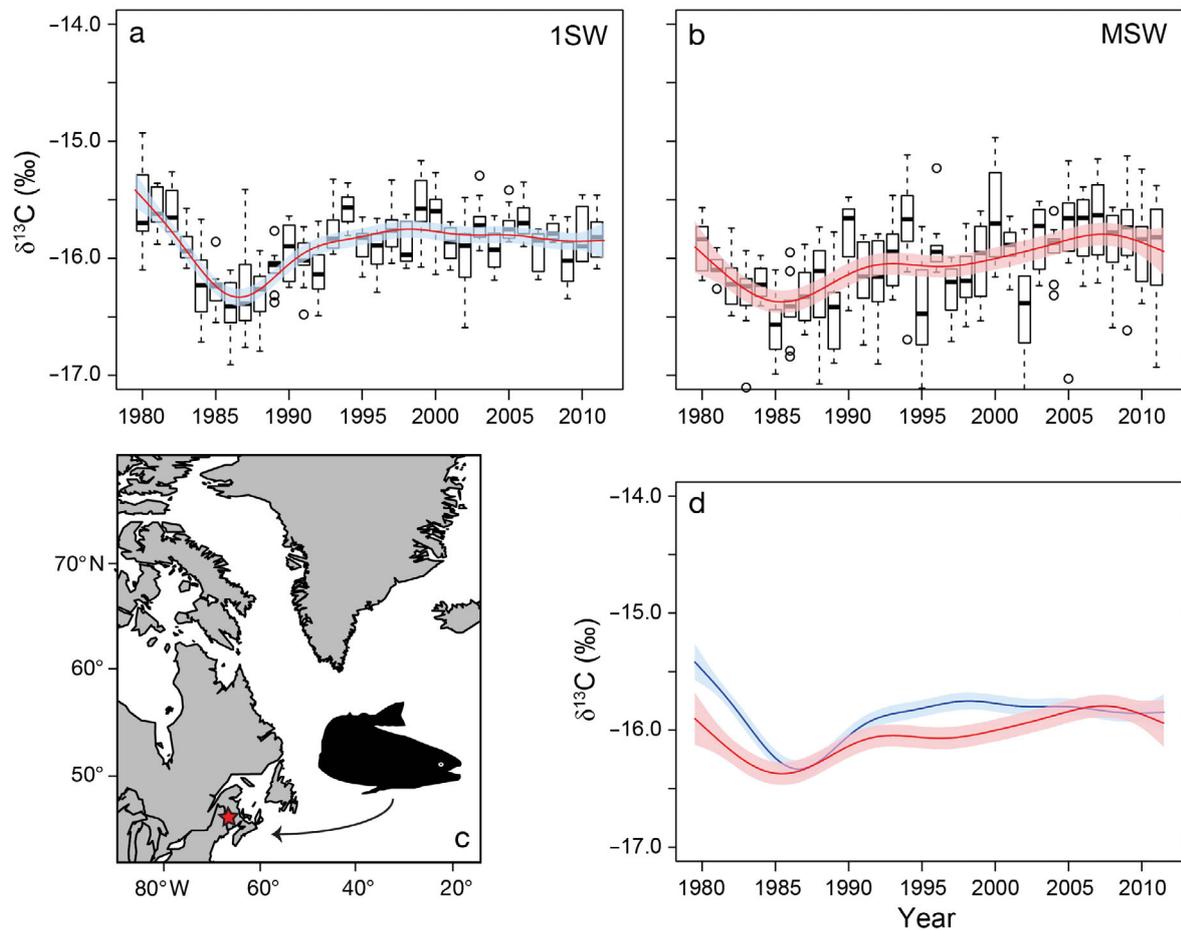


Fig. 2. Temporal patterns of scale $\delta^{13}\text{C}$ (Suess corrected) for adult Atlantic salmon returning to the St. John River after spending (a) 1 winter at sea (1SW) or (b) multiple winters at sea (MSW). Solid line shows the generalized additive model fit and the shaded area represents $2 \times \text{SE}$ on the smoother (blue: 1SW; red: MSW). (c) Location of the St. John River on the western North Atlantic Ocean. (d) Comparison of both temporal $\delta^{13}\text{C}$ patterns from panels (a) and (b)

in Nature Laboratory (SINLAB), Fredericton, Canada. Scales are mainly composed of collagen and carbonated bioapatite (Hutchinson & Trueman 2006). The carbonate component is volumetrically negligible in terms of its effect on bulk $\delta^{13}\text{C}$ values (Sinatamby et al. 2009), so no pre-treatment (i.e. acid washing) was performed. Relative isotopic abundances of carbon and nitrogen (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) were measured from sample gases derived from combustion in a Costech 4010 Elemental Analyzer (EA) using a DeltaPlus XP isotope-ratio mass spectrometer (Thermo-Finnigan). In-house calibrated standard materials (i.e. fish muscle, bovine liver and nicotinamide) were analyzed within the run to correct for drift and to normalize measured isotopic composition to the respective international stable isotope reference scale. All isotopic values are reported in the delta (δ) notation (in parts per thou-

sand, ‰) deviations from the international standard defined by: $\delta^{13}\text{C}$ (or $\delta^{15}\text{N}$) = $[(R_{\text{sample}} / R_{\text{standard}}) - 1]$, where R is the isotope ratio of the corresponding element ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample and the international standard (Vienna Pee Dee Belemnite, VPDB, or AIR; respectively). Analytical precision, measured as the standard deviation of replicate analyses, was better than $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$. Samples analyzed in duplicate ($n = 34$) had an average standard deviation of 0.1‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Tissue $\delta^{13}\text{C}$ values were corrected to account for the global decrease of atmospheric $\delta^{13}\text{C}$ values (i.e. the Suess effect) prior to further statistical and spatial analyses. The Suess effect is primarily caused by fossil fuel emissions and has occurred over the past 150 yr. Based on the global ocean average surface $\delta^{13}\text{C}$ rate of change (Gruber et al. 1999), we applied a time-dependent correction of -0.018‰ per year

relative to 2011 to all scale $\delta^{13}\text{C}$ values except 2011 scale samples. Temporal patterns of $\delta^{13}\text{C}$ values between salmon cohorts or sea age were compared using a generalized additive model (GAM) with $\delta^{13}\text{C}$ values modelled as a function of time. These GAM approaches are linearly based on unknown smooth functions of the variable 'year'. GAMs were fitted using the package 'mgcv' (Wood 2006, 2011) using a Gaussian error structure and an identity link function. Smoothing parameters were estimated using restricted maximum likelihood (REML), which optimizes smoothing terms to reduce overfitting. Residuals were randomly distributed with respect to the predictor variable 'year'. GAMs were fit to the full data series (including both sea ages), and the effect of including sea age as a covariate within the model was assessed using Akaike's information criterion (AIC) values.

SST vs. isotope analysis

Time series of SST were compiled from median summer SST records (March to October) of the 1° monthly gridded NOAA OI SST V2 data (provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at www.esrl.noaa.gov/psd/). The isotope data and SST records were thus reduced to 1 average value for each year to be ultimately correlated. As the temporal coverage of the NOAA SST dataset commences in November 1981 (Reynolds et al. 2002), we evaluated the temporal correlation for the period 1982–2011. We used an 8 mo timeframe (i.e. March to October) because, during scale sampling, annuli representing winter growth were discarded such that measured values approximated the period of marine growth. In this way, both temperature and scale collection was undertaken in the second summer of ocean growth in both cohorts to represent consistent timeframes for accurate comparisons (Dixon et al. 2015).

Potential marine feeding areas for each marine age were proposed based on the relative strength of linear correlations between temporal trends of SST and Suess-corrected scale $\delta^{13}\text{C}$ values (MacKenzie et al. 2011). This approach was based on the premise that the extent of carbon isotopic discrimination during photosynthesis by phytoplankton co-varies with temperature such that warmer waters lead to more ^{13}C -enriched particulate organic matter (POM) or higher $\delta^{13}\text{C}$ values (Laws et al. 1995, Hofmann et al. 2000, Barnes et al. 2009, Graham et al. 2010, Magozzi et al. 2017). For this analysis, we assumed that regional areas are broadly conserved during the period cov-

ered in the analysis, as implied by population differences in at-sea mortality and temporal isotopic patterns (Sinnatamby et al. 2009, MacKenzie et al. 2011, Trueman et al. 2012b). Salmon are thus more likely to have been feeding in any region showing a positive association between the time series of tissue $\delta^{13}\text{C}$ values and SST. Isotopic and SST time series data were reduced from a second-order LOESS fit with a span width of 0.3 to temporal data (scale $\delta^{13}\text{C}$ values/SST vs. year of return).

Scale circuli spacing data

Patterns of marine growth in each salmon cohort (marine age) were inferred by assessing the scale circuli spacing data from the same samples analyzed for stable isotope measurements. For comparison purposes, we divided the total number of years studied in 3 groups of 10 yr. Scale images were taken at 15–20× magnification with a calibrated scale bar as reference. Measurements of inter-circuli spacing in the marine phase of scales from both 1SW and MSW fish were made with Fiji (ImageJ) free software (Schindelin et al. 2012). This image-processing system was used to measure the distance between successive pairs of scale growth rings (inter-circuli spacing) in the section representing marine growth. Measurements were made along an assigned line perpendicular to the scale circuli (from focus to edge) after discarding the portion representing the freshwater life stage (Hubley et al. 2008). The end of the freshwater growth was considered circulus 0.

Statistical analysis

All spatial and statistical analyses were performed using the R package (R Core Team 2017). We analyzed the differences between groups using ANOVA when the assumption of normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test) were met at a level of significance of 0.05. When these assumptions were not met, a Kruskal-Wallis test (followed by a Mann-Whitney *U*-test for each group pair when needed) was conducted.

RESULTS

Sea surface temperatures averaged across the North Atlantic showed an increase of ca. 0.5°C decade⁻¹ during the last 3 decades as a response to cur-

rent global warming effects (Fig. S1 in the Supplement). Temporal patterns of SST differed among areas within the North Atlantic Sub-polar Gyre regions, with more pronounced warming trends in the eastern North Atlantic (Fig. S1). Regarding $\delta^{13}\text{C}$ patterns, including sea age as a fixed effect significantly improved the explanatory power of the GAM (AIC = 362 vs. 397) and we therefore infer that time series of $\delta^{13}\text{C}$ values were significantly different between salmon cohorts. There was an initial $\delta^{13}\text{C}$ decline in the early 1980s shared by 1SW and MSW fish. During the early 1990s, there was no evidence for different feeding or that regions used by fish shared temporal changes, but after the mid-1990s, the time series began to diverge. The $\delta^{13}\text{C}$ values in scales from MSW fish increased progressively from the late 1980s (Fig. 2b), implying a progressive increase in the average SST experienced by this population over time. By contrast, $\delta^{13}\text{C}$ values in scales from 1SW returning fish did not increase after the mid-1990s (Fig. 2a) and were relatively invariant at ca. -15.8‰ , implying feeding in a region or regions experiencing limited change in SST or tracking preferred SST.

Scale collagen $\delta^{13}\text{C}$ values laid down during summer foraging were significantly different between 1SW (mean \pm SD: $-15.9 \pm 0.3\text{‰}$) and MSW ($-16.1 \pm 0.4\text{‰}$) returning individuals (Kruskal-Wallis rank test; age cohort, $\chi^2_1 = 25.985$, $p < 0.001$; year, $\chi^2_{31} = 226.05$, $p < 0.001$; Fig. 2d), and within-year variability was higher in MSW salmon (average of SD = 0.22 for 1SW vs. 0.32 for MSW; ANOVA, $F_{1,62} = 22.73$, $p < 0.001$). The larger variance and wider range in observed $\delta^{13}\text{C}$ values for MSW returning fish could imply that MSW fish spread further due to their longer ocean residence period and larger size. The

absolute $\delta^{15}\text{N}$ values indicated a slightly cyclical temporal pattern but with minimal change over time (mean \pm SD all years, $11.3 \pm 0.5\text{‰}$ and $11.8 \pm 0.8\text{‰}$ for 1SW and MSW, respectively), which could reflect salmon trophic stability or changes in isotopic baselines (Fig. S3). Despite similar trends of $\delta^{15}\text{N}$ for 1SW and MSW salmon, there was no evidence for a progressive change in trophic level corresponding to the increase in ocean temperatures. In fact, the 2 $\delta^{15}\text{N}$ records had synchronous cyclicity, implying that ocean basin-scale effects influence the isotopic composition of nitrogen at the base of the food web.

Time series of $\delta^{13}\text{C}$ values in scales from both 1SW and MSW returning fish (Fig. 2) showed a sharp decline in $\delta^{13}\text{C}$ values (and therefore inferred SST) in the early 1980s, reaching time series minimum values in 1985. Time series of $\delta^{13}\text{C}$ values in scales from MSW fish showed a strong positive co-variation with basin-wide average North Atlantic SST trends ($R^2 = 0.56$, $p < 0.001$, Fig. 3), but relatively weak covariance with SST time series from individual sub-areas within the North Atlantic Ocean ($R^2 = 0.20\text{--}0.49$; Table 1). Consequently, $\delta^{13}\text{C}$ values in scales from MSW fish were most easily explained as each annual cohort consisting of individuals returning from a wide range of areas across the North Atlantic Ocean effectively producing a spatial average of ocean condition (Fig. 4). The relatively large between-individual variance in $\delta^{13}\text{C}$ values in scales from MSW fish supports this interpretation. Time series of $\delta^{13}\text{C}$ values in scales from 1SW-returning salmon were relatively weakly correlated with all Atlantic SST trends (for mean Atlantic, $R^2 = 0.28$, $p < 0.005$; for other sub-areas $R^2 = 0.09\text{--}0.18$; Table 1, Figs. 3 & 4). Sea areas experiencing SST trends more consistent with tem-

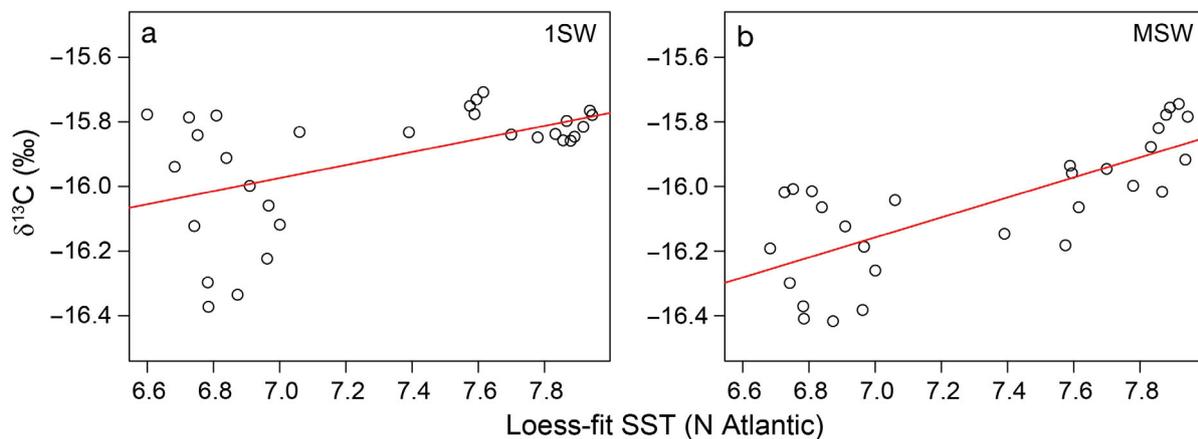


Fig. 3. Relationships between the LOESS fit of average sea surface temperature (SST) in the North Atlantic Ocean and $\delta^{13}\text{C}$ values in Atlantic salmon after spending (a) 1 winter at sea (1SW; $R^2 = 0.28$) or (b) multiple winters at sea (MSW; $R^2 = 0.56$) salmon. Note that SST from the year $X-1$ was correlated for MSW fish

Table 1. Correlation analysis between the LOESS fit of average sea surface temperature (SST) and $\delta^{13}\text{C}$ values in the North Atlantic Ocean scale and sub-basin scales for Atlantic salmon after spending either 1 winter at sea (1SW) or multiple winters at sea (MSW). Note that SST from the year $X - 1$ was correlated for MSW fish

Region	R^2	Coeff. corr.	p
1SW			
N Atlantic	0.28	0.53	<0.005
Norwegian Sea	0.18	0.43	<0.05
SW Greenland	0.12	0.34	0.06
Irminger	0.10	0.32	0.09
Faroes	0.09	0.30	0.11
MSW			
N Atlantic	0.56	0.75	<0.001
Norwegian Sea	0.49	0.70	<0.001
SW Greenland	0.20	0.44	<0.05
Irminger	0.27	0.52	<0.005
Faroes	0.34	0.59	<0.001

poral trends in $\delta^{13}\text{C}$ values in scales from 1SW returning fish included the western North Atlantic (e.g. Irminger Sea, SW Greenland or Labrador/Newfoundland), the southern North Sea and northern Norwegian Sea areas (Fig. 4). Of these isotopically consistent potential feeding areas, only the western North Atlantic region was considered likely for salmon returning as 1SW fish to the St. John River.

The numbers of MSW returning fish in the St. John River have steadily declined, and population trends closely matched the observed trends in $\delta^{13}\text{C}$ values in scales from MSW returning fish ($R^2 = 0.72$, $p < 0.001$), and, therefore, mean SST across the North Atlantic (Fig. 5). Returns of 1SW salmon to the St. John River showed similar long-term declining population trends as MSW returning fish. However, $\delta^{13}\text{C}$ values in 1SW returning fish were relatively invariant after the mid-1990s, and thus there was a weak temporal co-variance between $\delta^{13}\text{C}$ values (and inferred SST) and

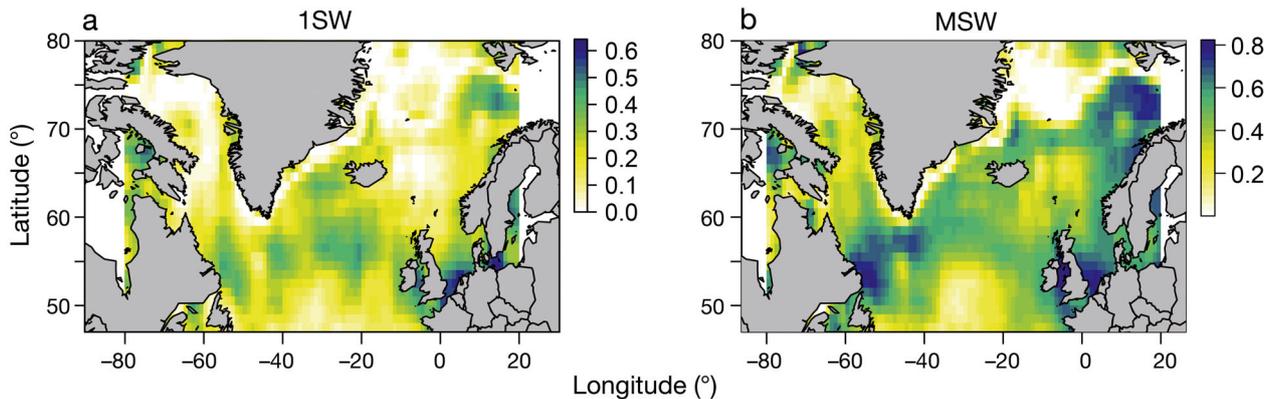


Fig. 4. Probable marine summer feeding locations derived from correlations of LOESS-fit scale $\delta^{13}\text{C}$ and yearly median sea surface temperature (SST) for Atlantic salmon after spending (a) 1 winter at sea (1SW) or (b) multiple winters at sea (MSW) and returning successfully to the St. John River during the period 1982–2011. Colours indicate the degree of correlation (R^2)

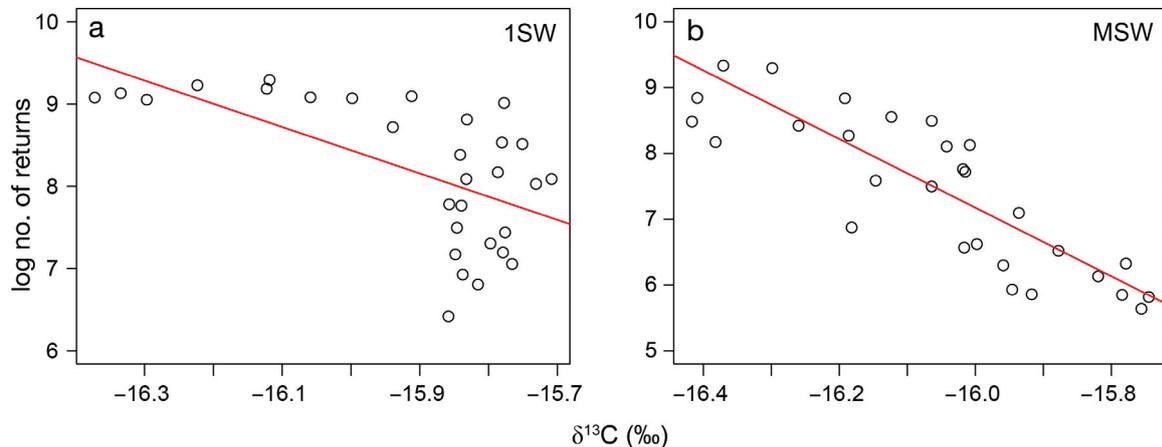


Fig. 5. Relationships between log-transformed annual returns in the St. John River and LOESS fit of $\delta^{13}\text{C}$ values for Atlantic salmon after spending (a) 1 winter at sea (1SW) or (b) multiple winters at sea (MSW) ($R^2 = 0.37$ and 0.72 , respectively). Salmon return data extracted from Jones et al. (2014)

return rates for 1SW fish ($R^2 = 0.37$, $p < 0.001$), and no significant covariance between $\delta^{13}\text{C}$ values and return rates if the time series after 1994 are explored ($R^2 = 0.1$; $p = 0.18$).

Since some summer marine feeding locations of Atlantic salmon could be more suitable for growth than others, we used scale circuli spacing to evaluate growth in the studied individuals during the period of study. On average, we found a significant decrease of 10% in the last summer's marine growth (circuli pairs 31–33) for 1SW salmon in the most recent decade (Kruskal-Wallis test, followed by Mann-Whitney U -tests, $p < 0.01$; Fig. 6). The average inter-circuli spacing of the last decade was up to 6 μm less than that of the 2 previously studied decades. In the case of MSW, there were significant differences in inter-circuli spacing (annuli growth) among decades. Significant growth decreases were found in the 2000s for circuli pairs 35–36 and in the 1980s for circuli pairs 44–52 (except for pair 45) relative to the other 2 decades (Kruskal-Wallis test, followed by Mann-Whitney U -tests, $p < 0.01$; Fig. 6). The maximum spacing of scale circuli of MSW salmon in the sampled area suggests a difference among decades, with growth peaks occurring progressively later from the 1980s to the 2000s.

DISCUSSION

Salmon returning to the St. John River as 1SW and MSW fish showed different temporal trends in scale $\delta^{13}\text{C}$ values (Fig. 2), and by inference experienced different trends in SST over the 30 yr sampling period. These 2 cohorts are likely to forage in different

regions of the North Atlantic (Dadswell et al. 2010). Salmon returning after spending 1 winter at sea experienced no significant long-term temporal changes in $\delta^{13}\text{C}$ values, and thus were probably able to track available, appropriate thermal habitat, over the measured time series. Such a probability makes sense since 1SW fish preferentially forage in warmer temperatures than MSW fish (Jákupsstovu 1988, Dadswell et al. 2010). Salmon returning after 2 or more winters at sea showed progressive increases in $\delta^{13}\text{C}$ values, and by inference experienced progressive increases in SST from 1985 to the present. The thermal environment experienced by 1SW and MSW returning populations apparently differed over time. Temporal co-variation in SST and $\delta^{13}\text{C}$ values suggests that MSW foraged over large areas of the North Atlantic (Dadswell et al. 2010) while 1SW fish were more spatially restricted, most likely foraging in regions of the western North Atlantic (Fig. 4).

Annual returns of 1SW and MSW adult Atlantic salmon for the St. John River population have been steadily and co-incidentally declining since the 1980s (Jones et al. 2010), similar to long-term trends in salmon and other diadromous fish populations across their native range (Limburg & Waldman 2009). Here we show for the first time that cohorts of salmon experiencing similar trends in adult returns fed in regions with markedly different expressions of recent ocean warming, despite the relatively constant smolt densities in the freshwater ecosystem for the river and period of study (Jones et al. 2010, Gibson et al. 2016). We therefore argue that warming in oceanic feeding areas cannot be the principal cause of synchronous population declines in 1SW and MSW salmon returning to the St. John River. Both cohorts

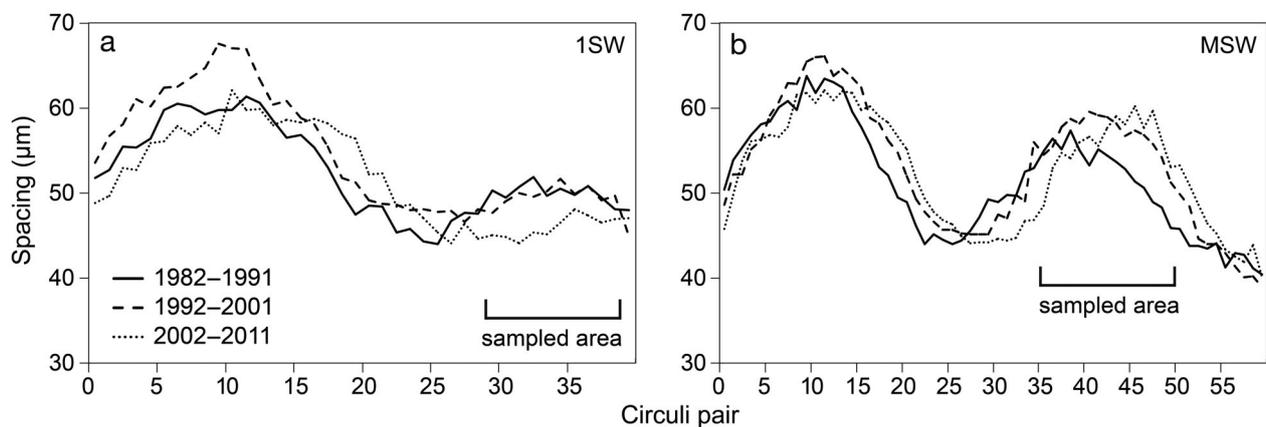


Fig. 6. Average inter-circuli spacing for each pair of circuli representing marine growth in Atlantic salmon scales for fish returning to the St. John River after spending (a) 1 winter at sea (1SW) or (b) multiple winters at sea (MSW). Each line shows the average spacing of individuals returning in the 1980s (1982–1991), 1990s (1992–2001) and 2000s (2002–2011). The approximate scale section sampled for stable isotope analysis is indicated in the graph

probably experienced similar environmental conditions and pressures (and presumably similar temporal trends in marine mortality) during the early post-smolt phase of life, where cohorts of similar size, prey requirements and metabolic demands share estuarine and coastal habitats. We therefore argue that the strong correlation between $\delta^{13}\text{C}$ values and population sizes of MSW-returning fish (Fig. 5b) is co-incident, reflecting a common factor of variation, and does not imply direct causal relationships between drivers of $\delta^{13}\text{C}$ change in oceanic feeding grounds and marine mortality. We thus conclude that environmental conditions in early post-smolt environments are the more likely causes of the synchronous population declines experienced by 1SW and MSW returning fish than conditions experienced during their time in open-ocean regions after the post-smolt year. Alternatively, freshwater conditions are also shared between both cohorts, and changes in conditions in fresh water can exert strong influences on population sizes, even in restored or relatively undisturbed ecosystems (Bernhardt & Palmer 2011, Ohlberger et al. 2016). However, as explained above, there is no indication of a potential link between the freshwater conditions and salmon adult returns in our system since the smolt population sizes in the St. John River watershed during the freshwater phase were consistently unaffected over this time.

In the St. John River, populations of MSW-returning fish have declined at higher rates than those of 1SW fish, and this pattern is commonly seen throughout the native range of Atlantic salmon on both sides of the North Atlantic (Figs. 1 & S2, Chaput 2012). Unlike 1SW returning fish, MSW salmon returning to the St. John River experienced progressive increases in SST over the time series. The question now becomes whether these temperatures would be detrimental for adult salmon during the second summer's growth. Adult salmon are found most commonly at temperatures of 2–8°C (mean about 4°C; Reddin & Shearer 1987, Jákupsstovu 1988, Rikardsen et al. 2008), and average North Atlantic SST and other regional oceanic areas are approaching or exceeding these preferred temperatures (Fig. S1). It is possible that the increased rate of population decline seen in MSW-returning fish reflects increased marine mortality associated with ocean warming, but further research is needed to test this hypothesis.

Our analysis of scale circuli spacing identified a growth decrease for 1SW fish in the most recent decade of study (2000s) for the last summer growth at sea. Maximum MSW growth was significantly delayed again in recent years (2000s). Poorer oceanic

growth of salmon, such as occurred for 1SW Atlantic salmon during the last decade (2000s), may cause individuals to stay longer at sea on average, and this reduced growth could therefore trigger a proportional increase in MSW returns in subsequent years (Piou & Prévost 2013). In relation to our results, a higher number of MSW fish in the ocean experiencing warming trends could increase the number of salmon suffering suboptimal conditions in the marine environment. No definitive causes for observed reduced or delayed growth have been found, apart from possible associations with climatic variables such as SST changes (Todd et al. 2008, Bacon et al. 2009, Jensen et al. 2011). Here we observed decreased growth in 1SW returning salmon with no accompanying evidence for significant changes in SST, major re-organisations in plankton communities, or differences in trophic level. On the other hand, a shift in the timing of growth peaks for MSW salmon in our data series appears to provide some evidence of longer search times for adequate resources or a change in marine distribution similar to the findings of Hubley et al. (2008) for returning salmon in the Big Salmon River (New Brunswick, Canada).

Our results suggest that warming in oceanic foraging regions during the second summer growth cannot account for synchronous population declines in 1SW and MSW cohorts of Atlantic salmon returning to the St. John River. Post-smolt fish destined to return after spending 1 or more winters at sea experience shared ecological and environmental conditions during their early post-smolt year, and we suggest that the principal drivers responsible for sustained population declines are likely to be found in habitats used by salmon in the post-smolt year. We do find evidence that salmon returning to the St. John River as MSW fish are experiencing progressive warming in response to global ocean change. The combined effects of changes in post-smolt and oceanic habitats may account for the greater rates of population declines seen in MSW returning salmon.

Atlantic salmon are commercially and culturally important fish throughout their native range, and considerable efforts and resources are expended attempting to reduce the declines in population trends. Our results support analyses identifying early post-smolt habitats as critical targets for conservation efforts focussed on reducing marine mortality of Atlantic salmon (Friedland et al. 2005, 2014, Thorstad et al. 2012). For the St. John River population at least, reductions in marine mortality achieved through conservation efforts in post-smolt habitats are un-

likely to be compromised or wasted due to warming-related mortality in the relatively uncontrollable open-ocean feeding grounds.

Acknowledgements. Fisheries and Oceans Canada provided samples from DFO archive collections of Atlantic salmon scales, with special thanks to R. Jones and L. Anderson. We are grateful to E. Weigum for considerable assistance in preparing and weighing scale samples; to R. Lagrifoul for helping with inter-circuli spacing measurements; and to A. McGeachy, M. Savoie and C. Paton for stable isotope analysis. We also thank B. Hayden for comments that improved an earlier version of the manuscript. Funding was provided by the Stable Isotopes in Nature Laboratory (SINLAB).

LITERATURE CITED

- Bacon PJ, Palmer SCF, MacLean JC, Smith GW, Whyte BDM, Gurney WSC, Youngson AF (2009) Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. *ICES J Mar Sci* 66:844–859
- Barnes C, Jennings S, Barry JT (2009) Environmental correlates of large-scale spatial variation in the $\delta^{13}\text{C}$ of marine animals. *Estuar Coast Shelf Sci* 81:368–374
- Bernhardt ES, Palmer MA (2011) River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecol Appl* 21:1926–1931
- Chaput G (2012) Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J Mar Sci* 69:1538–1548
- Dadswell MJ, Spares AD, Reader JM, Stokesbury MJW (2010) The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'Merry-Go-Round' hypothesis. *J Fish Biol* 77:435–467
- DFO (Fisheries and Oceans Canada) (2015) Status of Atlantic salmon in salmon fishing areas (SFAs) 19-21 and 23. Canadian Science Advisory Secretariat Science Response 2015/021. <http://waves-vagues.dfo-mpo.gc.ca/Library/363770.pdf>
- DFO (2016) Stock status update of Atlantic salmon in salmon fishing areas (SFAs) 19-21 and 23. Canadian Science Advisory Secretariat Science Response 2016/029. <http://waves-vagues.dfo-mpo.gc.ca/Library/40602916.pdf>
- DFO (2017) Stock status update of Atlantic salmon in salmon fishing areas (SFAs) 19-21 and 23. Canadian Science Advisory Secretariat Science Response 2017/020. <http://waves-vagues.dfo-mpo.gc.ca/Library/4062500x.pdf>
- Dixon HJ, Dempson JB, Power M (2015) Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis. *Fish Res* 164:112–119
- Friedland KD, Chaput G, MacLean JC (2005) The emerging role of climate in post-smolt growth of Atlantic salmon. *ICES J Mar Sci* 62:1338–1349
- Friedland KD, Shank BV, Todd CD, McGinnity P, Nye JA (2014) Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *J Mar Syst* 133:77–87
- Gibson AJF, Jones RA, MacAskill GJ (2016) Recovery potential assessment for outer Bay of Fundy Atlantic salmon (*Salmo salar*): population dynamics and viability. Canadian Science Advisory Secretariat Research Document 2016/032. <http://waves-vagues.dfo-mpo.gc.ca/Library/365817.pdf>
- Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes*. Springer, Dordrecht, p 299–318
- Gruber N, Keeling CD, Bacastow RB, Guenther PR and others (1999) Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. *Global Biogeochem Cycles* 13:307–335
- Guðjónsson S, Einarsson SM, Jónsson IR, Guðbrandsson J (2015) Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. *Can J Fish Aquat Sci* 72:1087–1098
- Hanson NN, Wurster CM, EIMF, Todd CD (2013) Reconstructing marine life-history strategies of wild Atlantic salmon from the stable isotope composition of otoliths. *Mar Ecol Prog Ser* 475:249–266
- Hofmann M, Wolf-Gladrow DA, Takahashi T, Sutherland SC, Six KD, Maier-Reimer E (2000) Stable carbon isotope distribution of particulate organic matter in the ocean: a model study. *Mar Chem* 72:131–150
- Hubley PB, Amiro PG, Gibson AJF (2008) Changes in scale circulus spacings of an endangered Atlantic salmon *Salmo salar* population: evidence of a shift in marine migration? *J Fish Biol* 73:2321–2340
- Hutchinson JJ, Trueman CN (2006) Stable isotope analyses of collagen in fish scales: limitations set by scale architecture. *J Fish Biol* 69:1874–1880
- Jákupsstovu SH (1988) Exploitation and migration of salmon in Faroese waters. In: Mills D, Piggins D (eds) *Atlantic salmon: planning for the future*. Springer, Dordrecht, p 458–482
- Jensen AJ, Fiske P, Hansen LP, Johnsen BO, Mork KA, Næsje TF (2011) Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. *Can J Fish Aquat Sci* 68:444–457
- Jones RA, Anderson L, Gibson AJF, Goff T (2010) Assessments of Atlantic salmon stocks in South Western New Brunswick (outer portion of SFA 23): an update to 2008. Canadian Science Advisory Secretariat Research Document 2010/118. <http://waves-vagues.dfo-mpo.gc.ca/Library/342473.pdf>
- Jones RA, Anderson L, Clarke CN (2014) Assessment of the recovery potential for the outer Bay of Fundy population of Atlantic salmon (*Salmo salar*): status, trends, distribution, life history characteristics and recovery targets. Canadian Science Advisory Secretariat Research Document 2014/008. <http://waves-vagues.dfo-mpo.gc.ca/Library/360849.pdf>
- Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[\text{CO}_2]_{\text{aq}}$: theoretical considerations and experimental results. *Geochim Cosmochim Acta* 59:1131–1138
- Limburg KE, Waldman JR (2009) Dramatic declines in North Atlantic diadromous fishes. *Bioscience* 59:955–965
- MacKenzie KM, Palmer MR, Moore A, Ibbotson AT, Beaumont WRC, Poulter DJS, Trueman CN (2011) Locations of marine animals revealed by carbon isotopes. *Sci Rep* 1:21
- MacKenzie KM, Trueman CN, Palmer MR, Moore A, Ibbotson AT, Beaumont WRC, Davidson IC (2012) Stable iso-

- topes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. *ICES J Mar Sci* 69:1637–1645
- ✦ Magozzi S, Yool A, Vander Zanden HB, Wunder MB, Trueman CN (2017) Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* 8:e01763
- ✦ Mills KE, Pershing AJ, Sheehan TF, Mountain D (2013) Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Glob Change Biol* 19:3046–3061
- ✦ Ohlberger J, Scheuerell MD, Schindler DE (2016) Population coherence and environmental impacts across spatial scales: a case study of Chinook salmon. *Ecosphere* 7:e01333
- ✦ Peyronnet A, Friedland KD, Ó Maoileidigh N (2008) Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. *J Fish Biol* 73:945–962
- ✦ Piou C, Prévost E (2013) Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. *Glob Change Biol* 19:711–723
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reddin DG, Shearer WH (1987) Sea-surface temperature and distribution of Atlantic salmon in the northwest Atlantic Ocean. *Am Fish Soc Symp* 1:262–275
- ✦ Renkawitz MD, Sheehan TF, Dixon HJ, Nygaard R (2015) Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. *Mar Ecol Prog Ser* 538:197–211
- ✦ Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An improved in situ and satellite SST analysis for climate. *J Clim* 15:1609–1625
- ✦ Rikardsen AH, Hansen LP, Jensen AJ, Vollen T, Finstad B (2008) Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78° N. *J Fish Biol* 72:1792–1798
- ✦ Robson J, Ortega P, Sutton R (2016) A reversal of climatic trends in the North Atlantic since 2005. *Nat Geosci* 9:513–517
- ✦ Schindelin J, Arganda-Carreras I, Frise E, Kaynig V and others (2012) Fiji: an open-source platform for biological-image analysis. *Nat Methods* 9:676–682
- Sinnatamby RN, Dempson JB, Chaput G, Caron F, Niemelä E, Erkinaro J, Power M (2009) Spatial and temporal variability in the trophic ecology of Atlantic salmon in the North Atlantic inferred from analyses of stable isotope signatures. *Am Fish Soc Symp* 69:447–463
- ✦ Straneo F, Heimbach P (2013) North Atlantic warming and the retreat of Greenland's outlet glaciers. *Nature* 504:36–43
- ✦ Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B (2012) A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *J Fish Biol* 81:500–542
- ✦ Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM (2008) Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Glob Change Biol* 14:958–970
- ✦ Trueman CN, MacKenzie KM, Palmer MR (2012a) Identifying migrations in marine fishes through stable-isotope analysis. *J Fish Biol* 81:826–847
- ✦ Trueman CN, MacKenzie KM, Palmer MR (2012b) Stable isotopes reveal linkages between ocean climate, plankton community dynamics, and survival of two populations of Atlantic salmon (*Salmo salar*). *ICES J Mar Sci* 69:784–794
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL
- ✦ Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36

Editorial responsibility: Stylianos Somarakis, Heraklion, Greece

Submitted: February 14, 2018; Accepted: June 25, 2018
Proofs received from author(s): August 4, 2018