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**Contemporary ocean warming and freshwater conditions contribute to delay the
completion of maturation in Atlantic salmon**

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Abstract. The completion of maturation in Atlantic salmon (*Salmo salar*) depends on environmental conditions that affect both feeding opportunities and growth, which would provide sufficient lipid stores for reproduction. However, if the level of energy reserves of a given fish is below a certain genetic threshold at a critical decision time further gonadal development is arrested and fully maturation postponed. This individual development pattern suggests that the proportion of fish maturing at a given sea age could vary from year to year according to the feeding opportunities in the oceanic migratory habitat, and the growth rate during freshwater residence that might be associated with growth at sea. In this study we show that sea age at maturity of adults caught in multiple Norwegian rivers has increased with increasing sea surface temperature (SST) experienced by the fish in autumn months during their first year at sea. Furthermore, freshwater conditions measured by river discharge during summer months one year ahead of seaward migration is positively related with increasing sea age at maturity. This result is discussed within the broad changes occurring in the North-east Atlantic pelagic food web mostly related with the current ocean warming, and river conditions influencing growth rates.

Introduction

Recent climate change is promoting multiple effects at population, community and ecosystem levels inducing extensive ecological changes well documented from various terrestrial, freshwater and marine systems (Letcher, 2009). The impacts of climate variability on aquatic ecosystems are widespread across their multiple components (e.g. Drinkwater *et al.*, 2010) and have effects on key life-history processes, including reproduction and maturation of fish (Rijnsdorp *et al.*, 2009). Age at reproduction is among the most important life history traits, having profound fitness effects and also important demographic implications (Stearns, 1992). In fish there is ample evidence that age at maturity has a significant additive genetic component, but also that this trait is highly plastic in response to changes in the environmental conditions (e.g. McDermid *et al.*, 2007). This is also the case for the Atlantic salmon (*Salmo salar* L.), a highly charismatic species with great economic and social value (García de Leániz *et al.*, 2007).

The life history of Atlantic salmon is complex (Webb *et al.*, 2007). Spawning occurs in freshwater in October–January. Juveniles (parr) stay in freshwater 1–6 years before transforming into smolt in spring and leaving their rivers to pursue oceanic feeding migrations. Post-smolt Atlantic salmon spend 1–4 years at sea until the attainment of sexual maturity, and return in May–October with high precision to their natal areas to spawn. Maturation may be reached after a single or multiple sea-winters and it is to some extent determined genetically (García de Leániz *et al.*, 2007). However, the biochemical processes leading to the completion of maturation are complex and depend on environmental conditions. Hence, the reproductive strategy is environmentally dependent but determined by the genetic structure, which sets a threshold level that prevent or permit an individual to continue further gonadal

development at a critical decision time and complete maturation (Thorpe, 1994). Several studies have shown that the determination whether to continue maturation occurs during autumn, a year ahead of spawning (Metcalf, 1998), and depends on adequate lipid reserves (Thorpe *et al.*, 1998). If the level of energy stores is insufficient for reproduction, that is, the genetically specified threshold level is not reached, the completion of maturation could be halted (Mangel & Satterthwaite, 2008). This arrest implies individual dependence on environmental opportunities, suggesting that the proportion of fish maturing at a given sea age would vary from year to year.

There is ample evidence that demonstrates the link between inheritance and maturation (García de Leániz *et al.*, 2007); however, the literature is inconclusive on the nature of the environmental effects across life-stages both in the river and in the ocean that in turn might affect maturity. During the parr stage, juveniles may be heavily affected by river discharge (e.g. Jensen & Johnsen, 1999) and river temperature (e.g. Jensen, 2003). Freshwater conditions might then influence pre-smolt growth rates that, in turn, might be associated with growth during the first year at sea and hence sea age at maturity. If so, age at maturity may partly be determined prior to sea entry, however, the shapes of these relationships are not clear. Some studies infer that smolt size and marine growth could be positively related (e.g. Salminen, 1997), whereas other authors have found an inverse relationship (e.g. Nicieza & Braña, 1993). In addition, increased growth rate during the first year at sea leads to postpone maturation (e.g. Jonsson *et al.*, 2003), while other studies argue the opposite (e.g. Friedland & Haas, 1996).

In this paper we use the proportion of two-sea-winter relative to one-sea-winter fish from the same smolt cohorts of Atlantic salmon to elucidate the plasticity in sexual maturation of salmon caught in 59 Norwegian rivers. By means of statistical modelling we estimate and determine the type of relationship between the sea age at maturity and

(i) the oceanic conditions experienced by post-smolt salmon in their seawater-foraging habitat, and (ii) the environmental conditions during the pre-smolt freshwater residence previous to the seaward migration. We expect that Atlantic salmon respond quickly to variations in either large scale (i.e. in the ocean) or local scale (i.e. in the river) environmental conditions by plastically changing their age at first maturation.

Material and methods

Biological data

The present study is based on the official statistics of nominal rod catch of adult Atlantic salmon for the period 1992 to 2007 over a wide geographical range of Norwegian rivers (58°19'–70°37' N and 5°07'–30°32' E). The legal fishing season is restricted to summer and early autumn, but differs somewhat among rivers. In Norway, systematic collection of data on salmonid fisheries began in 1876. Starting in 1979, Atlantic salmon were identified at the species level and differentiated into two weight categories (< 3 kg and ≥ 3 kg). The smaller group mainly corresponds to one-sea-winter (1SW) fish (grilse), and the larger group corresponds to multi-sea-winter (MSW) fish. Starting in 1993, the MSW group was categorized into two more weight classes (3–7 kg, and ≥ 7 kg) corresponding to 2SW and mainly 3SW fish, respectively (Jensen *et al.*, 1999). For the purpose of this study we used data from the 1SW (i.e. catches from years 1992 to 2006) and 2SW (i.e. catches from years 1993 to 2007) weight groups compiled from 59 Norwegian rivers. We based our analyses on the annual proportion of fish attaining maturity as two-sea-winter fish relative to one-sea-winter fish pertaining to the same smolt cohort (i.e. $2SW_t / (2SW_t + 1SW_{t-1})$) that is, smolt cohorts from years 1991 to 2005. Further detailed description of data handling and discussion on possible bias can be found elsewhere (Otero *et al.*, submitted).

Physical data

Sea surface temperature (SST in °C) changes have broad effects in the North Atlantic Ocean (e.g. Beaugrand, 2009), and they have been associated with growth rates (Todd *et al.*, 2008) and fluctuations of Atlantic salmon catch (Beaugrand & Reid, 2003). Therefore, we used basin scale SST as a surrogate of oceanic conditions. Optimum Interpolation sea surface temperature (SSTv2) data available at 1° latitude × 1° longitude grid resolution were obtained from the NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/psd/>). Monthly average data from a combination of satellite and *in situ* measurements (Reynolds *et al.*, 2002) were extracted for the period May-1991 to April-2006 to match appropriate time lags (see below), and delimited to the range of 55°–80° N and 15° W–30° E (note that the Baltic Sea was excluded from the analyses). This area covers most of the migratory and foraging habitat of Atlantic salmon originated from Norwegian rivers (Holm *et al.*, 2004) and included 794 grid boxes. The monthly SST time series were analyzed using Principal Component Analysis (PCA). A PCA was performed on the correlation matrix for each month (i.e. each of the 12 matrices: 15 years × p boxes, with the p number of boxes varying among months depending on the affection by sea ice) to identify long-term changes in SST (examination of principal components) and locate the geographical patterns (mapping of eigenvectors). These matrices were not of full rank, this means that there were fewer number of observations n (i.e. years) than descriptors p (i.e. grid boxes). However, when $n \leq p$ the first few axes, which are the ones of main interest, are little influenced (Legendre & Legendre, 1998).

Water discharge is used as a surrogate of freshwater conditions in terms of feeding opportunities and growth rates mediated, for instance, by river temperature (Forseth *et*

al., 2001). River conditions in midsummer would determine whether an individual would undergo smolt metamorphosis and ultimately define a sufficient energy status to survive emigration from the river the following spring (Mangel & Satterthwaite, 2008). Therefore, we considered average runoff in each river during the spring-summer (May–August) one-year ahead of smolt migration for the period 1990 to 2004 to match an appropriate time lag (see below). In doing so, daily discharge (runoff in $\text{m}^3 \text{s}^{-1}$) for each river catchment was estimated using a spatially distributed version of the Hydrologiska Byråns Vattenbalansavdelning model (HBV, http://www.smhi.se/foretag/m/hbv_demo/html/welcome.html) developed by the water balance section of the Swedish Meteorological and Hydrological Institute (see Beldring *et al.*, 2003 and references therein).

Statistical analyses

We first evaluated if there were a linear trend in the proportion of 2SW fish (measured in kg) from the same smolt cohorts (i.e. $2\text{SW}_t/2\text{SW}_t + 1\text{SW}_{t-1}$) in each river by means of ordinary least squares, and compared the individual slopes with latitude and various habitat characteristics which appear to be important for explaining the variation in grilse proportion (L'Abée-Lund *et al.*, 2004). Second, the proportion of 2SW fish was modelled using a restricted maximum likelihood (REML) linear mixed-effects model (random grouping factor comprises 59 rivers with 868 observations) following methods described in Pinheiro & Bates (2000). Although the response variable is a proportion, a linear model is adequate here since the observed proportions are not close to either 0 or 1. Selection of explanatory variables, random effects and correlation structure on error term was all performed using the Bayesian Information Criterion (BIC, Burnham & Anderson, 2002). A preliminary analysis indicated that inclusion of a random effect in

the intercept might be required to account for river-to-river variability while random effects related to the other regression coefficients were of less significance. According to these preliminary results we fitted a model of the form:

$$P_{i,t} = (\beta_0 + a_i) + \beta_1 \text{SST}_{t-n} + \beta_2 \mathbf{R}_{i,t-3} + \varepsilon_{i,t}$$

where P is the proportion of 2SW kg for each river i at a time t ; SST is the first principal component of the SST analyses lagged depending on the considered month, that is, SST from May to December was lagged two years (i.e. these months represent temperature effects during the smolt year), and months from January to April were lagged one year (i.e. these months represent temperature effects during the returning year for 1SW individuals); and R is ln-transformed runoff with a three year lag to represent effects during pre-smolt growth conditions the year before emigrating from the river. Note that R was also centered, by subtracting a river-specific mean. β_j are the fixed effects to be estimated; a is the random river (i) effect for the intercept assumed to follow a normal distribution with mean zero and variance σ_a^2 ; and $\varepsilon_{i,t}$ is the within-group error term assumed to be first-order autocorrelated (i.e., $\varepsilon_{i,t} = \phi\varepsilon_{i,t-1} + \eta_{i,t}$, where $\eta_{i,t} \sim N(0, \sigma^2)$).

Finally, heteroscedasticity was modeled using the following variance function:

$$\text{Var}(\varepsilon_{i,t}) = \sigma^2 |v_{i,t}|^{2\delta}$$

where δ is the power function of the fitted values ($v_{i,t}$) to be estimated.

All analyses were performed on R 2.6.2 software (R Development Core Team, 2008) and using the “nlme 3.1-86” package (Pinheiro & Bates, 2000).

Results

The proportion of 2SW Atlantic salmon generally increased across the rivers studied. Only 9 out of 59 rivers (~ 15%) showed a negative time trend (Fig. 1). The estimated slopes were not related with latitude neither with any habitat characteristics. SST changes in the North-east Atlantic in September (the month that gave the optimal fit in

the mixed-effects model, though note that April provided an equally likely model in terms of BIC criteria) shows a pronounced increase since 1991 with a peak in 2003 (Fig. 2a). This warming was especially apparent in the central Norwegian Sea and north of the Faroe islands (Fig. 2b), which is an area of distribution for Atlantic salmon post-smolt. By contrast, water flow was relatively stable in every studied river. The most remarkable feature occurred in 2000 with an apparent overall increase in runoff (Fig. 3). The optimal mixed-effects model shows that warmer ocean temperatures in autumn (September) and higher runoff in summer during the parr stage (the year before smolt transformation) give relatively more 2SW salmon (Table 1). The data strongly supported the model including both the ocean and freshwater effects compared to models considering isolated oceanic and riverine conditions (Table 2). Within group residuals were normally distributed and did not show any remaining variability. Random effects were also reasonable normally distributed.

Discussion

Here, we show that sea age at maturity in Atlantic salmon is strongly influenced by environmental conditions in the ocean during the post-smolt phase as well as in the river during the pre-smolt phase. To complete maturation and reproduce in autumn Atlantic salmon must initiate physiological changes well in advance. Mangel & Satterthwaite (2008) summarized this life history framework describing developmental switches that occur in the fish at a given decision time (Fig. 4). That is, in autumn fish compare the state of lipids and their rate of change with a genetically determined threshold (switch designated as G_1). If the state is sufficiently high gonadal development continues; otherwise maturation is inhibited. The following spring a similar comparison between the state of lipids and their rate of change with a second threshold occurs (switch

designated as G_2). Therefore, one-sea-winter (1SW) fish has followed a path where $G_1 = 1$ and $G_2 = 1$, whereas two-sea-winter (2SW) fish has followed a path where either $G_1 = 0$ or $G_1 = 1$ but $G_2 = 0$. Thorpe *et al.* (1998) have provided evidence supporting this modelling framework. Overall, our results show that the analyzed Norwegian rivers are becoming more 2SW rivers over the last 15-year period, meaning that the proportion of Atlantic salmon from a given cohort that attains maturity after 2 years at sea is increasing. This increase does not vary according to latitude neither depends on any river characteristic.

The control of maturation of Atlantic salmon has been tested in aquaculture experiments providing strong evidence that gonadal development is halted by poor feeding opportunities and concluding that the amount of lipid stores would probably be the critical resource governing the direction of maturity at the critical decision time (see Thorpe *et al.*, 1998 and references therein). Low levels of stored lipids would lead to postpone maturation. Therefore, it would be expected that the less favourable feeding conditions at sea the higher the proportion of Atlantic salmon arresting maturity. The current ocean warming has been related to poorer feeding opportunities and decreased growth conditions of the returned 1SW salmon (Todd *et al.*, 2008). In turn, this leads to poor recruitment (Friendland *et al.*, 2009), and reduces the catches in the eastern North Atlantic (Beaugrand & Reid, 2003). In this study, we found that warmer SST is related with an increase in sea age at maturity and this relationship is probably related to the temperature-induced changes in food web structure and consequently reduced feeding conditions. Therefore, we here suggest that our findings are a result of well-described changes in the eastern North Atlantic food web, specifically related with the changes on zooplankton assemblages occurring as a consequence of ocean warming (Beaugrand, 2009). That is, growth at sea might be compromised by the quantity and quality of prey

items available providing insufficient energy to reach the lipid threshold needed to complete maturation. For instance, the increase in temperature has profound effects on the food web (plankton) composition and is enhancing a decrease of the size of copepods (Beaugrand, 2009) that in turn would have a lower concentration of lipids (e.g. Pepin & Head, 2009). Copepods (*Calanus* spp.) are not a significant prey item of the diet of post-smolt salmon (Jacobsen & Hansen, 2001), however, they are the most important constituents of the pelagic ecosystem serving as food for organisms at higher trophic levels. These organisms include various salmon preys, for instance, amphipods, lantern fishes, pearlsides, euphausiids, shrimps or herring (Jacobsen & Hansen, 2001; Haugland *et al.*, 2006), which are decisive for energy –lipid– flux (Jensen *et al.*, 2007; Petursdottir *et al.*, 2008). The effects of climate variation on biochemical ecology are, however, poorly known, although significant variability on the lipid contents are expected through changes in the availability of essential fatty acids by changing physical oceanography (e.g. Litzow *et al.*, 2006). Therefore, our result is consistent with the decision paths described earlier in a sense that conditions in the ocean during autumn are correlated with the sea-age proportion of fish caught later in the rivers. That is, increasing sea surface temperature in September suggests that more fish are following the path $G_2 = 0$ and hence postponing maturation for another year. As a result the relative catch of 2SW fish is higher compared to 1SW fish of the same smolt cohort (Fig. 4). However, we cannot distinguish if $G_1 = 0$ or $G_1 = 1$, i.e., whether growth opportunities before the first developmental switch were not sufficient to exceed the threshold associated with G_1 or ongoing environmental conditions before G_2 were poor. Moreover, note that oceanic conditions in April appeared to be equally important in the model selection procedure, which would serve as an indication of the importance of the secondary switch (G_2).

Several studies have addressed the effects of temperature on multiple traits of Atlantic salmon life history. For instance, it is generally accepted that warmer SST during the first weeks of foraging at sea promote high growth-mediated survival for 1SW fish (e.g. Friedland *et al.*, 2000). However, the literature is strongly contradictory when describing relationships across life-stages and the implication of environmental factors. Studies within (Jonsson *et al.*, 2003) and among Atlantic salmon populations (Hutching & Jones, 1998) have shown that higher growth rate at sea seems linked to an increase in sea age at maturity. Sea age at maturity and growth rate is suggested to be linked with ocean climate such that fish reaching a certain size threshold postpone maturation and become 2SW when the sea is warmer (Jonsson & Jonsson, 2004a). Given this framework, relatively more 2SW than 1SW salmon would then be expected with favourable growth conditions at sea at higher water temperatures. This is a model directly in opposition to the one presented by Mangel & Satterthwaite (2008) and to the results found in this study. It is also in opposition to the more general observations based on theory and data that life history transitions happen later when growth rate decreases (e.g. Day & Rowe, 2002). A number of other studies in Atlantic salmon support our conclusions. For instance, Friedland & Haas (1996) found a positive relationship between growth during late summer and the fraction of post-smolt attaining maturity after one year at sea. Moreover, Salminen (1997) depicted as well a negative relationship between marine growth rate and sea age at first maturity. Furthermore, Jonsson & Jonsson (2004b) showed that the percentage of adults maturing as 1SW and their mean body mass increase from smolts to 1SW fish were positively related to the North Atlantic Oscillation (NAO) from February to April and in May, respectively. These authors suggested that benign conditions at the time of sea entry would be important to define the later size of spawners and would favour less inhibition of

maturation increasing the percent maturing. The SST variability associated with the winter NAO shows marked spatial structure with cold anomalies in part of the post-smolt foraging habitat and warm anomalies along the Norwegian coast at high values of NAO (Hurrell & Dickson, 2004). Therefore, ocean climate effects on Atlantic salmon early and later performance, including the decision to mature, are not unequivocal; rather they seem to be complex and presumably differ at various spatio-temporal scales.

Growth performance of Atlantic salmon during freshwater residence affects smolt age and size that in turn might be related to post-smolt growth and presumably with ultimate effects on size and age at maturity. However, correlation analyses between stage-specific traits are again inconclusive. For instance, on the one hand, it has been shown that smolt size and marine growth could be positively (e.g. Salminen, 1997) or negatively related (e.g. Nieceza & Braña, 1993). On the other hand, pre-smolt growth in freshwater might be negatively linked with growth at sea (e.g. Einum *et al.*, 2002), whereas Friedland *et al.* (2006) provided no evidence for a relationship among growth rates between life stages. Furthermore, among-population studies have shown that the smaller the fish at seaward migration, the higher the subsequent growth at sea (Jonsson & Jonsson, 2007). Notwithstanding, we found an increase of sea age at maturity with increasing values of water flow from May to August during the pre-smolt growth and at the time of deciding to emigrate the following spring (Thorpe *et al.*, 1998) (Fig. 4). Experimental studies have shown lower growth rate and lipid content of parr at higher water flow, suggesting that the energetic costs for foraging in response to increased discharge and water velocity are high enough to reduce performance of Atlantic salmon (Kemp *et al.*, 2006). Moreover, high water flow during summer reflects rainy weather with low air and water temperatures resulting in reduced growth of salmon parr (Forseth *et al.*, 2001). Therefore, elevated runoff seems to promote poor growth in freshwater.

However, the relationship between lower growth rate in the river and delaying maturity at sea is not clear. Concurrent with our findings, Nieceza & Braña (1993) and Salminen (1997) showed that smaller smolts (slower growth in the river) would mature at older (sea) ages. However, it has been reported that salmon growing poorly in freshwater grows faster at sea (e.g. Jonsson & Jonsson, 2007). If this would be the case, and to be coherent with our previous argument of more 2SW at lower sea growth, we would expect more 1SW fish, contrary to what we found. More 2SW would be expected, however, if current poor ocean conditions were outweighing the benefits of fast growth at sea (and slow growth at freshwater). Finally, the influence of river conditions in determining sea age at maturity could be actually of minor importance in determining maturity (Table 3).

Changes in age –and size– at maturity in exploited fish could, however, be an evolutionary consequence of continuous fishing. Selective exploitation can cause detectable evolutionary changes in multiple life traits, but separating phenotypic plasticity from genetically based responses is still complex (Hard *et al.*, 2008). For Atlantic salmon, for instance, Kuparinen *et al.* (2009) have shown a decrease in age at maturity in synchrony with changes in growth trajectories suggesting the effect of a common factor driving the observed changes at the population level including fisheries induced evolution. Furthermore, cessation of high seas fishing activities seemed to be responsible of observed changes in size at maturity of other salmon species (e.g. *Oncorhynchus keta*, Fukuwaka & Morita, 2008). In line with this, the Norwegian drift net fishery was closed in 1989. Jensen *et al.* (1999) showed changes in populations from Norwegian and Russian rivers, however, evolutionary effects for sea age at maturity are less likely due to the fact that this fishery targeted the spawning run, that is, individuals that have already made the decision to mature. Therefore, it seems that environmental

conditions would be overwhelming evolution, though, we can not rule out completely the hypothesis of evolutionary effects of fishing derived from responses to the fishery in the foraging area to the north of the Faroe Islands.

All in all, it seems that growth condition at sea of Atlantic salmon is decreasing resulting in a reduction of size at maturity within the returned individuals (Jonsson & Jonsson, 2004b; Todd *et al.*, 2008). However, it is not that clear whether a decrease in growth rate at sea is related with an increase or decrease in sea age at maturity. Our finding that the proportion of 2SW over the last 15-year period has increased concurs with similar results of various Pacific salmon species attributing the changes in size and age at maturity to a phenotypic response to a reduced growth rate caused by changes in the environmental conditions (see Morita & Fukuwaka, 2007 and references therein). It is therefore likely that sea age at maturity will increase, contrary with what has been recently suggested (Jonsson & Jonsson, 2009), as projected effects of climate change predict a continuous rise of SST, and derived bottom-up alterations in the pelagic ecosystem of the eastern North Atlantic Ocean and adjacent seas (Ito *et al.*, 2010). Moreover, climate models point towards an increase of precipitation and springtime flooding events (Benestad & Haugen, 2007) that would potentially affect growth rate in freshwater.

We can conclude that warming in the foraging habitat of post-smolt Atlantic salmon since the 1990s promotes poor growth opportunities delaying the completion of maturation by not reaching the desired level of stored lipids and therefore increasing the sea age at maturity. Furthermore, increased water discharge at the pre-smolt stage promotes poor growth during freshwater residence, though the (in)direct effects on posterior oceanic growth and later on the sea age at maturity remain unclear. Hence it seems that current changes in developmental opportunities (Thorpe, 2007) are playing a

fundamental role in determining –delaying– the completion of maturation of Atlantic salmon from Norwegian rivers.

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Table 1 Results from analyses of the influence of SST and runoff on the proportion of two-sea-winter relative to one-sea-winter fish (in kg) from the same smolt cohort of Atlantic salmon obtained from the optimal mixed-effects model with River as random grouping factor (59 levels). SST = sea surface temperature (°C), R = runoff (m³ s⁻¹), c.i. = confidence interval, s.d. = standard deviation, n.a. = not applicable.

Fixed effects	Estimate	95% c.i.	<i>t</i> -value	<i>P</i> -value
Intercept	0.4008	0.3615; 0.4401	20.0307	9.18e-73
SST _{September}	0.0024	0.0019; 0.0029	9.1206	5.83e-19
R	0.0612	0.0243; 0.0981	3.2582	1.17e-3
Random effects (s.d.)				
Intercept (σ_a^2)	0.1507	0.1247; 0.1820	n.a.	n.a.
Correlation structure				
ϕ	-0.1248	-0.1974; -0.0508	n.a.	n.a.
Variance function				
δ	0.1877	0.0650; 0.3105	n.a.	n.a.
Residual s.d. (σ^2)	0.1563	0.1368; 0.1785	n.a.	n.a.

Table 2 Comparison of mixed-effects models fitted to the proportion of 2SW Atlantic salmon being produced by 1991–2005 cohorts from 59 Norwegian rivers using different fixed effects. Models were fitted using maximum likelihood estimation (ML) for meaningful comparisons. Note that SST corresponds to the PC1 of the SST analysis in September. SST = sea surface temperature, R = runoff, BIC = Bayesian Information Criterion.

Modelled effects	Model structure	Parameters	BIC	Δ BIC
Oceanic + freshwater	$P_{i,t} = (\beta_0 + a_i) + \beta_1 \text{SST}_{t-n} + \beta_2 \text{R}_{i,t-3} + \varepsilon_{i,t}$	7	-863.59	0
Oceanic	$P_{i,t} = (\beta_0 + a_i) + \beta_1 \text{SST}_{t-n} + \varepsilon_{i,t}$	6	-858.51	5.09
Freshwater	$P_{i,t} = (\beta_0 + a_i) + \beta_1 \text{R}_{i,t-3} + \varepsilon_{i,t}$	6	-792.97	70.63

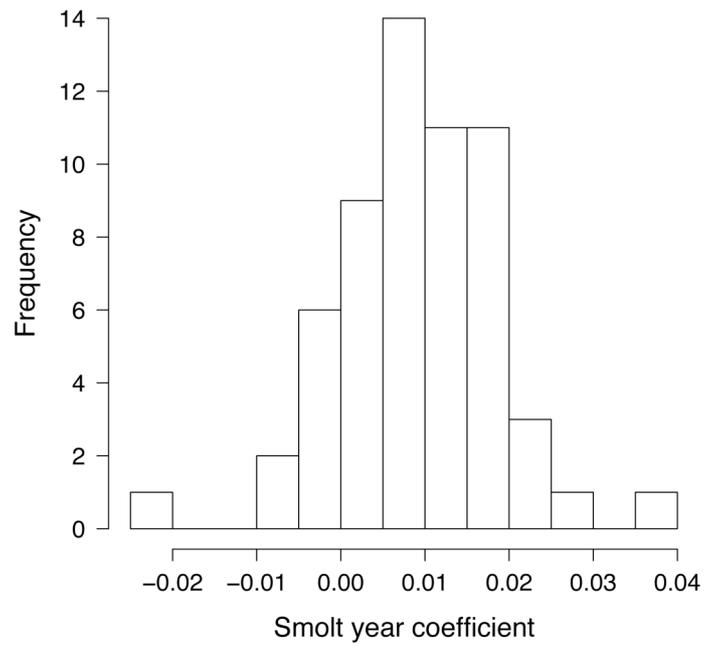


Fig. 1 Histogram of the time trend (i.e. smolt year slope) of the proportion of 2SW Atlantic salmon cohorts in 59 Norwegian rivers during 1991–2005.

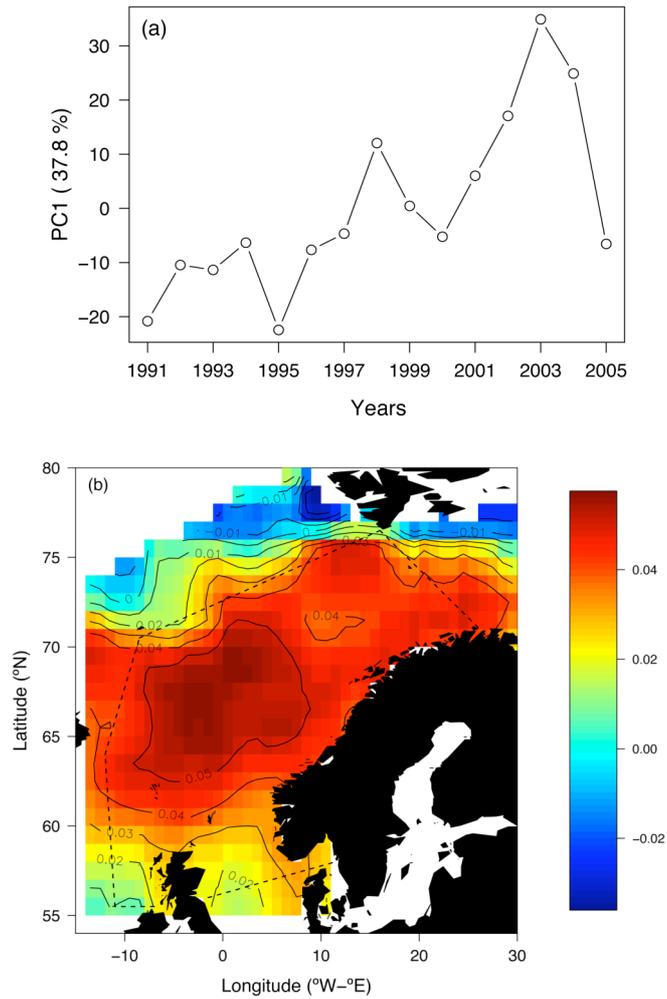


Fig. 2 Long-term changes in SST in the Norwegian Sea. (a) First principal component of SST in September over the period 1991–2005 accounting for 37.8% of the total variance. (b) Spatial mapping of the loadings (correlations) of each grid cell on the first principal component. The dashed line delimits the approximate area of distribution of post-smolt Atlantic salmon according to Holm *et al.* (2004). Note that the Baltic Sea data were excluded from the analysis. Northernmost white areas were affected by sea ice.

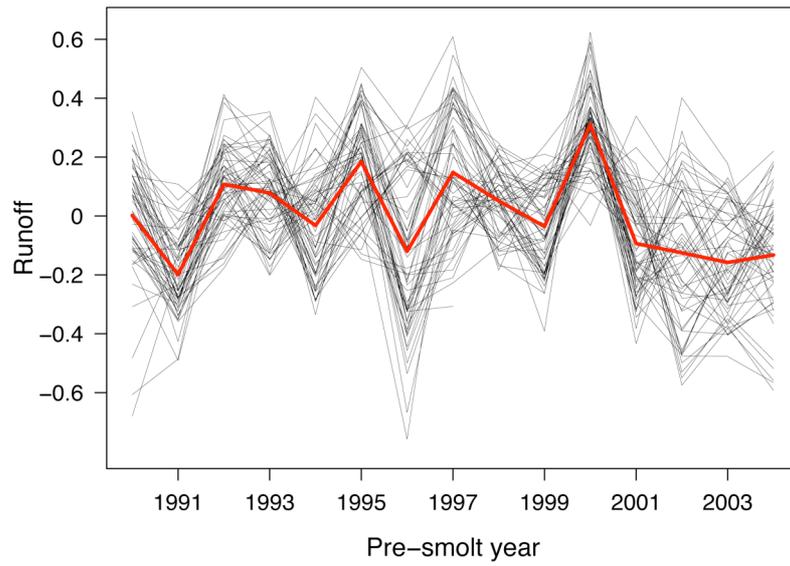


Fig. 3 Mean estimated ln-transformed runoff ($\text{m}^3 \text{s}^{-1}$) from May to August in the year prior to Atlantic salmon smolt transformation during the years 1990–2004. Thin lines represent river-specific centered runoff in each of 59 rivers; thick red line shows the annual mean.

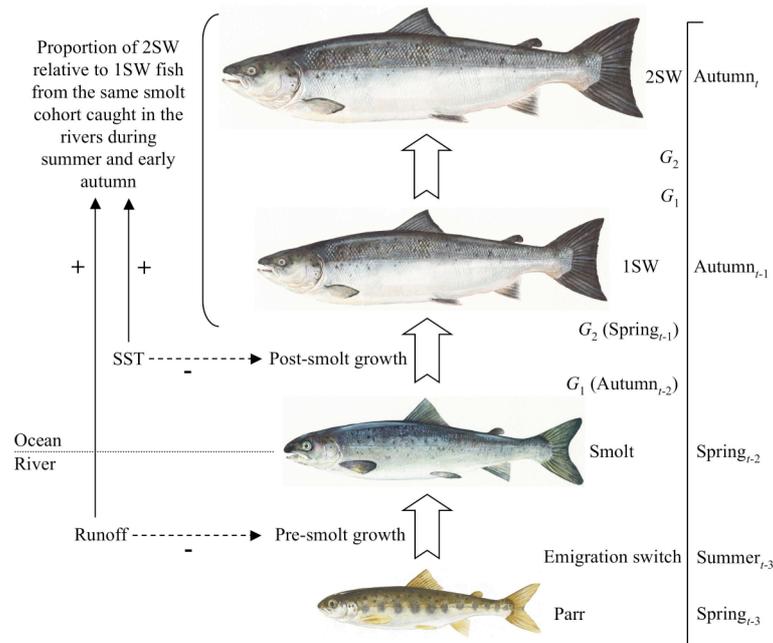


Fig. 4 Schematic representation of the Atlantic salmon life cycle and the relationships reported in this study. Fish mature after one-sea-winter (1SW) or two-sea-winters (2SW) depending on the route determined by the responses to the developmental switches (G_1 and G_2). Black arrows indicate the (positive) relationships modelled in this work, whereas dashed arrows show the hypothetical (negative) effects of sea surface temperature (SST) and runoff on post-smolt and pre-smolt growth, respectively. The modelling framework by Thorpe *et al.* (1998) inspired this sketch. See the main text for further discussion on the potential nature of the relationships involved. Drawings credits: © Atlantic Salmon Federation (www.asf.ca) / J.O. Pennanen.