1 **Basin-scale phenology and effects of climate variability on global timing of**

2 **initial seaward migration of Atlantic salmon (*Salmo salar*)**

3

4 **Running title:** Climate and emigration timing of *Salmo salar*

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70   **Type of Paper:** Primary Research Article

71

72   **Abstract**

73   Migrations between different habitats are key events in the lives of many organisms. Such
74   movements involve annually recurring travel over long distances usually triggered by
75   seasonal changes in the environment. Often, the migration is associated with travel to or from
76   reproduction areas to regions of growth. Young anadromous Atlantic salmon (*Salmo salar*)
77   emigrate from freshwater nursery areas during spring and early summer to feed and grow in
78   the North Atlantic Ocean. The transition from the freshwater ('parr') stage to the migratory
79   stage where they descend streams and enter salt water ('smolt') is characterized by
80   morphological, physiological and behavioural changes where the timing of this parr-smolt
81   transition is cued by photoperiod and water temperature. Environmental conditions in the
82   freshwater habitat control the downstream migration and contribute to within- and among-
83   river variation in migratory timing. Moreover, the timing of the freshwater emigration has
84   likely evolved to meet environmental conditions in the ocean as these affect growth and
85   survival of the post-smolts. Using generalized additive mixed-effects modelling, we analysed
86   spatio-temporal variations in the dates of downstream smolt migration in 67 rivers throughout
87   the North Atlantic during the last five decades and found that migrations were earlier in
88   populations in the east than the west. After accounting for this spatial effect, the initiation of
89   the downstream migration among rivers was positively associated with freshwater
90   temperatures, up to about 10 ℃ and levelling off at higher values, and with sea-surface
91   temperatures. Earlier migration occurred when river discharge levels were low but increasing.
92   On average, the initiation of the smolt seaward migration has occurred 2.5 days earlier per
93   decade throughout the basin of the North Atlantic. This shift in phenology matches changes in
94   air, river, and ocean temperatures, suggesting that Atlantic salmon emigration is responding to
95   the current global climate changes.
96

Introduction

98 Many organisms migrate between different habitats during their life cycle (Dingle, 1996).

99 These movements may occur at different timescales and allow species to (i) take advantage of

100 dietary or reproductive opportunities available in discrete and often distant habitats; and (ii)

101 avoid certain habitats during periods such as winter when conditions may be intolerable.

102 Migrations are usually triggered by seasonal changes in environmental conditions and by

103 internal physiological processes. Habitat shifts may involve annually recurring travel over

104 long distances, such as those undertaken by many species of birds, mammals, reptiles, fishes

105 and insects (Dingle, 1996).

106 In diadromous fishes, life history strategies and migratory movements between fresh

107 water and the ocean constitute key life history events in the life cycle of these species.

108 Atlantic salmon (*Salmo salar*) typically emigrate from freshwater in the spring after having

109 reached a growth-dependent size threshold (Økland *et al*., 1993). Age at emigration is 1–6

110 years and total length 12–25 cm. Once they reach the ocean, the subsequent growth is

111 compensatory and very rapid (Hogan & Friedland, 2010). After 1–4 years at sea they return

112 with high precision to their natal river to breed, although a small proportion strays to other

113 rivers (Jonsson *et al*., 2003).

114 Prior to the seaward migration Atlantic salmon undergo a major transformation often

115 called smolting, which comprises morphological, physiological and behavioural changes. This

116 allows individuals to change from the territorial and relatively sedentary juvenile ('parr')

117 stage to the migratory ('smolt') stage, during which they move downstream and are able to

118 enter sea water (Hoar, 1976). The parr-smolt transformation is typically associated with

119 increasing temperatures in spring, and is regulated by photoperiod and water temperature

120 through effects on the neuroendocrine system (McCormick *et al*., 1998). Controlled

121 laboratory studies indicate that photoperiod is the dominant cue of the parr-smolt

122 transformation, with local temperatures playing a subordinate role (McCormick et al., 2002).

123 Once the smolt transformation has been completed there is a short period of time during

124 which the fish are physiologically prepared for seawater entry. Smolt that do not complete

125 their seaward migration within this period desmolt, but may smolt again in the subsequent

126 spring (McCormick et al., 2009). In general, smolt migration occurs in spring or early

127 summer (Thorstad et al., 2012), and the timing of the initiation of the downstream migration

128 differs among rivers.

129   A number of different environmental factors may trigger the downstream migration.

130 These factors can be river-specific such as water temperature, flow and turbidity (Jonsson &

131 Ruud-Hansen, 1985; McCormick et al., 1998), or related to light conditions in the river

132 (Hansen & Jonsson, 1985; Hvidsten et al., 1995). Also the presence of other migrants and

133 predators may affect out-migration (McCormick et al., 1998).

134   Many factors affect post-smolt survival, but the timing of the smolt migration is an

135 important predictor of survival to adulthood (Antonsson et al., 2010). In addition to proximal

136 conditions like river temperature, other mechanisms can also affect survival, including

137 predators, parasites and pathogens, feeding opportunities, and temperatures in the ocean

138 (McCormick et al., 1998; McCormick et al., 2009). Each of these factors has the potential to

139 exert selective pressure on the migratory timing, with reduced survival associated with both

140 too early (Kennedy & Crozier, 2010) and delayed migrations (Castro-Santos & Haro, 2003;

141 McCormick et al., 2009). Thus, there exists a critical period of downstream migration

142 ('environmental smolt-window') in which fitness is maximized by arrival at the marine

143 environment when conditions are optimal for both survival and growth (McCormick et al.,

144 1998). These are the necessary conditions for stabilizing selection, leading to genetic and

145 phenotypic differentiation among populations of several salmonid species (Stewart et al.,

146 2006; Spence & Hall, 2010).

147   In fisheries biology, the critical period concept (Cushing, 1990) postulates that survival

148   and recruitment are maximized when there is a temporal match between a predator's

149   phenology and that of its prey. Climate change might, however, alter the patterns of food

150   availability leading to a mismatch if the resource base does not react in a similar way (Durant

151   *et al*., 2007). Thus, there is evidence that the timing of seasonally recurring biological events

152   (i.e. phenology) is shifting as a result of global increases in temperature (e.g. Parmesan,

153   2007). However, shifts in phenology appear to vary across taxa (Jonzén *et al*., 2006; Menzel

154   *et al*., 2006; Parmesan, 2007; Kauserud *et al*., 2012), and at different trophic levels (e.g.

155   Edwards & Richardson, 2004), and have important effects on population dynamics and

156   systems ecology (Miller-Rushing *et al*., 2010); however, the fitness consequences may vary

157   widely (McNamara *et al*., 2011).

158   Compared with terrestrial taxa, knowledge of the relationships between the timing of

159   environmental changes and seasonal activities in fishes is sparse (Parmesan, 2007; but see

160   Anderson *et al*., 2013). Furthermore, despite being a group with numerous species, there is

161   little knowledge of the likely impacts of climate change on the dynamics of migratory fishes

162   (Robinson *et al*., 2009). In anadromous salmonids some long-term studies have provided

163   evidence that migration from freshwater to saltwater is occurring at earlier dates during a

164   period of environmental warming for both Atlantic (Kennedy & Crozier, 2010) and Pacific

165   (Kovach *et al*., 2013) species. In any case, productivity of Atlantic salmon has been declining

166   throughout its distribution (Jonsson & Jonsson, 2004), raising major conservation and

167   management concerns (Dempson *et al*., 2004). This reduction in fish abundance may be due,

168   in part, to an alteration in timing of life history decisions affecting later survival (Hindar *et al*.,

169   2011). Thus, there is a need to better understand the factors related to the initiation of global

170   seaward migration pattern of Atlantic salmon.

171   In this paper we analyze large-scale variations in the timing of migration in Atlantic

172   salmon at two migratory audit points (dates of 25 and 50% total smolt emigration) from fresh

173   to salt water. We examine data sampled during 50 years from 1961 to 2010 from 67 North

174   Atlantic rivers. The objective was to study the relationship between the smolt descent and

175   environmental factors in both fresh and salt water while accounting for geographic variability.

176   Further, we tested if there has been a global phenological shift and whether this possible shift

177   can be linked to changes in global and local environmental conditions.

178

179   **Materials and Methods**

180   *Study area and smolt sampling*

181   Atlantic salmon are naturally distributed throughout the basin of the North Atlantic Ocean. In

182   the western part of its distribution, they occur from Ungava Bay, Québec, Canada in the north

183   to the Connecticut River, USA, in the south. In the eastern part Atlantic salmon are found

184   from Petchorskaya and the Ural mountains in Russia in the Northeast, along the coast of the

185   European continent south to the River Miño in Spain in addition to Iceland and the British

186   Isles (Jonsson & Jonsson, 2011). Data on timing of smolt downstream migration were

187   obtained from 70 sites on 67 rivers covering most of this east-west and north-south gradient

188   for the period 1961 to 2010 (Fig. 1a, Table 1). Some sites were situated close to the river

189   mouth, others were in tributaries either close to the confluence with the main river or in the

190   upper reaches, and others were located in the central part of the main stem of a river. Thus

191   most sites were situated between 1.2 and 34.8 km upstream of the river mouth

192   (Supplementary Material and Methods). Downstream migrating smolts were monitored by

193   various methods. In most cases only a fraction of the river width was screened for smolts.

194   However, it is assumed that the sampling schemes provide representative observations of the

195   daily migration pattern and timing. Smolt trapping facilities were typically placed at sites

196   where they could be operated across as broad a spectrum of river discharges as possible.

197   However, such traps may have reduced efficiency during flood events. In some rivers, Wolf

198   traps (Wolf, 1951) spanned the whole width of the river. Most Wolf traps are operated

199   continuously and independent of the discharge. However, others are located on weirs and are

200   subjected to operational constraints related to flows. Video cameras have also been used in

201   some rivers. Cameras were anchored to the riverbed perpendicular to the running water and

202   enabled a sample of migrating smolts to be recorded and subsequently counted. The number

203   of cameras used in each transect depended on river width and water turbidity.

204   Descending smolts were usually monitored throughout the whole migration period. This

205   extended from March to June in southern rivers and from June to August in northern systems

206   (Table S1). The initiation of downstream migration for a given site and year was defined as

207   the day of the year when 25% of the total smolt run had been enumerated (referred to as the

208   onset of the smolt emigration), and the median emigration day was defined as the day of the

209   year when 50% of the total smolt emigration had been counted. These quartiles were chosen

210   because they are standard audit points of the smolt run in Atlantic salmon literature

211   (Antonsson & Gudjonsson, 2002), and describe well the temporal migratory dynamics of each

212   smolt cohort (Kennedy & Crozier, 2010).

213

214   *Environmental data*

215   *River conditions*. To test for association between time of emigration and relevant

216   environmental conditions in freshwater we estimated the mean temperature ($\bar{T}$ in ºC) and the

217   mean discharge ($\bar{Q}$ in $m^3\ s^{-1}$) for the 10-day period preceding the 25% and 50% smolt

218   descent dates. Further we estimated the relative change in discharge as the discharge-day

219   relationship (slope, ΔQ) for that period. Such levels or changes in environmental conditions

220   may act as triggers initiating the downstream migration. Discharge in each site was highly

221 skewed thus it was ln-transformed before analysis. Temperature and discharge were mostly

222 recorded using data loggers at the smolt counting station, or as close to this as possible

223 (Supplementary Material and Methods).

224

225 *Sea surface temperature*. Optimum Interpolation sea surface temperature

226 (NOAA_OI_SSTV2) data available at weekly 1º latitude × 1º longitude grid resolution from a

227 combination of satellite and *in situ* measurements (Reynolds *et al*., 2002) were obtained from

228 the NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/) for the period

229 1982 to 2010 (Fig. 1a-c). To evaluate the potential association between downstream migration

230 dates and sea surface temperature (SST in ºC) at sea entry we used the average SST for the 7-

231 day period preceding the date of 25% and 50% descent for those cells whose centers were

232 located nearest to the ocean entry point of a given river. In eleven rivers where smolt

233 sampling started before the availability of the satellite data set, SST was obtained from

234 different sources (Supplementary Material and Methods). Sampling sites were located at

235 various distances from the river mouth. The time (25 and 50% dates) for smolts to reach the

236 ocean was adjusted for this variation using the distance from the sampling station to the river

237 mouth and an average migration speed of about 32 km d^{-1} obtained from measurements

238 recorded in various rivers (Table S2).

239

240 *Chlorophyll* a. Phytoplankton concentration is important for defining suitable pelagic habitats

241 and might be a surrogate for oceanic feeding conditions (e.g. Bi *et al*., 2007). To test if timing

242 of sea entry is adjusted to a period of sufficient primary production, we compiled data on

243 satellite-derived chlorophyll *a* concentration (8-day composites on surface concentration,

244 Chla, in mg m^{-3}) from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) at 1º latitude ×

245 1º longitude grid resolution for the period 1998 to 2010 (Fig. 1d-f). For the same SST coastal

246   cells we used the ln-transformed (to make the distribution more symmetrical) concentration of

247   chlorophyll *a* from the 8-day composite previous to the 25 and 50% downstream dates

248   (Supplementary Material and Methods).

249

250   *Air temperature*. Water temperature was for most rivers obtained daily during the smolt

251   migration period and not all year round. Moreover, many rivers were sampled during a few

252   years only; accordingly, the length of the water temperature time series was shorter than ten

253   years in many cases. This makes it difficult to reliably estimate global trends in freshwater

254   conditions. Thus, air temperature, which correlates with river temperature (Fig. S14) was used

255   as a surrogate to generate a global description of the thermal environment faced by each

256   sampled river. Therefore, we collected data on daily mean air temperatures (Table S3) using

257   the   'WeatherData'   function

258   (http://reference.wolfram.com/mathematica/ref/WeatherData.html)   in   Mathematica   8.04

259   (Wolfram Research, Inc., 2010) (Supplementary Material and Methods).

260

261   *Statistical analyses*

262   Information from 70 locations was used in the analyses; each site was sampled over multiple

263   but not necessarily consecutive years implying repeated longitudinal measures (Table 1 and

264   Table S1). Data were analysed by means of generalized additive mixed effects models

265   (GAMM; Wood, 2006) that allow for non-linearity and the inclusion of both fixed and

266   random effects such as in the following model:

267     $$\text{DoY25}_{t,i} = \alpha + f_1\left(\overline{\text{T}}_{t,i}\right) + f_2\left(\text{SST}_{t,i}\right) + f_3\left(\text{Y}_{t,i}\right) + g\left(lo_i, la_i\right) + a_i + b_i + \varepsilon_{t,i} \tag{1}$$

268   where DoY25 is the day of the year when 25% of the smolt have descended (i.e. the onset of

269   seaward migration) in year *t* at site *i*. α is an intercept, and the f_n's and *g* are one- and two-

270   dimensional   nonparametric   smoothing   functions   describing   the   effect   of $\overline{\text{T}}$ (river

271   temperature), SST (sea surface temperature), Y (year), and site location at longitude *lo* and

272   latitude *la*. We assumed that including a function of longitude and latitude would act as a

273   'catch-all' proxy for factors that vary spatially such as photoperiod and seasonal freshets. The

274   smoothing functions were fit by penalized cubic regression splines and a thin plate regression

275   spline with 3 and 15 knots for the one- and two-dimensional functions, respectively (Wood,

276   2006). If any of the nonparametric relationships are essentially linear, those covariates can be

277   modelled as parametric terms within the GAMM formulation. For instance, the relationship

278   with SST is linear (see below), thus that term in equation 1 becomes $\beta_1 \times \mathrm{SST}_{t,i}$ where β_1 is a

279   coefficient that describes the change in the date of emigration for a unit change in SST. a_i is a

280   random intercept allowing for variation between sites, and b_i is a random slope allowing, for

281   instance, the relationship with SST to differ by site. Random effects are assumed to be

282   normally distributed with mean 0 and variances σ_a^2 and σ_b^2. The residuals $\varepsilon_{t,i}$ are a normally

283   distributed random error with mean 0 representing the within-site variation. Given the

284   sequential nature of the data a residual correlation structure was added to the model. An

285   autoregressive correlation of order 1 is suitable for regular spaced data. Because our data were

286   commonly irregularly spaced in time, we tested if including a linear spatial correlation

287   structure (Pinheiro & Bates, 2000), that can accommodate the imbalance in time, improved

288   the model fitting. In addition, the variance in residual dates (σ^2) was further modelled as a

289   function of possible covariates included in equation 1, for instance:

290      $$\mathrm{var}\left(\varepsilon_{t,i}\right) = \sigma^2 \exp\left(2\delta \overline{\mathrm{T}}_{t,i}\right) \qquad\qquad (2)$$

291   where δ is a parameter to be estimated that describes the estimated change in variance with $\overline{\mathrm{T}}$.

292   This model of the residual variance was compared with other variance structures through

293   selection criteria.

294   The difference between river temperature ($\overline{T}$) and sea surface temperature (SST) can be

295   related to the onset of migration (Kennedy & Crozier, 2010). Therefore we explored this

296   potential effect running a separate model that included the thermal difference (T_{Dif}) between

297   both environments as a covariate. Water flow records were unavailable for numerous site-year

298   combinations (Table 1), thus substantially reducing the migration information. Therefore,

299   discharge was not used in equation 1. It was, however, included in a separate model that

300   contained only those sites with sufficient data. The same happened with chlorophyll *a* that

301   was available only from 1998 to 2010.

302   For any equation, model selection was performed iteratively. First, with all fixed effects

303   included in the model, appropriate random effects and residual correlation structure were

304   selected using the Bayesian Information Criterion (BIC) that puts a heavier penalty on models

305   with more parameters. Model parameters were estimated by means of restricted maximum

306   likelihood (REML). Second, the variance models were selected. Third, the optimal fixed

307   effects were determined by means of maximum likelihood (ML) parameter estimation.

308   Finally, with the optimal fixed structure in place the random effects were reassessed and

309   model parameters presented were estimated by REML (Zuur *et al.*, 2009). The same

310   procedure was used to model the median of downstream migration (i.e. DoY50).

311   For each river, air and sea surface temperature time series, individually average warming

312   rates and changes in the timing of seasonal warming were computed (Supplementary Material

313   and Methods).

314   All analyses and treatment of data were performed with R 2.15.0 language (R

315   Development Core Team, 2012) and using the "mgcv 1.7-13" (Wood, 2006) and "nlme 3.1-

316   103" (Pinheiro & Bates, 2000) packages.

317

318

319 **Results**

320 *Summary of smolt migration patterns*

321 Downstream migration timing varied among and within sites. The earliest onset of emigration

322 occurred in the Tea River (Spain) where 25% descent was recorded on the 20th March in

323 2000, whereas the latest onset date was recorded on the 3rd August 1995 in the Vesturdalsa

324 River (northern Iceland) (Table S1). Collectively, the observations of time of 25 and 50%

325 descent (river and year combinations) showed that *c.* 75% were within a 30-day period

326 between the beginning of May (~day 120s) and the beginning of June (~day 150s) (Fig. 2a).

327 In addition, the difference between the 50 and 25% emigration date occurred within a narrow

328 time window with 75% of the observations (river and year combinations) extending over a

329 period of less than 6 days, though a maximum difference of 27 days was recorded in

330 Vesturdalsa River in 1998. The variability of this difference was not related to latitude (Fig.

331 2b). However, on average, time between 50 and 25% of emigration dates appeared to be

332 shorter when the onset of emigration occurred later (Fig. 2c).

333

334 *Onset of emigration*

335 Model selection favoured a random intercept indicating high variability in emigration dates

336 from site to site, and also a random slope allowing the relationship with SST to differ by site

337 (Table S4). Within-site residual correlation structures did not improve the model fitting (Table

338 S4). The optimal model of the onset of emigration timing revealed a strong spatial trend

339 showing a clear west-east and south-north gradient (Fig. 3a). The average onset of

340 downstream migration was about the 18th May (day 138) (Table 2) at 45ºN in the western

341 Atlantic, whereas in the eastern Atlantic this date occurred approximately at 63ºN (isopleth

342 zero in Fig. 3a). This resulted in the mean onset of emigration date in Northern Norway,

343 Finland and Russia occurring about 90 days later than in Spain, at the southern limit of the

species distribution in Europe (Fig. 3a). After accounting for the spatial trend, river

temperature ($\bar{T}$) had a slight non-linear effect on the among-river onset of emigration

reaching a plateau at about 10 ℃ (Fig. 3b). In addition, there was evidence for changes in the

spread of the onset of emigration related to $\bar{T}$ (Table 2 and Table S5). The estimated

exponential variance parameter corresponds to a 14.9% increase in variance with a 2 ℃

warming in river temperature.

When the smolt migrated later the SST at the oceanic entry point was warmer (Fig. 3c).

This effect resulted in an estimated average (± s.e.) increase of 2.1 ± 0.3 days in onset of

emigration per 1 ℃ increase in SST. Furthermore, the model also revealed a slight non-linear

shift towards earlier onset of emigration timing during the last fifty years (Fig. 3d). Modelling

the long-term trend as a parametric component resulted in an earlier downstream migration of,

on average, 2.5 ± 0.3 days per decade, which means that, over the entire 50 years studied, the

data showed an earlier onset out-migration of 12.7 ± 1.4 days.

There were variability in mean emigration onset dates from site to site, and also the

relationship with SST differed by site (Table 2). Furthermore, there was a positive correlation

between the random effects indicating that sites that had larger intercepts (i.e. later

emigration) also had larger slopes (i.e. a stronger relationship with SST) (Fig. 4). Moreover,

this pattern slightly varied with geography with larger intercepts and slopes occurring at

higher latitudes.

Finally, residuals of the optimal model did not show any apparent heterogeneity or major

departures from normality (Fig. S16-S17). The estimated random effects were also reasonably

normal (Fig. S18). Moreover, there was no spatial pattern in residuals; there was no clear

clustering of positive (or negative) averaged residuals per sampling site (Fig. S19).

Further examination of the combined effects of temperature in both fresh- and saltwater

habitats showed a nonlinear relationship between the among-river onset of migration and the

369   thermal difference between both environments (Table S7). This mostly revealed that when

370   freshwater temperature was 3 ℃ warmer than the ocean SST the onset of smolt emigration

371   occurred earlier (Fig. 5).

372   Regarding water flow, the onset of emigration occurred later at higher average discharge

373   ($\bar{Q}$) (Fig. 6a). This relationship implied that a one percent increase in $\bar{Q}$ would result in a

374   0.011 ± 0.003 day delay in the average onset date of emigration. Furthermore, the model also

375   revealed a nonlinear relation between the onset date and the change in water flow (ΔQ), with

376   earlier emigration when the rate of change in discharge tended to increase (Fig. 6b).

377   Chlorophyll *a* was not correlated with the onset of emigration. Running a model from

378   1998 to 2010 ($n = 443$) that included surface concentrations of chlorophyll *a* (Fig. 1d) at the

379   oceanic entry point as a new covariate, revealed no association (P-value > 0.1).

380   The onset and median emigration dates were correlated ($r^2 = 0.97$), thus the modelling

381   yielded similar results (Table S9 and Fig. S22).

382

383   *Trends and seasonal shifts in air, river and sea surface temperature*

384   Overall, the analysis of temperature trends in rivers with at least 10 years of data revealed an

385   increase in water temperature at an average rate ($\pm$ s.e.) of 0.36 ± 0.06 ℃ per decade (Fig. 7a).

386   This warming corresponded well with air temperature records at stations close to the smolt

387   sampling locations, for which the mean increase was 0.25 ± 0.03 ℃ per decade (Fig. 7b). The

388   SST at the ocean entry points warmed at a mean rate of 0.33 ± 0.02 ℃ per decade (Fig. 7c).

389   Furthermore, it was observed that seasonal warming (air temperature stations and the coastal

390   cells) generally occurred earlier in the year. These shifts revealed an advance of seasonal

391   warming in air temperatures at an average rate of 2.70 ± 0.34 days per decade (Fig. 7d), and

392   an earlier arrival of seasonal warming in SST at an average rate of 5.02 ± 0.49 days per

393   decade (Fig. 7e). Finally, the among-river date of onset of emigration was related to the date

394   of seasonal warming in air temperatures (Fig. 7f).

395

396   **Discussion**

397   In this work, we examined the geographical pattern of the initial timing of the downstream

398   migration of young anadromous Atlantic salmon (smolts) throughout its natural distribution

399   and found that timing of downstream migration varies strongly among rivers. This variation is

400   probably a response to selection driven by prevailing regional conditions (Thorstad *et al*.

401   2011), and thus we could expect large-scale patterns that reflected these spatial environmental

402   differences. Results showed that –in addition to the latitudinal cline with southern populations

403   migrating earlier than northern ones (Hvidsten *et al*., 1998)– the timing of out-migration

404   differed strongly between the East and West Atlantic, with western populations migrating to

405   sea at later dates than eastern populations at corresponding latitudes.

406   What may be the selective agent leading to this geographic pattern in downstream

407   migration? Geographical variation in timing is most probably driven by the spatial pattern of

408   average SST (compare isotherms in Fig. 1a with isopleths in Fig. 3a). In particular there is

409   large variation in SST between the East and West part of the Atlantic, which is the result of

410   both the organization of atmospheric circulation forcing and oceanic current systems (Deser *et*

411   *al*., 2010; Fig. S23). The latitudinal variation in SST is also well known. However, even if

412   SST is the selective force leading to differences in phenology, salmon smolts cannot use it as

413   a cue for initiating the downstream migration. A cue that might be associated with SST may

414   be used. Consequently, the latitudinal patterns in phenology are most probably cued by the

415   geographic variation in photoperiod (Fig. S24). Photoperiodism is widespread across multiple

416   taxa (Bradshaw & Holzapfel, 2007), and Atlantic salmon are shown to assess and use day

417   length to initiate the physiological changes associated with smolting. However, the response

418   to photoperiod may be adjusted by variation in local environmental factors such as river

419   temperatures (McCormick *et al*., 2002). Long-term selection may then lead to changes in how

420   salmon populations respond to these cues.

421   After accounting for this geographical variation, among-river migratory patterns of

422   Atlantic salmon were related to freshwater conditions. The onset of the smolt emigration was

423   positively associated with river temperatures up to about 10 ºC, levelling off or potentially

424   decreasing at higher temperatures. This result indicates that the onset of the freshwater

425   emigration does not occur beyond a given day of the year (or temperature) despite continued

426   temperature increase. In rivers and years with the latest onset dates the temperature at smolt

427   descent ranged from 10 to 17 ºC, values that are close to the seasonal peak temperature for

428   those rivers. This agrees well with previous knowledge about the secondary role of river

429   temperature in impairment of the fishes tolerance of saltwater (McCormick *et al*., 2002;

430   2009). In addition, emigration dates were more heterogeneous in rivers and years

431   experiencing elevated temperatures, though this effect might be a result of scarce data at high

432   temperatures.

433   Water temperature has been already identified as a primary environmental factor cuing

434   downstream migration (Thorstad *et al*., 2012). Some studies suggest that the initiation of the

435   smolt run require passing a certain temperature threshold (e.g. 10 ºC) for wild (Antonsson &

436   Gudjonsson, 2002) and hatchery reared smolt (Jutila *et al*., 2005). However, when pooling

437   rivers across the distribution of Atlantic salmon there was no clearly defined lower

438   temperature limit associated with the commencement of the smolt migration, and the lower

439   thermal threshold appears river-specific (McCormick *et al*., 2002). At high water

440   temperatures smolt characters (e.g. salinity tolerance) are lost sooner and quicker

441   (McCormick *et al*. 2009). Consequently, it is important for the smolts to emigrate from

442 freshwater well before reaching very high water temperatures. Our results suggest that also

443 the upper thermal limit is river-specific.

444   Downstream migration timing has frequently been related to water flow (McCormick *et*

445 *al.*, 1998) showing that migration of Atlantic salmon smolts can be initiated by increased

446 water discharge during spring freshets (Hvidsten *et al.*, 1995) albeit this correlation may be

447 highly variable (Jonsson & Jonsson, 2009). We found that earlier migration among rivers

448 occurred at lower average water flow and at a higher positive change (increase) in flow. This

449 might indicate that smaller rivers (low average flow) with an increase in the rate of change in

450 discharge are more unstable in their hydrology and thus emptying the smolts out earlier.

451 Alternatively, because rivers with larger discharge are usually longer some of the observed

452 relationship could be due to longer migration distances to saltwater from multiple headwater

453 streams.

454   Among-river variation in downstream migration was associated with oceanic thermal

455 conditions at the sea entry point with later migrants finding higher sea temperatures. This

456 relationship also varied from site to site, with sites that had later emigration also had a

457 stronger relationship with SST. Several studies have reported the thermal regime experienced

458 by smolts during the initial marine migration. For instance, Antonsson & Gudjonsson (2002)

459 showed that smolts leaving northern Icelandic rivers would enter seawater at 5 ℃, Hvidsten *et*

460 *al.* (1998) reported a consistent SST of *c*. 8 ℃ for smolts emigrating from five rivers in

461 Norway, and Kennedy & Crozier (2010) showed that smolt in Northern Ireland would

462 experience a thermal regime ranging from 7 to 12 ℃. Our analysis shows that among-river

463 variation in smolt emigration was associated with a range of SST of about 0 to 15 ℃, and this

464 further suggests that populations would be adapted to emigrate from the rivers and enter salt

465 water at a particular and prevailing regional sea temperature. The specific sea temperature at

466 which each population reaches the ocean environment should be consequently connected with

467 a specific value of photoperiod (Fig S24c), the main cue used by the salmon to initiate

468 smolting.

469   Year-to-year variability in the timing of the smolt run within rivers has often been related

470 to variation in water temperature, resulting in delayed migration in cooler springs (Jonsson &

471 Ruud-Hansen, 1985; Jensen *et al*., 2012). We found that the timing of migration for the whole

472 set of rivers and years was related to the thermal difference between fresh and salt water.

473 When temperature in fresh water was ~3 ºC warmer than in the sea outside the river mouth,

474 the migration occurred earlier. Earlier onset of migration at an increased temperature contrast

475 between fresh and saltwater was previously shown for the River Bush, Northern Ireland

476 (Kennedy & Crozier, 2010). Therefore, we conclude that smolts migrate earlier in warm river

477 years, and that river temperature influences the timing of the smolt run, but selection has

478 regulated the fish's ability to use photoperiod as a priming mechanism for the migration. This

479 is consistent with laboratory studies that have shown clear physiological linkages between the

480 photoperiod and the physiological preparation for smolting with local temperature serving a

481 subordinate role (McCormick *et al*., 2002). The onset of migration, although accompanied

482 and mediated by physiological changes, is a behavioural response. As such, priming

483 mechanisms prepare animals for migration, and tend to be synchronized with long-term

484 average conditions that are associated with selective drivers of migration. Releasing

485 mechanisms are often de-coupled from these priming mechanisms, however, and allow

486 animals to fine-tune behavioural responses to maximize their ability to take advantage of

487 variable conditions (Dingle, 1996). Our data are consistent with this interpretation: salmon in

488 each site would use specific day length to initiate smolting and entry the saltwater at a

489 particular sea surface temperature. Photoperiod as a priming mechanism would tend to

490 stabilize dates of migratory onset, but local temperatures and flow would be responsible for

491 annual variation.

492   Time of ocean entry of Atlantic salmon influences post-smolt survival (Hansen &

493   Jonsson, 1989; Antonsson *et al*., 2010) as has also been shown for several Pacific salmon

494   species (Scheuerell *et al*., 2009). Therefore, natural selection would favour migration at a time

495   when conditions are favourable (Hansen & Jonsson, 1989; Hansen & Jonsson, 1991). During

496   this time window the ionoregulatory ability of the fish may be optimal, with smolts that

497   migrate too early or too late experiencing physiological stress (Handeland *et al*., 1998) and

498   increased mortality (Antonsson *et al*., 2010). Increased mortality might be related to predation

499   and its interaction with the physiological status of the smolts (Handeland *et al*., 1996), to food

500   availability (Hvidsten *et al*., 2009), or to other stressors (Thorstad *et al*., 2012). Matching the

501   sea temperature that is optimal for iono-regulation and antipredator behaviour, and the link

502   with resource peaks that favour rapid growth is crucial for survival. For instance, Jutila *et al*.

503   (2005) showed that for hatchery reared salmon smolt survival in the northern Baltic Sea was

504   related to SST in June during the smolt emigration, and this relationship followed a dome-

505   shaped pattern with optimal survival at 9 to 12 ℃. Furthermore, warmer sea temperatures at

506   the time of ocean entry increase subsequent catches of salmon that have spent one winter at

507   sea (Otero *et al*., 2011).

508   Various factors, including food availability affect marine survival (Beaugrand & Reid,

509   2012). We therefore used data-rich satellite information on chlorophyll *a* as a proxy for

510   productivity. We found no support for a positive association between migration timing and

511   chlorophyll *a* concentration at sea entry, and chlorophyll *a* concentration did not track SST or

512   was connected with photoperiod. This suggests that smolt emigration is probably not adjusted

513   to chlorophyll peaks, and that phytoplankton abundance is a poor indicator for early post-

514   smolt feeding conditions. Successful initial feeding might be better represented by the

515   abundance of fish larvae, large crustaceans, and nekton (Hvidsten *et al*., 2009; Renkawitz &

516   Sheehan, 2011) and various other prey groups not available at the scale of this study.

517 Information on these prey types would probably allow evaluation of the temporal connection

518 of marine resources with migratory cues. Nevertheless, successful feeding for early post-

519 smolts is crucial to enhance growth and avoid predators (Rikardsen & Dempson, 2011). In

520 addition, a "correct" migration timing should ensure that post-smolts arrive at distant water

521 feeding grounds during periods of high prey abundance. Distance from the river to the feeding

522 area in the North Atlantic increases with decreasing latitude notably for the south European

523 populations and it is important to be present in the north at the start of the growth season

524 (Friedland *et al*., 2013). Moreover, the importance of a precise timing at ocean entry is further

525 emphasised by the fact that smolts entering seawater outside the narrow migration window

526 stray more to other rivers when returning to spawn (Hansen & Jonsson, 1991).

527 We found a shift towards earlier onset of downstream migration for the Atlantic salmon

528 smolts during the last five decades. For diadromous fishes, habitat shifts are key life history

529 events subject to environmental variation. The downstream migration of species seems to be

530 population-specific (Crozier *et al*., 2008; Jensen *et al*., 2012), but often with a trend towards

531 earlier timing in recent years as noted for Atlantic salmon (Kennedy & Crozier, 2010), and a

532 number of Pacific salmon species (Kovach *et al*., 2013). Nevertheless, our combined dataset

533 estimated an overall out-migration advancement across the North Atlantic of 2.5 days per

534 decade in the initial time of migration. This value parallels current mean estimates of global

535 shifts of phenological responses of 2.8 days per decade in spring across the northern

536 hemisphere for multiple taxonomic groups (Parmesan, 2007). Our estimate is, however,

537 slightly faster than the 1.5 days shift per decade observed for a number of Pacific salmon

538 species in an Alaskan river (Kovach *et al*., 2013). It is generally hypothesized that earlier

539 phenology might be associated with the impacts of current climatic changes, and especially

540 related to warming. However, different organisms respond differently, even when

541 experiencing similar climatic trends (Parmesan, 2007). Further, the patterns of climatic

542   changes are highly heterogeneous across Earth, thus very different responses are expected

543   among species. However, despite the differences in sensitivity to temperature, organisms

544   should maintain their thermal niches by tracking temperature patterns (Cleland *et al*., 2012).

545   Recent global analyses show that, despite spatial and seasonal heterogeneity, oceanic and

546   terrestrial ecosystems (Burrows *et al*., 2011) and coastal regions (Lima & Wethey, 2012) have

547   experienced significant increases in temperature since the middle of the last century. In

548   addition, seasonal shifts in temperature towards earlier spring arrival have been identified.

549   However, Burrows *et al*. (2011) concluded that despite land temperatures warming three

550   times faster than the ocean, the seasonal shifts were generally greater in the sea than on land.

551   At the scale of our analysis, we found similar trends. First, we observed comparable average

552   warming rates of freshwater, air, and sea surface temperatures at the coastal entry points.

553   Second, we also observed earlier seasonal warming of air and sea surface temperatures, and

554   an association between the onset of emigration and the timing of seasonal warming in air

555   temperature. Increasing water temperature results in earlier migration (Jonsson & Ruud-

556   Hansen, 1985). This effect has been described also for other salmonids such as brown trout

557   (*Salmo trutta*) (Jonsson & Jonsson, 2011), and Arctic charr (*Salvelinus alpinus*) (Jensen *et al*.,

558   2012). Thus, it is plausible that global downstream smolt migrations have advanced due to

559   increased river temperatures as changes in climate (Burrows *et al*., 2011), together with

560   hydrological changes, are driving the current river temperature trends (van Vliet *et al*., 2011),

561   which ultimately might have multiple implications for salmonid resources (Isaak *et al*., 2012).

562   Thus, global warming could lead to a greater disconnect between cues for migration

563   (photoperiod that is insensitive to climatic changes and water temperature) and the

564   environmental conditions in the receiving marine environment with potential implications for

565   fitness and productivity (Piou & Prévost, 2013). This effect might point to further long-term

566   stock depression because it would no longer be possible to optimize survival if the cues are

567   disconnected from the environment. This mis-timing would have a survival cost; however,

568   population dynamics could still be quite stable due to compensatory dynamics (Reed *et al*.,

569   2011).

570   Whether this change in migration timing of Atlantic salmon smolts is due to phenotypic

571   plasticity or has a genetic basis remains to be understood. Despite evidence that adaptive

572   microevolution can occur rapidly in many populations, separating the contribution of genetic

573   adaptation and phenotypic plasticity is difficult (Hoffmann & Sgrò, 2011). For salmonids

574   recent studies have shown that evolutionary and plastic responses can explain a phenotypic

575   trend towards earlier migration into freshwater of sockeye salmon (*Oncorhynchus nerka*)

576   (Crozier *et al*., 2011). Similarly, a genetically based change towards earlier upstream

577   migration of pink salmon (*O. gorbuscha*) has been documented (Kovach *et al*., 2012).

578   Nonetheless, our analysis cannot distinguish between the two responses and additional

579   research is needed.

580   Timing of downstream migration may vary depending on smolt age and size. Slower-

581   growing and older smolts tend to migrate earlier in spring within a river (Jonsson *et al*., 1990;

582   Jutila & Jokikokko, 2008; but see Jensen *et al*., 2012). Recent analyses suggest that juvenile

583   salmon now tend to grow faster and migrate to sea at younger ages and smaller sizes (Jonsson

584   & Jonsson, 2005), but with large variation among rivers (Russell *et al*., 2012). The cause of

585   this change in size and age may partially be ascribed to the hydrological regime and to an

586   increase in temperature that regulate parr growth and age at smolting. Unfortunately it was not

587   possible to assess the influence of smolt age on emigration timing since information on smolt

588   age was lacking for most rivers and years.

589   We conclude that downstream migration timing of Atlantic salmon is strongly spatially

590   structured as a result of photoperiodicity. Photoperiod would be linked with the spatial pattern

591   of sea surface temperature at the time of ocean entry and would then be a priming mechanism

592 differentiating the latitudinal among-river initiation of the smolt emigration. An overall trend

593 towards earlier smolt migration was evident and probably associated with observed warming

594 trends in the freshwater habitat. Global warming could lead to a reduced connection between

595 the cues for migration and the environmental conditions in the receiving marine environment

596 with potential implications for salmon survival through a mismatch with seawater conditions

597 affecting population fitness and productivity. Declining survival would probably be

598 associated with suboptimal ionoregulatory conditions causing an altered antipredator

599 behaviour of the early post-smolts. Moreover, growth opportunities might be reduced if

600 emigration timing does not match with the production of prey items that are experiencing

601 changes in their own phenology inducing further food web alterations.

602

611

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809

810   **Supporting Information legends**

811   **Supplementary Material and Methods:** Detailed information on smolt sampling in each

812   river is provided. Further additional details on the environmental variables are also provided

813   here. Files: Otero et al_Supplementary Material and Methods.pdf; Otero et al_Supplementary

814   Material and Methods_Table S3bis.xls

815   **Supplementary Results:** Here we present details on model selection, model validation, and

816   other illustrative figures. File: Otero et al_Suplementary Results.pdf

817   **Supplementary References:** Literature cited in the Supplementary Material. File: Otero et

818   al_Supplementary References.pdf

819   **Table 1** Summary of the information used in the analyses. Years indicate the earliest and latest year with available data for any site within a

820   country, and the total number of observations (sites and years) in that country is indicated in parenthesis. Relevant comments for each country are

821   also provided. Further specific information for each sampling site is provided in Table S1 in the Supplementary Material and Methods.

Country	N° sites	Years (n)	Sampling methods	Comments
1. Canada	9	1970–2010 (192)	Fence, Rotary screw trap	River temperature predicted from air records in 3 observations. Water flow non-recorded for 41 observations. SST filled in for 16 observations.
2. USA	7	1993–2010 (76)	Rotary screw trap, Inclined screen samplers	River temperature predicted from air records for 24 observations. Water flow non-recorded for 36 observations.
3. Iceland	3	1987–2008 (52)	Fence, Fyke net	River temperature predicted from air records for 2 observations. Water flow non-recorded for 31 observations.
4. Scotland	2	1975–2010 (48)	Wolf trap, Smolt trap	River temperature predicted from air records for 29 observations. Water flow non-recorded for 2 observations. SST filled in for 7 observations.
5. Ireland	2	1970–2010 (74)	Wolf trap	River temperature predicted from air records for 12 observations. Water flow non-recorded for 41 observations. SST filled in for 16 observations.
6. England	6	1981–2010 (59)	Smolt trap, Rotary screw trap	River temperature predicted from air records for 19 observations. Water flow non-recorded for 8 observations. SST filled in for 1 observation.

7. Wales	2	2000–2010 (17)	Rotary screw trap	River temperature predicted from air records for 1 observation.
8. France	2	1985–2010 (42)	Smolt trap	Water flow non-recorded for 2 observations.
9. Spain	2	1999–2009 (21)	Smolt trap	River temperature predicted from air records for 4 observations. Water flow non-recorded for 1 observation.
10. Russia	1	1988–1995 (6)	Fence	Water flow non-recorded for 8 observations.
11. Finland	9	1972–2009 (90)	Fyke net, Video camera	River temperature predicted from air records for 1 observation. Water flow non-recorded for 38 observations. SST filled in for 8 observations.
12. Norway	20	1976–2010 (203)	Wolf trap, Net trap, Fence, Video camera, River fish lift	River temperature predicted from air records for 32 observations. Water flow non-recorded for 13 observations. SST filled in for 6 observations.
13. Sweden	5	1961–2010 (23)	Rotary screw trap, Wolf trap, Smolt trap	Water flow non-recorded for 5 observations. SST filled in for 17 observations.

822

823 **Table 2** Parameters for the optimal generalized additive mixed-effects model using 25% dates

824 as the response variable obtained from 70 sampled sites (n = 903 observations). See model

825 selection in Tables S4-S6 in the Supplementary Results. $\bar{T}$ = Mean River Temperature; SST =

826 Sea Surface Temperature; Y = Year. These covariates were centred by subtracting 9 and 7º C,

827 and year 1986, respectively before inclusion in the model. lo = longitude; la = latitude; S.D. =

828 standard deviation; S.E. = standard error; C.I. = 95% confidence interval; E.d.f = estimated

829 degrees of freedom. Note that exploratory generalized additive models revealed a linear

830 relationship with SST (e.d.f = 1), thus this term was modelled as a parametric term.

Parameter	Estimate	S.E.	C.I.	t-value	E.d.f	F-value	P-value
Fixed effects							
Intercept	138.60	0.85		163.41			<0.0001
$\bar{T}$					1.86	9.23	<0.0001
SST	2.07	0.32		6.55			<0.0001
Y					1.26	69.92	<0.0001
lo,la					10.81	61.63	<0.0001
Random effects (S.D.)							
σ_a	5.81		4.68; 7.21				
σ_b	1.28		0.80; 2.06				
σ	6.01		5.72; 6.32				
Variance function							
δ	0.035		0.016; 0.053				

831
832

Figure legends

Fig. 1 North Atlantic environmental conditions. Basin-scale SST (a) and ln-Chlorophyll *a* (d) at 1º × 1º grid resolution annually averaged from 1982 to 2010 and 1998 to 2010, respectively. Seasonal effects were not removed. Note also that specific monthly averages showed the same spatial patterns for both variables. Seasonal pattern and long-term trend of SST (b, c) and ln-Chlorophyll *a* (e, f) for the whole region are also shown. Numbers in (a) indicate the regions examined in this study (see Fig. S1-S13 for detailed maps of each area).

Fig. 2 Emigration data. Distribution of observed onset (grey hatched bars) and median (open black bars) downstream migration dates (a). Relationship between the difference in days between the median date (50%) and the onset date (25%) in each site, and latitude (b), and onset date (c). Curves in (b) and (c) show the results of fitting a Poisson generalised linear model corrected for overdispersion. Slopes were non-statistically significant (P-value = 0.156), and significant (P-value < 0.0001), respectively.

Fig. 3 Main model fixed effects results. Spatial trend of the onset of seaward smolt migration across the North Atlantic Ocean (a). Isopleths indicate the number of days of earlier (negative values) or later (positive values) migration than the zero isopleth (day of the year ~138, Table 2). The broken lines are the confidence bands (±1 s.e.), and the dots indicate the location of the sampling sites. Partial plots showing the effects of mean river temperature ($\bar{T}$) (b), and sea surface temperature (SST) (c) on the onset of seaward migration. The long-term trend during the last five decades is shown in (d). See Fig. S15 for a plot showing the distribution of the data in (b-d). Smolt drawing credits in panel (a): © Atlantic Salmon Federation (www.asf.ca) / J.O. Pennanen.

858 **Fig. 4** Main model random effects results. Scatter plot showing the correlation (0.76, 95%

859 C.I.: 0.30–0.93) between the site-specific random effects estimates for the intercepts ($\alpha + a_i$)

860 and SST slopes ($\beta_1 + b_i$) obtained from the optimal model depicted in Table 2. The colour

861 scale indicates a gradient of increasing latitude, and the dot size shows the differences in

862 longitude. The dotted lines show the population intercept (α) and slope (β_1).

863

864 **Fig. 5** Relationship with temperature difference. Partial plot showing the effect of the

865 temperature difference (T_{Dif}) between fresh and seawater on the onset of seaward migration.

866 See full results of this model in Table S7 and Fig. S20.

867

868 **Fig. 6** Relationships with river discharge. Partial plot showing the effect of ln-transformed

869 mean river discharge ($\bar{Q}$) (a), and the discharge-day slope for the 10-day period preceding the

870 25% smolt descent dates (ΔQ) (b) on the onset of seaward migration. See full results of this

871 model in Table S8 and Fig. S21.

872

873 **Fig. 7** Temperature patterns. Frequency histograms of water temperature trends in rivers with

874 at least 10 years of data (a), of air temperature records at stations close to the smolt sampling

875 locations (b), and sea surface temperature (SST) at the coastal entry cells (c). Frequency

876 histograms of changes in timing of seasonal warming in air temperature records (d), and in

877 sea surface temperature (e). Relationship between the geographically adjusted date of onset of

878 the smolt emigration and the date of seasonal warming in air temperature, defined as the

879 annual achievement of the first day in each year during April and August exceeding the 75th

880 percentile of the entire air temperature data set for each site (f). See Supplementary Material

881 and Methods for details on the individual estimation of the patterns in (a-e). Note that on

882 panels (c) and (e) there appear two extreme values. If removed, SST would warm at a mean

883 rate of 0.30 ± 0.02 ℃ per decade, and an earlier arrival of warmer SST would occur at an

884 average rate of 4.44 ± 0.25 days per decade.