

# Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon

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## Abstract

Ocean climate impacts on survivorship and growth of Atlantic salmon are complex, but still poorly understood. Stock abundances have declined over the past three decades and 1992–2006 has seen widespread sea surface temperature (SST) warming of the NE Atlantic, including the foraging areas exploited by salmon of southern European origin. Salmon cease feeding on return migration, and here we express the final growth condition of year-classes of one-sea winter adults at, or just before, freshwater re-entry as the predicted weight at standard length. Two independent 14-year time series for a single river stock and for mixed, multiple stocks revealed almost identical temporal patterns in growth condition variation, and an overall trend decrease of 11–14% over the past decade. Growth condition has fallen as SST anomaly has risen, and for each year-class the midwinter (January) SST anomalies they experienced at sea correlated negatively with their final condition on migratory return during the subsequent summer months. Stored lipids are crucial for survival and for the prespawning provisioning of eggs in freshwater, and we show that under-weight individuals have disproportionately low reserves. The poorest condition fish (~30% under-weight) returned with lipid stores reduced by ~80%. This study concurs with previous analyses of other North Atlantic top consumers (e.g. somatic condition of tuna, reproductive failure of seabirds) showing evidence of major, recent climate-driven changes in the eastern North Atlantic pelagic ecosystem, and the likely importance of bottom-up control processes. Because salmon abundances presently remain at historical lows, fecundity of recent year-classes will have been increasingly compromised. Measures of year-class growth condition should therefore be incorporated in the analysis and setting of numerical spawning escapements for threatened stocks, and conservation limits should be revised upwards conservatively during periods of excessive ocean climate warming.

*Keywords:* anomaly, Atlantic salmon, bottom-up control, condition factor, fecundity, lipid reserves, NAO, ocean warming, *Salmo salar*, spawning, SST, time series

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## Introduction

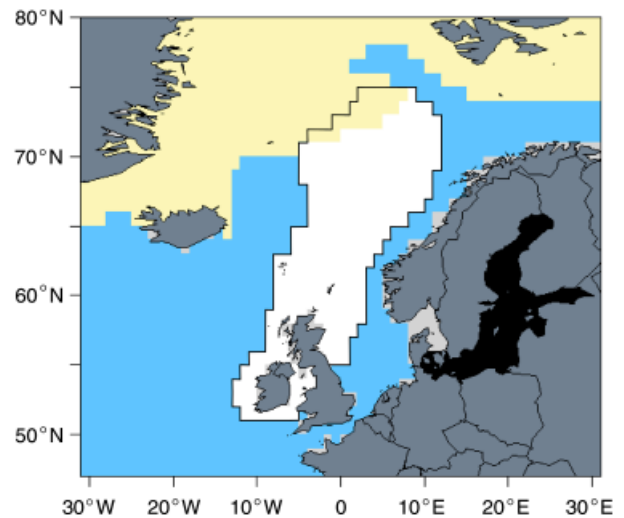
Atlantic salmon (*Salmo salar* L.) are generalist and opportunistic predators of zooplankton and nekton at the ocean surface (Jacobsen & Hansen, 2001; Lacroix & Knox, 2005; Haugland *et al.*, 2006). In recent years, salmon population abundances have fallen sharply to

historical lows (Friedland *et al.*, 2003a; Anon, 2007), probably due to a long-term decline in marine survivorship over the past three decades (Friedland *et al.*, 2003b; Jonsson & Jonsson, 2004a). The juvenile smolts emigrate from freshwater in springtime and occupy specific, northern oceanic areas of restricted surface temperature range for most of their marine residence (Friedland, 1998; Hansen & Jacobsen, 2000; Friedland *et al.*, 2003b; Jonsson & Jonsson, 2004a). North Atlantic surface zooplankton communities have undergone marked distri-

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butional changes since the 1960s, with both poleward extension of warm-water species in the eastern North Atlantic and increases in the number of Arctic species in the western North Atlantic; these changes have been related to variability in ocean circulation and climate (Beaugrand *et al.*, 2002). The eastern and western North Atlantic are influenced differently by the subpolar and subtropical gyres, and consequently show differing patterns of decadal variability, but since the early 1970s sea surface temperatures (SST) on both sides of the North Atlantic – including the salmon foraging areas – has risen markedly. Large-scale, climate-driven biogeographic shifts in the epipelagic ecosystem are likely to have exerted substantial bottom-up impacts on generalist predators high in the food web (e.g. Crick, 2004; Richardson & Schoeman, 2004; Frederiksen *et al.*, 2006), including Atlantic salmon.

Management assessments of salmon stock health are based largely on estimates of oceanic abundance, adult return rates and spawning escapements of the one sea-winter (1SW) and multi sea-winter (MSW) population components (Anon, 2007). 1SW salmon return to spawn after a migration of only 13–18 months, while MSW fish remain at sea for two to five winters. North American 1SW stocks primarily exploit the western North Atlantic (Labrador Sea, Greenland), whereas European 1SW salmon typically migrate to the eastern North Atlantic (Norwegian Sea, Fig. 1; Reddin & Shearer, 1987; Friedland *et al.*, 1998, 2000; Holm *et al.*, 2000; Hansen & Jacobsen, 2003; but see also Spares *et al.*, 2007 for a different view). The International Council for the Exploration of the Sea (ICES) separates European stocks into the two maturity groupings and, according to river of natal origin, further distinguishes ‘northern’ (Russia–Scandinavia–North/East Iceland) and ‘southern’ (south/west Iceland–British Isles–France) components for the purposes of developing management advice and pre-fishery abundance estimates (Potter *et al.*, 2004). Atlantic salmon smolts weigh only ~30 g on entering seawater, but their growth rates at sea are high; southern European 1SW adults returning to freshwater after 13–15 months typically weigh between 1 and 4 kg, but juvenile mortality early in the marine phase is high (Friedland *et al.*, 1998, 2000). Growth and survivorship of Atlantic salmon clearly are linked to ocean climate variation (Reddin & Shearer, 1987; Friedland, 1998; Friedland *et al.*, 1998, 1993; Jonsson & Jonsson, 2004a, b), but the responses are still poorly understood and may differ fundamentally for North American and European stocks (Friedland *et al.*, 2005). Notwithstanding these biogeographic complexities, it is likely that the general pattern of stock decline throughout the North Atlantic



**Fig. 1** The eastern North Atlantic Ocean posts molt migratory habitat for 1SW Atlantic salmon of northern British Isles origin (white) (compiled from Friedland *et al.*, 1998, 2000; Hansen & Jacobsen, 2000, 2003). The northernmost extent probably is set by the Barents Sea polar front, to the east of Bear Is. (74°N 19°E), which is indicated in Fig. 3 by the intersection of contrasting patterns of cooling/warming. Baltic Sea (black) SST data were excluded from correlation analyses. Light grey indicates incomplete coastal boxes and yellow includes grid boxes that were seasonally affected by sea ice: the latter were excluded also from the SST analyses for those months. 1SW, one-sea winter; SST, sea surface temperature.

region over the past three decades has been a response, at least in part, to global climate change (Friedland *et al.*, 2003a). Here, we focus not on salmon abundances or survivorship, but on annual variation in final adult growth condition (mass at standard length) of southern European 1SW salmon, and its linkage to ocean climate during the period 1992–2006.

The first studies to draw connections between ocean–atmosphere climate linkages and Atlantic salmon abundance focused on North American stocks and the fishery at West Greenland (Templeman, 1972; Dunbar & Thomson, 1979; Reddin & Shearer, 1987). Both positive (Friedland *et al.*, 1993, 2000; Friedland, 1998) and negative (Friedland *et al.*, 2003a, b) correlations between SST and juvenile growth and survivorship have been shown for European and North American stocks, respectively, and survivorship appears to be strongly growth mediated (Friedland *et al.*, 2000). It is very likely that marine survival, growth, and age at maturity (Friedland, 1998; Jonsson & Jonsson, 2004b), probably all will to an extent be density independent (Jonsson *et al.*, 1998) and influenced directly (physiologically) and/or indirectly (trophically; bottom-up control) by ocean climate (Beamish & Bouillon, 1993; Friedland

*et al.*, 2000, 2005; Beaugrand & Reid, 2003). First entry to seawater is physiologically demanding for smolts, and positive, direct effects of warmer SST have been reported for European juveniles (Friedland *et al.*, 2005). However, during the latter part of their ocean residence, indirect, temperature-driven effects on epipelagic prey assemblages may be especially important both to growth of individual preadult salmon and to population abundance (e.g. Friedland *et al.*, 2006). The possibility remains that positive, direct effects of warmer SST on juvenile postsmolts might not extend to preadults during their one winter at sea.

The distinct year-classes of 1SW fish offer a better opportunity than MSW fish for assessing environmental effects on growth condition integrated throughout the ocean residence period. None the less, year-class or cohort means for salmon length and weight typically show strong fluctuations (Fleming, 1998). To obtain an integrative measure of fish quality that is independent of within- and between-year variation in mean length, we here express the growth condition for each year-class of returning 1SW adults as the predicted weight (PWt) at a standard length on a fixed date. We analysed residuals in correlating SST anomalies with two independent time series of final growth condition (PWt), one from a fishery that targets a mixture of stocks and the other for a single identifiable river stock. For salmon of southern European origin we show that PWt has fallen steadily over the past decade, and is negatively correlated with the midwinter (January) SST anomaly that each of the respective 1SW year-classes would have experienced.

## Methods

### *SST and North Atlantic Oscillation (NAO)*

Monthly SST data for the eastern North Atlantic were extracted from the NOAA Optimum Interpolation SSTv2 grid data set (NOAA-CIRES Climate Diagnostics Center, Boulder, CO, USA, <http://www.cdc.noaa.gov>). The monthly averaged data are generated on a  $1^\circ$  latitude  $\times$   $1^\circ$  longitude grid from a combination of satellite and *in situ* measurements (Reynolds *et al.*, 2002). Throughout this study, we delimited the gridded SST anomaly data to the range of  $45\text{--}80^\circ\text{N}$  and  $30^\circ\text{W}\text{--}30^\circ\text{E}$ . This ensured an oceanic coverage that more than embraced the known migratory habitat of Atlantic salmon of southern European origin (Friedland *et al.*, 1998, 2000; Hansen & Jacobsen, 2003) and included 1441  $1^\circ \times 1^\circ$  grid boxes. For preliminary descriptive purposes we calculated the overall 1991–2005 trends for each grid-box in the eastern North Atlantic using a simple linear fit to the time series data.

For the subsequent analyses of correlation between SST anomalies and the two salmon time series, all grid boxes in the Baltic Sea were excluded because this semi-enclosed basin certainly is outwith the salmon migratory habitat. Furthermore, many of the northern grid boxes within our prescribed coverage are seasonally affected by sea ice and these also were excluded in months for which sea ice was a feature. Before analysis, the average seasonal cycle (climatology), calculated for the period 1971–2000, was removed from the OISSTv2 data. This climatology (Reynolds *et al.*, 2002) is available from NOAA-CIRES alongside the OISSTv2 data set ([http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn\\_SmithOiv2/.climatology/.dataset\\_documentation.html](http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOiv2/.climatology/.dataset_documentation.html)). The deseasoned, monthly anomaly time series then was detrended by application of a Gaussian-weighted running mean ( $\sigma = \pm 1$  year).

The NAO is the dominant pattern of atmospheric pressure variability in the North Atlantic, and can be a useful index when relating long-term changes in ecological conditions to variability in climate. Hurrell's December–March winter NAO Index (<http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html>) was detrended by application of a polynomial, and the residuals used for correlation with residuals of the two detrended salmon PWt time series. We sought correlations between year-matched PWt and the NAO index for the one winter that each year-class was at sea, in addition to the NAO lagged by  $-1$  year.

### *Salmon time series*

Fourteen year-classes (1992–1993 to 2005–2006 inclusive;  $n = 5269$ ) of returning adult 1SW salmon were sampled repeatedly throughout each summer netting season (weeks 23–33) from commercial coastal trap nets at Strathy Point (SP), North Scotland ( $58^\circ 36'\text{N}$   $04^\circ 00'\text{W}$ ). SP is a mixed-stock, interceptory fishery; salmon caught here are mostly in home waters, have ceased feeding and have completed their marine growth, but are destined for numerous rivers throughout north, west and east Scotland, with some returning to Ireland (Shearer, 1986). The United Kingdom and Ireland together dominate the ICES southern European stock component, and data from SP arguably are indicative or representative of the multiple stocks within that grouping. Furthermore, fish taken at SP have not been subject to prior fishery pressure, which may be size selective.

Comparable data also were collected from larger, and more frequently repeated, samples from the commercial net fishery in the River North Esk (RNE) estuary, E Scotland ( $56^\circ 46'\text{N}$   $02^\circ 26'\text{W}$ ). At either site we therefore

were able to sample between June and August the fully grown 1SW adults derived from the May (spring) emigrant smolt run of the previous year. Samples from RNE were available both earlier and later in the season compared with SP, and typically for multiple days in each week. The weekly SP samples generally commenced around 21 June and the season closes on 26 August, 5 days earlier than RNE. Annual sample totals at SP ranged from 115 (1999) to 689 (1996) fish, with a median of 346. To ensure comparability with SP, the RNE sample dates were reduced to include a starting date as close to 21 June (Day 172), and a median approximating Day 200 (the overall median for SP). Catch data from RNE are commercial-in-confidence, but the minimum annual sample size (1995) was 305 fish and, with the exception of 1995, all RNE sample sizes exceeded those from SP. The fishing personnel, methods, gear and net mesh sizes at both sample locations were consistent throughout the time series.

Sample dates at either site when  $\leq 5$  1SW fish were caught were deleted from the analyses. Scale readings allowed confirmation of the 1SW status of all fish analysed, and all MSW fish, escaped farm fish and previously spawned individuals were excluded from analysis. The sweep-net fishery at RNE is confined to the tidally influenced river estuary. Following heavy rainfall and spate conditions in the river, some fish, which evidently had entered the river some days or weeks previously, can drop back downstream and become available to the nets once again. All such 'coloured' fish were excluded from the RNE data set.

#### *Calculation of PWt*

Condition factor indices provide measures of 'quality', or marine growth condition, for individual fish and are an expression of the observed weight relative to the expected weight for a fish of that length. Various indices, based on length/weight relationships (Marshall *et al.*, 2004), can be calculated for individual fish and thence for populations or year-classes. Most measures of condition factor are, however, vulnerable to length-dependence (Blackwell *et al.*, 2000), which is especially problematic because male 1SW salmon returning in summer typically are longer and heavier than females, and both sexes tend to increase in length and weight as the summer sample season progresses. Simple population mean values for separate year-classes are therefore liable to gender- and sample date-related bias. PWt at standard length was our measure of choice because it is less subject to bias and provides a single summary statistic that integrates weight-at-length variation for either sex into a compar-

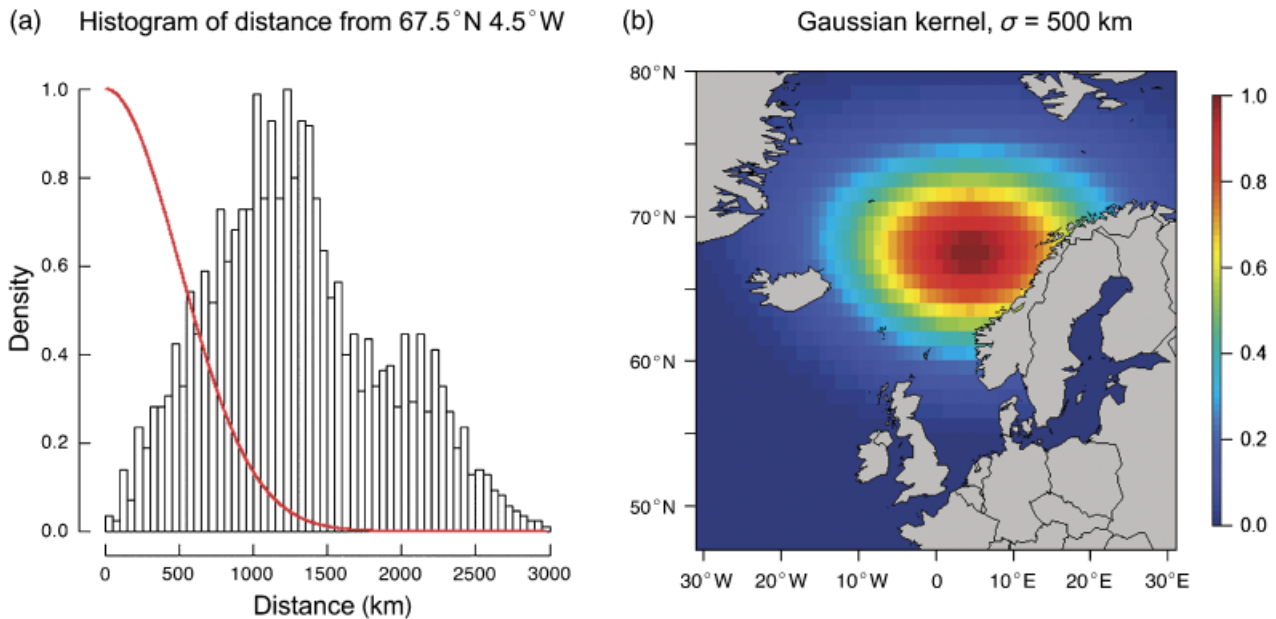
able measure of year-class growth condition, or adult 'quality'.

The overall means for salmon captured at the two sites were 60 cm (SP) and 58 cm (RNE), and these respective standard lengths were used in generating the single annual value of PWt for each time series. We used a Generalized Additive Model (GAM) to obtain PWt at the nominal median sample Day 200 for each year. Variations in weight through the sample season were modelled as a smooth function of Day of the year. Year ( $n = 14$ , 1993–2006) and Location ( $n = 2$ , SP, RNE) were included as GAM factors, in order to allow variations in intercept of the fitted parameters for given combinations of factor levels. Fish length was included as a covariate, thereby controlling for the allometric length/weight relationship in obtaining the estimate of PWt. The validity and utility of models including sex of individuals as an additional factor also were investigated, using the General Cross Validation (GCV) procedure.

#### *Time series data processing and analysis*

In the present study, it was possible to generate  $> 18\,000$  correlations between the salmon time series and each of the  $1^\circ \times 1^\circ$  gridded SST anomalies for the 13 months during which all fish in a year-class were at sea before capture. With multiple comparison studies of such large scale, there appears to be no general agreement on the most appropriate statistical method or conceptual strategy in protecting both Types 1 and 2 error rates by, for example, adjusting probabilities (Perneger, 1998; García, 2004; Nakagawa, 2004; Garamszegi, 2006). Therefore, for time series correlation analysis with PWt, we sought single, monthly average SST anomalies for the prescribed area of the eastern North Atlantic ( $30^\circ\text{W}$ – $30^\circ\text{E}$ ,  $45^\circ\text{N}$ – $80^\circ\text{N}$ ), and from May 1992 to 2006. This reduced the analyses to just 13 when correlating PWt with the SST time series anomalies [i.e. May of the previous year (= smolt emigration), to May of the year of capture].

Following deseasoning of the SST data, single average monthly anomalies for the eastern North Atlantic were obtained by a spatially weighted analysis, whereby weights were assigned to each  $1^\circ \times 1^\circ$  grid box according to its distance from a reference grid box ( $67.5^\circ\text{N}$   $4.5^\circ\text{E}$ ). The reference grid box was chosen to represent the assumed centre of southern European salmon distribution at sea (Fig. 1), and weights were defined using Gaussian kernels (Fig. 2). Because SST effects on salmon growth condition are most likely to be bottom-up and indirect (i.e. manifest by temperature-driven alterations of epipelagic prey availability) it was considered expedient to assess possible SST effects not only coincident with the migratory habitat, but also at



**Fig. 2** (a) Histogram of the frequencies of SST grid boxes of varying distance from the assumed centre of salmon distribution in the Norwegian Sea (67.5°N 4.5°E). Six different weightings (Gaussian kernel  $\sigma = 250, 500, 750, 1000, 1500, 2000$  km) were used for calculating the mean monthly SST anomalies at increasing spatial scales. The illustrated example (red plot) is for  $\sigma = 500$  km. (b) Colour density illustration of the eastern North Atlantic Ocean grid box weightings applied for  $\sigma = 500$  km. SST, sea surface temperature.

distances outwith that known oceanic habitat area, and particularly to the south and west. To examine the effects of spatial scale on the correlations, we calculated monthly means using six Gaussian kernels ( $\sigma = 250, 500, 750, 1000, 1500$  and  $2000$  km).

Correlation of, for example, steadily rising SST anomalies with falling PWt over time would result in widespread and strong negative results throughout the eastern North Atlantic. However, and while that might hint at a causal relationship, autocorrelation effects would preclude the individual years and months being classed as independent variables. Detrending, or pre-whitening (Pyper & Peterman, 1999), of the PWt and SST anomaly time series by running means (with Gaussian weighting windows of  $\sigma = \pm 1$  year) permitted removal of the predominant, low-frequency trend in PWt while retaining the high-frequency, year-on-year variation which was considered most relevant in detecting an effect of ocean climate on salmon growth condition. Following detrending, we calculated the residuals of mean monthly SST anomalies and salmon PWt for the definitive correlation analyses. By investigating the residuals of the 13 monthly time lags throughout the period that each sampled year-class was at sea we were able to assess any seasonal restriction of significant correlations.

Here, as recommended by Nakagawa (2004), for the definitive correlation analyses we report the significant

Pearson's correlation coefficients and their probabilities. The six (250–2000 km) spatial comparisons within each of the 13 lagged analyses included the same SST data and cannot be considered to be independent. Therefore, adjustments of probabilities were made for 13 (monthly) tests and we identify those that satisfied control for False Discovery Rate (FDR) (Benjamini & Hochberg, 1995).

#### *Lipid extraction and analyses of individual condition factor ( $W_R$ )*

Given that fecundity of female salmon is strongly dependent upon both absolute body mass (Jonsson *et al.*, 1996; Fleming, 1998; Jonsson & Jonsson, 2003) and probably also the levels of stored lipid reserves, we wished to ascertain whether poorer condition fish have similar lipid concentrations to fish of high condition factor. Total lipids were extracted for individual 1SW salmon ( $n = 35$ , length range 49.5–70.0 cm, weight range 1.06–3.98 kg), sampled at SP during July and August 2006. Condition factor of these individual fish was calculated as the relative mass index,  $W_R$  (Blackwell *et al.*, 2000).  $W_R = W/W_S$ , whereby  $W$  is the observed mass and  $W_S$  is the standard mass predicted from a specific mass/length regression equation for salmon sampled at SP ( $n = 5269$ ). The  $W_S$  predictive equation (log weight in kg =  $3.084 \times \log$  length in cm – 5.068;

$r^2 = 1$ ) was derived by the RLP method (Blackwell *et al.*, 2000), treating the 14 year-classes as separate populations and by regressing the logarithm of the 75th percentiles for weight at each 1 cm grouping against the logarithm of length.

Fish for lipid extraction did not comprise a random sample because they were specifically chosen to include the range of both lengths and condition factors available through the 2006 netting season. To ensure direct comparability of lipid concentrations among individual fish only the section of the body between the posterior insertion of the dorsal fin and the anus was excised and homogenized. This morphologically defined section is the standard quality control cut approved by the Norwegian salmon aquaculture industry. Homogenized sections included the scales and bones, but not the posterior intestine. Lipids were determined gravimetrically for subsamples of homogenate ( $n = 4$  replicates, each  $\sim 20$  g wet weight) treated initially with 40 mL of chloroform only, followed by three 100 mL extractions in chloroform, water and methanol (Bligh & Dyer, 1959). Each of the four extractions was left to stand for 24 h.

Nonlinear regression was applied to ascertain the optimal model to describe the relationship between percent lipid (Norwegian section) and fish condition factor ( $W_R$ ). Regression residuals confirmed the optimal transformation for the percent lipid data to be the arcsine, and the optimal nonlinear model structure was identified by the Akaike Information Criterion score.

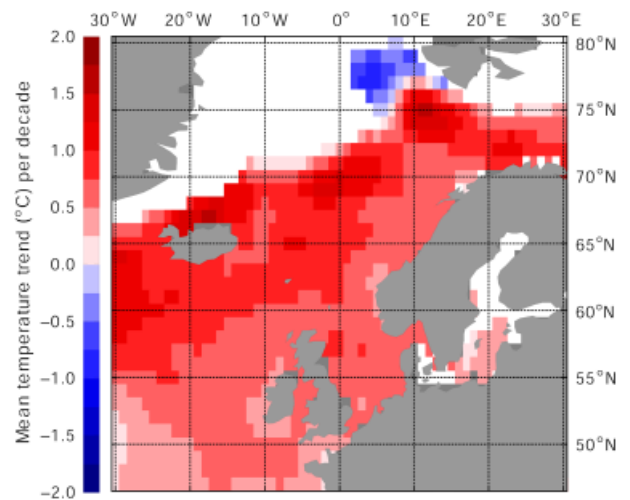
## Results

### Trends in SST

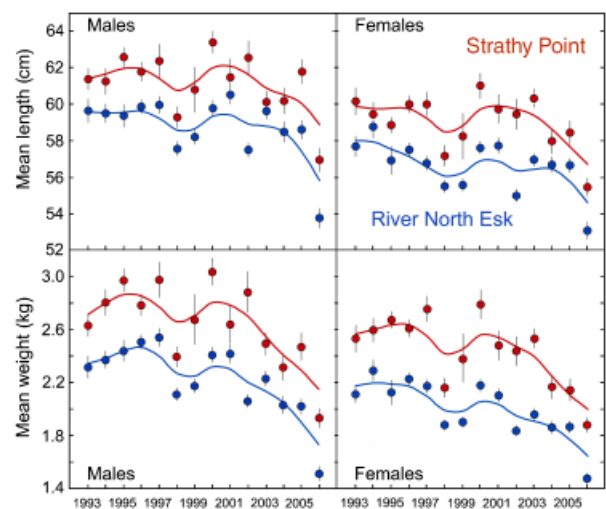
SST in the eastern North Atlantic has risen at a rate of between 0.5 and 1.5 °C decade<sup>-1</sup> since the 1990s (Fig. 3), although this period of accelerated warming may have peaked in 2003. Given that Atlantic salmon spend most of their time in surface waters (but do undertake brief feeding excursions to colder subsurface depths; e.g. Reddin *et al.*, 2006), and that the preferred oceanic habitat of postsmolts in the subpolar gyre lies only within a narrow temperature range (Friedland *et al.*, 1993; Friedland, 1998; Jonsson & Jonsson, 2004a), such rates of ocean surface warming are very likely to have marked and possibly detrimental consequences for growth and/or survivorship of salmon at sea.

### Trends in mean length and weight of salmon

1SW salmon sampled at SP typically are longer and heavier than those taken at RNE, but the consistent



**Fig. 3** The linear trend in annual mean SST in the eastern North Atlantic Ocean, 1991–2005. In red grid boxes the annual mean SST has increased since 1991, in blue boxes SST has decreased. White areas have sea ice cover for part of the year; trends have not been calculated for these areas. SST, sea surface temperature.



**Fig. 4** *Salmo salar*. Mean lengths and weights (back-transformed logarithm;  $\pm 95\%$  confidence intervals) for males and females at both sites. The fitted trend lines are weighted running means with a Gaussian window of  $\sigma = \pm 1$  year.

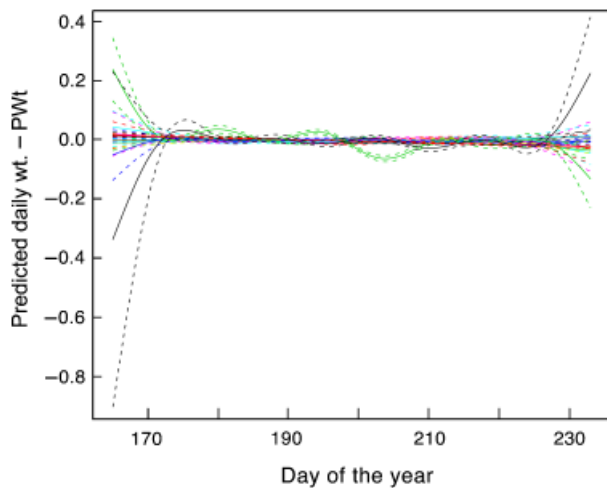
within-site differences in size of males and females are clear at both sites (Fig. 4). The interannual variation in both weight and length for both time series was considerable, with 2006 being characterised by fish that were both exceptionally short and of disproportionately low mass. Following the observed peak in 2000, the overall trend decrease (at either site) in mean length was  $\sim 5\%$  but mean weight fell more markedly, by

~22%. The recent pattern has, therefore, been one of 1SW salmon returning in increasingly poor condition (i.e. slightly shorter, but much thinner and of low absolute mass). Given that mean body mass varied disproportionately compared with mean length, the overall year-class growth condition (PWt) was expected to show a different temporal pattern to that for mean length or weight alone.

#### GAM analysis and derivation of PWt

In deriving the measures of PWt, models including sex of individuals as an additional factor were discarded on the basis of their GCV score being virtually identical to a simpler model excluding the sex effect. While there was a general size difference between males and females (Fig. 4), this difference was already controlled for in the model by the inclusion of the length covariate because within sites males and females of a given length have similar mass. Similarly, a more complex model including separate smooth terms for each year (essentially allowing the shape of the seasonal PWt changes to vary between years) was discounted on the basis of similarities in GCV score to the simpler model. This indicated that the seasonal change in PWt was very similar within years, despite the marked variation in PWt among years. Overall, the within-year changes in PWt were nonsignificant and Day 200 was, therefore, deemed an appropriate standard date for calculating PWt for each site and year-class. The final, most parsimonious, model for the two time series was used to obtain PWt (Day 200) for each year-class.

GAM analysis showed no significant within-year variation in PWt, with the exception of 1995 (Fig. 5): if fish returning early in a given season showed generally either good or poor condition, they continued to do so throughout that season. This unexpected result affirmed that growth condition essentially is 'set' for entire year-classes of return migrants, irrespective of stock substructuring (Youngson *et al.*, 2003) or date of migratory return within a year. Moreover, the very high correlation ( $r = 0.923$ ;  $P < 0.001$ ) between the two PWt time series (Fig. 6a) confirms that year-class growth condition is determined by factors in the shared oceanic environment that are common to multiple stocks within the ICES southern European component, rather than it being a response to variation in the freshwater habitat, or attributable to a specific river catchment. The general increase in eastern North Atlantic SST anomaly over the observational period (Fig. 6b) shows a clear and opposite trend to salmon PWt and is strongly indicative of a causal relationship between ocean climate and salmon growth condition.



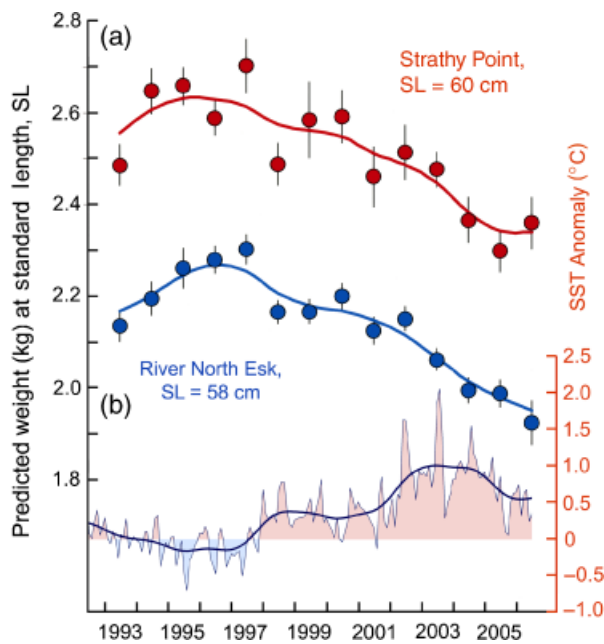
**Fig. 5** Within-season variation for log predicted weight (PWt) at standard length (SP 60 cm, RNE 58 cm) minus the log PWt on Day 200. The median sample date (Day 200) was used for determining PWt for subsequent correlation analyses. The 14 years are shown in different colours and each smoothed prediction is plotted with its 95% confidence intervals (broken plots). 1995 (light green) was the only year to show marked fluctuations in weight at standard length during the season. PWt, predicted weight; RNE, River North Esk; SP, Strathy point.

#### NAO

Pearson's correlations between the residuals of the detrended winter NAO index and detrended salmon time series were nonsignificant both for year-matched data (SP  $r = 0.193$ ,  $P = 0.508$ ; RNE  $r = -0.223$ ,  $P = 0.444$ ) and for the winter NAO Index lagged by  $-1$  year (SP  $r = -0.355$ ,  $P = 0.234$ ; RNE  $r = -0.318$ ,  $P = 0.290$ ). The lack of significant correlation with the NAO was perhaps to be expected because it accounts only for a proportion of the variability in atmospheric pressure over the North Atlantic, and over short timescales is not always clearly related to changes in ocean conditions. Since the turn of the millennium, for example, patterns such as 'Atlantic ridges' of high pressure have been more prevalent during the winter months (Hurrell *et al.*, 2003) and the NAO Index has been both weak and variable.

#### Correlation analyses (PWt and SST anomaly residuals) and adjustments for multiple comparisons

Prewhitening removed all autocorrelation from the salmon PWt time series, while (positive) autocorrelation did remain, albeit only at  $+1$  month, for the SST monthly mean values. The qualitative similarity of the pattern of lagged correlations between the residuals of monthly SST anomaly and the two PWt time series (Fig. 7) is pronounced. A significant positive correlation

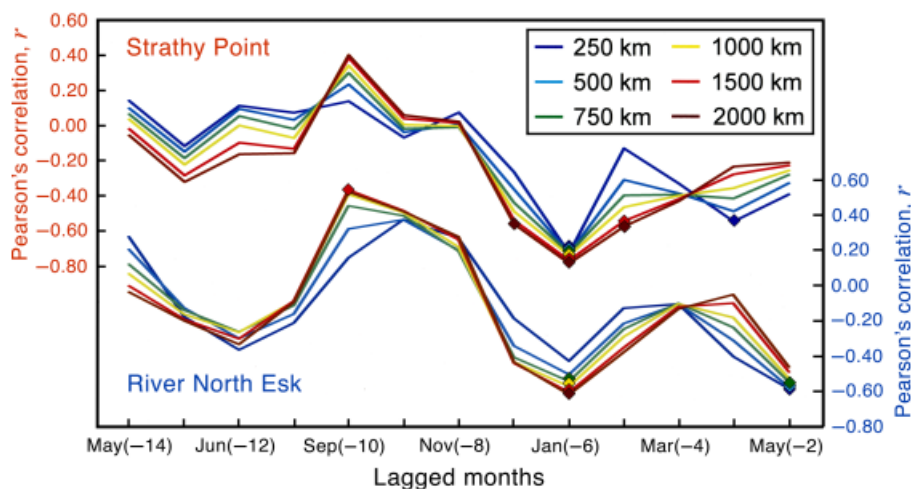


**Fig. 6** (a) Predicted weight (PWt)  $\pm 95\%$  CI at standard length (SL) for adult 1SW Atlantic salmon. A Generalized Additive Model, including a term for site, was used to obtain estimates of PWt on the median sample date (Day 200) at the observed overall mean lengths of 58 cm (RNE) and 60 cm (SP) for each year-class. (b) Example mean monthly SST anomalies for the eastern North Atlantic Ocean, calculated with a weighting kernel of  $\sigma = 500$  km. For all time series, weighted running means ( $\sigma = \pm 1$  year) were used to detrend the data to generate residuals for lagged correlation analysis. SST, sea surface temperature; PWt, predicted weight; RNE, River North Esk; SP, Strathy Point; 1SW, one-sea winter.

was found for RNE in September, but only at a large ( $\sigma = 1500$  km) spatial scale (Fig. 7). This result probably is not ecologically relevant because it is attributable to strongly negative, late summer SST anomalies in the high Arctic, to the north of the polar front and beyond the migratory range of Atlantic salmon. SST there has tended to fall over the time series (Fig. 3), perhaps due to increased rates of melting of Arctic ice. The unadjusted probabilities for the 13 lagged monthly analyses (Table 1) showed the major significant feature common to both salmon time series to be negative correlations between midwinter SST anomaly and salmon growth condition, and these were especially intense for SP at all spatial scales. Given the positive autocorrelation at +1 month for the residuals of SST anomalies, we confine the interpretation of a significant negative effect of SST on salmon condition to January only. Although the correlations at RNE were not sufficiently strong to remain significant after adjustment for FDR, those in January at SP, and for all six spatial scales, did remain significant.

#### *Variation in lipid reserves in relation to individual condition factor*

The overall trend decrease in PWt since 1997 (Fig. 6a) was 0.27 kg (−11%) and 0.30 kg (−14%) for SP and RNE, respectively, which will have considerable implications for individual female fecundity even if stored lipid concentrations for high condition and poor condition fish were found to be comparable. Figure 8 shows a strong sigmoid relationship between lipid content and condition factor and the optimal nonlinear model

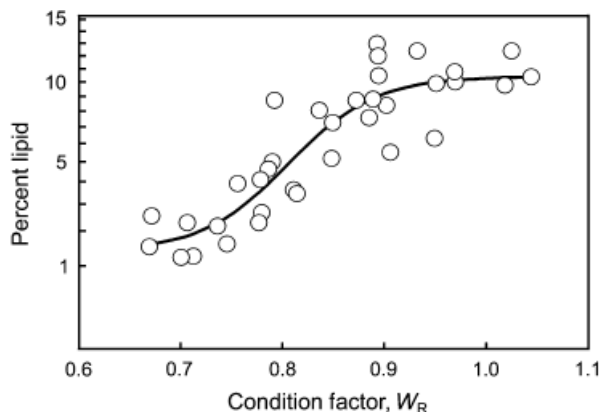


**Fig. 7** Summary of correlation analyses between residuals for the two salmon PWt time series and eastern North Atlantic Ocean mean monthly SST anomalies. The six analyses for each site included weighting kernels ranging from  $\sigma = 250$  to 2000 km for the calculation of monthly mean SST anomalies. Significant correlations are denoted by diamond symbols. SST, sea surface temperature; PWt, predicted weight.

**Table 1** Significant coefficients (Pearson's *r*) from correlation analyses between residuals of salmon predicted weight (Strathy Point, SP; River North Esk, RNE) and monthly SST anomalies

Month	Pearson's <i>r</i>	Spatial kernel (km)	Unadjusted Probability	FDR
<i>Strathy Point (SP)</i>				
April (-3 month)	-0.538	250	0.04741	No
February (-5 month)	-0.535	1500	0.04869	No
February (-5 month)	-0.567	2000	0.03466	No
January (-6 month)	-0.719	250	0.00383	Yes
January (-6 month)	-0.719	500	0.00383	Yes
January (-6 month)	-0.719	750	0.00384	Yes
January (-6 month)	-0.731	1000	0.00299	Yes
January (-6 month)	-0.759	1500	0.00166	Yes
January (-6 month)	-0.777	2000	0.00109	Yes
December (-7 month)	-0.553	2000	0.04024	No
<i>River North Esk (RNE)</i>				
May (-2 month)	-0.580	250	0.02953	No
May (-2 month)	-0.573	500	0.03236	No
May (-2 month)	-0.543	750	0.04505	No
January (-6 month)	-0.539	750	0.04694	No
January (-6 month)	-0.567	1000	0.03439	No
January (-6 month)	-0.599	1500	0.02358	No
January (-6 month)	-0.613	2000	0.01981	No
September (-10 month)	0.536	1500	0.04833	No

Monthly lags are given in parentheses and the standard deviations of the spatial kernels within months are given in km. The uncorrected probabilities are shown, and annotated as to whether or not they remain significant after adjustment and control for False Discovery Rate (FDR) (Benjamini & Hochberg, 1995). SST, sea surface temperature.



**Fig. 8** Percent lipid content (arcsine scale) of somatic tissue (Norwegian section) of adult 1SW Atlantic salmon of varying body length (range 49.5–70.0 cm) and condition factor ( $W_R$ ) captured at SP, July–August 2006. Extracted lipids were determined gravimetrically. The best fit nonlinear model was a modified logistic ( $r^2 = 0.808$ ). 1SW, one-sea winter; SP, Strathy Point.

was a modified logistic [arcsine percent lipid =  $a / (1 + \exp(b - cx)) + d$ , whereby  $a = -12.12$ ,  $b = -18.90$ ,  $c = -23.44$  and  $d = 18.83$ ;  $r^2 = 0.808$ ]. High condition fish ( $W_R \geq 1$ ) in 2006 typically attained a threshold lipid content (Norwegian section) of  $\sim 10\%$  but lipid reserves

fell steeply as  $W_R$  declined. The poorest condition fish, which were  $\sim 30\%$  underweight, showed lipid reserves reduced by  $\sim 80\%$  compared with the highest condition fish. Irrespective of effects on fecundity, the probability of the poorest condition fish – with lipid reserves as low as 1–2% – successfully migrating upriver and surviving to spawn in November is likely to be extremely low.

## Discussion

Detailed evidence for ocean–atmosphere climate linkages to salmon abundance was first derived specifically for North American stocks (Reddin & Shearer, 1987; Friedland *et al.*, 2003a, b), whereby the NAO was found to be in negative phase with the area of conducive ( $4\text{--}8^\circ\text{C}$ ) winter thermal habitat in the NW Atlantic (Friedland *et al.*, 1993, 2003b; Friedland, 1998). Years of more expansive suitable thermal habitat were associated with higher abundances of subsequently returning adults. None the less, other analyses of North American stock abundances (Friedland *et al.*, 2003a), estimated from NW Atlantic commercial landings over the period 1910–1997, have also shown negative correlations with winter and spring SSTs, respectively, in the Gulf of Maine and Gulf of St Lawrence. The winter thermal habitat area concept applied to the NW Atlantic

has not been demonstrable in explaining variation in abundance of European stocks occupying the NE Atlantic but, over the period 1965–1993, for two European river populations migrating to the Norwegian Sea, warmer springtime (May) North Sea and coastal Norwegian SSTs did correlate positively with marine survivorship of juveniles (Friedland *et al.*, 1993, 2000; Friedland, 1998), and their subsequent return rates as 1SW adults (Friedland *et al.*, 1998).

Notwithstanding the biogeographic complexities apparent in the above analyses, the emerging paradigm for Atlantic salmon at sea has been one of growth-mediated survival showing positive correlations with warmer SSTs, although recent analyses of the first 3–4 months of marine growth of postsmolts that returned to Scotland as 2SW spawning adults between 1964 and 1993 do indicate a negative effect of higher temperatures (Friedland *et al.*, 2005). It is important to emphasize that the data analysed in the aforementioned studies of European salmon predate the present time series, and that their focus was on survivorship and not growth condition of returning adult 1SW fish. As Figs 3 and 6b illustrate, the eastern North Atlantic in recent years has been characterized by anomalously high, year-round SST.

SST in the eastern North Atlantic shows a strong seasonal cycle, which generally exceeds interannual variability. Typically, temperatures range seasonally by  $\sim 5^{\circ}\text{C}$  in the central North Atlantic, to  $\sim 10^{\circ}\text{C}$  in coastal regions, and even  $>20^{\circ}\text{C}$  in certain eastern areas such as the southern North Sea and the Baltic Sea. Since the late 19th century, global average ocean SST has increased by  $0.074^{\circ}\text{C decade}^{-1}$  but the rate of warming calculated over the period 1981–2005 has been higher, at  $0.177^{\circ}\text{C decade}^{-1}$  (IPCC, 2007). In addition to this general rising trend, SST in the North Atlantic also fluctuates with decadal and multi-decadal periods. The multi-decadal fluctuation in SST has been in a rising phase since the mid 1980s and is thought to be contributing to the accelerated warming that has been observed over the measurement period (IPCC, 2007; Fig. 6b). North Atlantic SST anomalies are strongly related to changes in patterns of atmospheric pressure across the North Atlantic (Hurrell *et al.*, 2003), but these are not well described by the Hurrell December–March winter NAO index for our relatively short measurement period (Hughes & Holliday, 2006). Previous studies have shown correlations between the NAO and either salmon abundance (Friedland *et al.*, 1993, 2003a; Jonsson & Jonsson, 2004a, b), or year-class variation in growth (Jonsson *et al.*, 1998); but we could show no correlations of residuals between the winter NAO index and the two salmon PWt time series. Short time series are vulnerable to a lack of statistical power, but even

relatively long time series may show alternating patterns of correlation. Thus, for example, whereas Friedland *et al.* (2003a) found significant negative correlations between the NAO and salmon abundances in the second half of the 20th century, there was no correlation in the first half.

Given a dynamic thermal environment it is to be expected that cold-water fish with narrow oceanic temperature preferences, such as Atlantic salmon, will show considerable variations in growth and survivorship on annual to decadal time-scales. A multidecadal analysis of 1SW salmon captured in commercial river-mouth nets on the River Dee (E Scotland) over the period 1876–1972 (Martin & Mitchell, 1985) showed considerable fluctuations in mean weight, and latterly a steady increase from  $\sim 2$  to  $\sim 2.9$  kg throughout the 1960s and into the early 1970s. Those data must be interpreted with some caution: for example, fish were categorized as 1SW only ‘by eye’ (not by scale reading), and males and females were not distinguished. None the less, the indications are that long-term fluctuations in growth success of 1SW year-classes of Atlantic salmon of southern European origin are typical. That we can show fluctuations and recent declines in mean length, weight and growth condition of 1SW salmon is, therefore, not unexpected, although the extent and persistence of the downward trend in PWt over the past decade is particularly striking.

In seeking to identify the likely processes that underlie the strong patterns in PWt, two initial results stemming from the PWt data themselves were strongly indicative: first, growth condition is ‘set’ for entire year-classes of 1SW salmon, irrespective of their date of migratory return within the season. Second, the two PWt time series – for mixed stocks and for an identifiable single river stock – showed closely similar temporal patterns. Those findings, in addition to the significant correlations between PWt and midwinter SST anomaly in the ecologically relevant area of the Norwegian Sea, point unequivocally to an oceanic causal factor, be it direct or indirect.

While a direct physiological effect of ocean warming on salmon metabolism is possible, other evidence suggests it is more likely that the negative correlations (Fig. 7) are manifest in bottom-up control (i.e. reduced prey availability) for preadult 1SW salmon throughout the later winter and spring months of their ocean residence, just before their migratory return. There are recent observations of breeding failure for European seabirds correlating with ocean warming and reduced (fish) prey availability (e.g. Durant *et al.*, 2003; Crick, 2004), and of declining somatic condition and lipid content of piscivorous tuna (*Thunnus thynnus*) in the NW Atlantic (Golet *et al.*, 2007). Although we can show fluctuations and general declines in both mean length

and weight of 1SW salmon, the PWt time series show that their primary response has been one of disproportionate and inexorable decreases in weight at length. Some individuals in every year return in very high condition, but the observation that year-class mean body length has to a large extent been maintained, while mass at length has declined markedly, is strongly suggestive of fish essentially starving and catabolising both their energy reserves and muscle protein during the latter part of their marine residence. The sigmoid relationship between somatic condition factor and lipid content (Fig. 8) affirms the extent to which energy reserves have been compromised in the poorest condition fish.

Subcutaneous adipose deposits and lipids within the musculature comprise the main energy reserves (Jonsson *et al.*, 1997), and 1SW adults of lower condition factor ( $W_R$ , Fig. 8) have disproportionately low fat reserves. The poorest condition fish extracted were ~30% underweight for their length, yet their somatic lipid reserves were ~80% lower than for a full-condition fish ( $W_R = 1$ , Fig. 8). Because salmon cease feeding during their migratory return and subsequently rely on somatic reserves, the declines in both mean weight (Fig. 4) and growth condition (Fig. 6a) of recent year-classes will have exerted marked reductions in female fecundity. Egg production is a major investment of female salmon, which potentially are iteroparous although most are semelparous (Jonsson & Jonsson, 2004a; Niemelä *et al.*, 2006). Stored lipids are essential for vitellogenesis and prespawning provision of eggs in freshwater: the ovaries alone comprise ~30% of the female's total energy reserves at spawning (Jonsson *et al.*, 1996) and represent about half of the energy expended in maturation, upstream migration and reproduction combined (Fleming, 1998; Jonsson & Jonsson, 2003). For a standard 58 cm female 1SW fish at RNE, the trend decrease in PWt (Fig. 6a) between 1996 and 2006 was ~14%. From body mass calculations alone, this would result in a reduction of individual egg production of ~12% (Fleming, 1998).

It is likely that the qualitative sigmoid form of the relationship between lipid reserves and individual condition factor will be consistent among years, but probably the upper and lower thresholds, for high and low condition fish, respectively, will vary: in 'good' years fish may well return with significantly higher lipid reserves than individuals of a similar condition factor in 'poor' years. Lipid reserve data for more years clearly are necessary, but the present data show that recent year-classes inevitably will have displayed fecundity reductions even greater than those indicated by declining body mass alone (Figs 4 and 6a). Notwithstanding the likely density-dependent effects on embryos and juveniles in freshwater, such progressive and persistent

year-on-year declines in adult quality, and hence egg deposition, have important implications for current population status and management, and especially so for the many relatively small river systems in Scotland (Youngson & Hay, 1996) and Ireland with spawning populations dominated by 1SW adults.

The effects of ocean climate on Atlantic salmon growth and survival clearly are both pervasive and complex (Reist *et al.*, 2006). For example, while there has been a general pattern of marked stock declines over the past three decades this does not extend to all northern European rivers (e.g. Niemelä *et al.*, 2004). None the less, our analyses indicate that SST warming of the sub-Arctic North Atlantic Ocean over the past decade has been excessive to the point of constraining, rather than promoting, adult growth condition of multiple stocks within the ICES southern European grouping (Fig. 6a and b). While we favour an indirect, bottom-up controlling effect of surface warming on zooplankton and nekton prey availability to salmon, it has to be acknowledged that thermal growth optima need not necessarily match variations in food availability (Friedland *et al.*, 2006). Our finding that adult salmon growth condition over the 14-year period has declined as winter SST anomalies have risen does not necessarily conflict with previous reports of positive effects of warmer SST on growth-mediated survival of juvenile postsmolts (Friedland, 1998; Friedland *et al.*, 1998, 2000; Jonsson & Jonsson, 2004a), and may well concur with recent changes in eastern North Atlantic zooplankton assemblages (Beaugrand *et al.*, 2002; Beaugrand & Reid, 2003; Richardson & Schoeman, 2004). If the multiple-stock data for SP are indeed indicative of the broader ICES southern European stock component, the growth condition variation observed here (Fig. 6a) does reflect a geographically widespread, and ecologically profound, response of Atlantic salmon to prevailing ocean climate. This is in marked contrast to some other studies which have found that the relationship between ocean thermal conditions and salmon growth/survivorship responses might be stock- or population-specific (e.g. Jonsson & Jonsson, 2004a; Friedland *et al.*, 2005).

Commensurate with present stock abundances being at unprecedented lows, the sharp decline in growth condition that we show for the southern European 1SW maturity grouping, and the spatially extensive negative correlations with midwinter SST anomalies in the eastern North Atlantic, provide strong evidence of a recent, marked and continuing deterioration in ocean climate for wild Atlantic salmon. Growth condition reductions of this magnitude and temporal extent for a generalist marine predator are perhaps indicative of recent and large-scale ecological shifts in the eastern North Atlantic epipelagic ecosystem, and the likely importance of

bottom-up control in the food web (e.g. Frederiksen *et al.*, 2006). There is little that freshwater salmon fishery managers can do to alleviate such problems, but ICES presently considers the abundances of both the 1SW and MSW management groupings of southern European salmon to be at risk of suffering reduced reproductive capacity (Anon, 2007). While acknowledging that abundance estimates will remain the focus of stock management strategies, we argue that growth condition and measures of lipid reserves, as indicators of pre-spawning quality and fecundity, provide valuable additional empirical tools in assessing the performance and reproductive status of wild Atlantic salmon. Our results suggest that population conservation and enhancement measures in freshwater should perhaps be more stringent during periods of excessive SST warming, and likely reductions in individual fecundity also should be considered when setting and revising precautionary spawning escapements for given stocks.

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