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Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale

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Abstract

1. Understanding the geographical scales at which environmental variables affect an individual's body size, and thus their mortality risk, can inform management strategies to help conserve wild populations under climate change. Yet, our current understanding of these relationships is based on studies done at different scales that report inconsistent findings. We predicted that temperature-related variables (e.g. winter temperature) influence body size at a "regional" scale, that is, affecting individuals in geographically independent catchments similarly, whereas non-temperature-related variables (e.g. conspecific competitor density) exert a "local" influence, that is, affecting individuals in geographically independent catchments differently.

2. We developed statistical models to test our predictions using body length measures of a large and long-term sample of juvenile Atlantic salmon (*Salmo salar*) from three rivers in the U.K. and France. We developed mixture models to predict the individual juvenile salmon ages objectively from their body length. We then developed linear mixed models to describe inter-annual changes in mean length of the youngest (age 0) cohort of juvenile salmon from river-specific seasonal variables, and tested whether they exerted their influence at a "local" or "regional" scale. All models accounted for spatio-temporal differences in sampling protocols and individual reproductive strategy. We estimated and interpreted coefficients using Bayesian theory.

3. Our findings supported our predictions. Juvenile salmon were longer in years of higher overwinter water temperature and this effect was best parameterised as a single "regional" coefficient applicable to all three rivers. Similarly, spring mean temperature was best parameterised with a single "regional" nonlinear coefficient. In contrast, juvenile salmon were shorter in years of high densities of competing conspecifics and their interaction with total mean discharge and these effects were represented by "local" river-specific coefficients. Summer droughts had a negative effect on juvenile salmon length but was best parameterised as a single "regional" coefficient, contrary to our expectations.

4. We show that environmental variables affect biological processes at different but predictable geographical scales. Temperature-related variables affect body

sizes of exothermic animals at a regional scale, whereas non-temperature variables, such as the density of conspecific competitors and water abstraction, exert their influence at a local scale. These findings highlight the importance of integrating local and regional management plans to mitigate the impacts of climate change on the body size, and ultimately the conservation, of exothermic species.

1 | INTRODUCTION

Survival is positively related to body size in a wide range of plants and animals, from phytoplankton to mammals (McCoy & Gillooly, 2008). The mechanism(s) underpinning this relationship could be intrinsic because larger individuals have lower metabolic rates and lower rates of cell damage (Brown, Gillooly, Allen, Savage, & West, 2004) and/or extrinsic because larger individuals have a competitive advantage or lower *per capita* predation risk (Sogard, 1997). Nevertheless, evidence of this relationship is widespread and some researchers postulate that the "bigger is better" paradigm (*sensu* Sogard, 1997) should be an ecological "rule" (McCoy & Gillooly, 2008). Size-dependent survival is important for population conservation because there is mounting evidence that individual body size is shrinking in response to climate change. Sheridan and Bickford (2011) found that 38 of 85 (45%) studies of taxa from plants to mammals relating body size with climatic variables reported a decrease in size, compared to just 9 of 85 (11%) reporting an increase (45% reported equivocal results). These changes are (in part) ascribed to the direct or indirect effects of changing mean temperature and precipitation and their variability, including their extremes (Sheridan & Bickford, 2011). Together, these findings suggest that climate change negatively impacts wildlife populations through reduced survival of shrinking individuals.

As ectotherms, freshwater fish are strongly influenced by environmental conditions that act on their metabolic rates, affecting their growth and size (Atkinson, 1994). Experimental studies have shown that temperature and energy consumption are among the most important factors affecting somatic growth of fish (Brett, 1979). Evidence from empirical field studies is less common and suggests that climate change will drive decreasing body size-at-age in wild freshwater fish (e.g. in cyprinids; Daufresne, Lengfellner, & Sommer, 2009), and that smaller fish will suffer higher mortality (Sogard, 1997). Consequently, there is a mounting urgency to understand how environmental variables affect freshwater fish growth in natural systems (Jonsson & Jonsson, 2009). For example, Bacon, Gurney, Jones, Mclaren, and Youngson (2005) found positive correlations between spring temperatures and individual juvenile Atlantic salmon (*Salmo salar*, Family Salmonidae; hereafter, *salmon*) growth and basal metabolic and assimilation rates in a tributary of the river Dee, Scotland. Davidson, Letcher, and Nislow (2010) describe how juvenile salmon growth varied with seasonally changing river discharge in a

tributary of the Connecticut River, U.S.A., decreasing when discharge was low. Another variable—conspecific density (or density of salmon of the same cohort)—has also been shown to negatively affect fish growth, as individuals compete for limited local resources. For example, Bal, Rivot, Prevost, Piou, and Baglinière (2011) found that salmon and brown trout brown trout (*Salmo trutta*, Family Salmonidae) juvenile density had a strong effect on juvenile salmon growth on the river Oir, France.

Many empirical field studies investigating how environmental variables affect wild freshwater fish growth have considered only a single waterbody at a single scale, that is, a river or lake. Findings from single waterbodies are, however, often inconsistent because local conditions differ between waterbodies (e.g. habitat availability; Lobón-Cerviá, 2005) or environmental variables and their analysis differ between studies (e.g. including interactions [Crozier, Zabel, Hockersmith, & Achord, 2010] or nonlinear effects [Parra, Almodovar, Ayllon, Nicola, & Elvira, 2012]). Alternatively, environmental variables could influence biological processes at different geographical scales, rendering findings from single waterbody studies location-specific (Folt, Nislow, & Power, 1998). Fausch, Nakano, and Ishigaki (1994) found that the relationship between overlap in distributions of congeneric Char (*Salvelinus* sp., family Salmonidae) on Hokkaido Island, Japan, and temperature varied depending on the scale at which the observations were collected.

Poff and Huryn (1998) postulated that some variables, such as water temperature, affect wild salmon at regional scales (e.g. continent-wide), whereas others, such as species' interactions, affect them at local scales (e.g. habitat patches). Mechanistically, a "regional" effect of temperature on juvenile salmon growth could reflect its ubiquitous and strong effect on individual metabolic rate, which transcends geographical boundaries (Folt et al., 1998). Conversely, a "local" effect of a non-temperature variable, for example, species' interactions or river discharge, on growth could reflect river-specific processes, such as localised habitat availability, rainfall events or differences in water abstraction regimes (Folt et al., 1998). Evidence supporting (and opposing) Poff and Huryn's hypotheses from studies across multiple waterbodies is presented in Table 1 and generally supports the hypothesis of a regional temperature effect and a local conspecific density effect. The evidence supporting a local effect of river discharge is, however, more equivocal. For example, Gudmundsson, Tallaksen, and Stahl (2011) found spatio-temporal correlations in a wide range of discharge measures over a network

TABLE 1 Environmental explanatory variables used to describe inter-annual changes in mean juvenile salmon length on the rivers Frome, Oir and Scorff, their description, their hypothesised influence and citations of studies that suggest their influence will be apparent at a local (river-specific) or a regional (similar across all rivers) geographical scale

Name	Description	Influence	Suggested scale of effect	
			Local	Regional
Temperature				
Winter degree days (WDD)	Degree days from 1 January to 31 March	Positive influence due to better egg growth conditions or early hatching	1	2
Winter degree days^2 (WDD2)	Squared WDD to allow nonlinear relationship	Negative influence at high values due to low oxygen during development	—	2
Spring mean temperature (SPT)	Mean temperature from 1 April to 30 June	Positive influence due to better growth environment, particularly primary productivity	—	3
Spring mean temperature^2 (SPT2)	Squared SPT to allow nonlinear relationship	Negative influence at high values due to thermal stress	—	4
Summer maximum temperature (SMT)	Maximum mean temperature during seven consecutive days from 1 July to 31 September	Positive influence due to high productivity	—	5
Summer maximum temperature^2 (SMT2)	Squared SMT to allow nonlinear relationship	Negative influence at high value due to thermal stress	6	5
Discharge				
Total mean discharge (TMF)	Mean discharge from 1 April to 31 September	Positive influence due to increased food availability and available habitat to reduce density dependent effects	7	8
Summer minimum discharge (SMF)	Minimum discharge during seven consecutive days from 1 July to 31 September	Negative influence due to thermal stress and less available food	9	9
Other				
Conspecific density (DEN)	Conspecific density at site and time of capture	Negative influence due to less per capita available food	6	10
Conspecific density × spring mean temperature (DENSPT)	Interaction between conspecific density and spring mean temperature	Negative influence of less per capita available food will be offset by the positive influence of increased primary productivity	—	10
Conspecific density × total mean discharge (DENTMF)	Interaction between conspecific density and total mean discharge	Negative influence of less per capita available food will be offset by the positive influence of increased food availability	11	—
Winter NAO index (NAO)	Mean North Atlantic Oscillation index from 1 December to 31 March	Proxy for WDD	—	2

References: (1) Crozier et al., (2008); (2) Elliott & Elliott, (2010); (3) Jensen, Forseth, & Johnsen, (2000); (4) Swansburg et al., (2002); (5) Parra et al., (2012); (6) Lobon-Cervia, (2005); (7) Crozier & Zabel, (2006); (8) Gudmundsson et al., (2011); (9) Nislow & Armstrong, (2012); (10) Crozier et al., (2010); (11) Teichert, Kvingedal, Forseth, Ugedal, & Finstad, (2010).

of semi-natural European rivers although measures of low discharge were less correlated over space. Milner, Cowx, and Whelan (2012) suggest that the effects of river discharge on salmonids may be localised because of differences in river geomorphology and water abstraction regimes.

In this study, we aim to (1) identify environmental variables influencing inter-annual changes in juvenile wild salmon lengths recorded on three geographically independent rivers, and (2) test which of those were influencing their lengths at a regional scale. We define a regional scale as the geographical area encompassing the three independent catchments of the rivers Frome, Oir and Scorff; many studies in Table 1 investigate patterns across non-independent rivers, that is, rivers in the same catchment. In contrast, we define a local scale as the geographical area encompassing the single catchment of

each river. As recommended by Folt et al. (1998), we estimated the effect of environmental variables on inter-annual changes in average juvenile salmon lengths with a multi-scale analysis, that is, allowing the data to estimate whether and at what scale environmental variables effect salmon lengths. Despite the difficulties associated with such an analysis (Folt et al., 1998), we feel that the spatial and temporal extents of our data (three independent catchments, followed for up to 25 years), the large number of individuals measured (approximately 100,000) afford us the empirical and statistical power to address these aims without bias. We predict that (1) temperature-related variables will act at the regional scale because temperature effects growth at the level of individual physiology, and (2) non-temperature variables, for example, discharge and conspecific density, will act at the local scale because their effects are modified by local-

scale processes and activities, such as precipitation, water abstraction regimes and spawning stock size. Finally, we investigate whether the winter North Atlantic Oscillation index can be used in place of locally measured temperature variables (Hallett et al., 2004) to further test the hypothesis that temperature-related variables operate a large geographical scales.

2 | METHODS

2.1 | Study species and locations

Atlantic salmon spawn in coastal rivers and a few inland systems in the West Atlantic North America from Ungava Bay to Connecticut River and in the East Atlantic from Petchora in Russia to Lima in Portugal. Adults spawn *eggs* in freshwater river gravel beds, which hatch and grow to become juvenile salmon *parr* that undergo physiological changes and migrate to sea as *smolts*. At sea, they grow and (usually) attain sexual maturity and become *adults*, which eventually return to their natal rivers to spawn. Depending on latitude, this life-cycle can take between 3 and 10 years. Although the reasons are still unclear (but see, e.g. Beaugrand & Reid, 2012), Atlantic salmon populations are in decline throughout their geographical range, raising concerns for their persistence, particularly in southern and central Europe.

Parr data were collected on three rivers separated by the English Channel: the Frome (Dorset, U.K.), Oir (Normandy, France) and Scorff (Brittany, France) (Figure 1). These rivers were chosen for two reasons: (1) they have significant regional salmon populations whose parr have been monitored using consistent methods for 10–25 years, and (2) they drain geographically independent catchments (Table S1). All three rivers are "index rivers" that report salmon stock estimates to the International Council for the Exploration of the Seas.

2.2 | Data collection and preparation

Parr were captured by electrofishing from September to October on each river in each year, when they are large enough to be electrofished and marked. Electrofishing surveys were part of long-term monitoring programmes on each river and followed consistent protocols with standardised effort. Each parr was measured from the tip of the snout to the tail fork (hereafter *length* to the nearest millimetre, *mm*), examined for evidence of sexual maturity (mature if it had a soft and distended underbelly from enlarged gonads [Frome] or produced milt when massaged gently [Oir and Scorff]) and aged from a scale or—more often—by visual assessment from length. *River*, *Site*, *Year* and *Day of Year* were also recorded for each parr. All procedures were carried out under appropriate national licences and regulations.

River water temperature and discharge were measured on each river at a sub-daily (usually 15 min) interval. Each dataset had missing data, complicating the calculation of consistent explanatory environmental variables. To overcome this, we imputed missing data using the impSeqRob function of R package rrcovNA using spatially and temporally consistent E-Obs gridded data (version 10.0; http://eca.knmi.nl/dailydata/index.php) as predictors. We chose impSeqRob over alternative methods because it performed better in a small simulation experiment (Supporting Information). We used the resulting complete daily river water temperature and discharge datasets to calculate environmental variables purported to influence inter-annual changes in parr lengths in the scientific literature (Table 1).

Parr used in these analyses were caught at sites sampled consistently over time as part of river-specific long-term monitoring programmes and for which a relative index of annual parr density could be calculated. Total annual parr captures at each site were used as a site-specific index of relative annual changes in
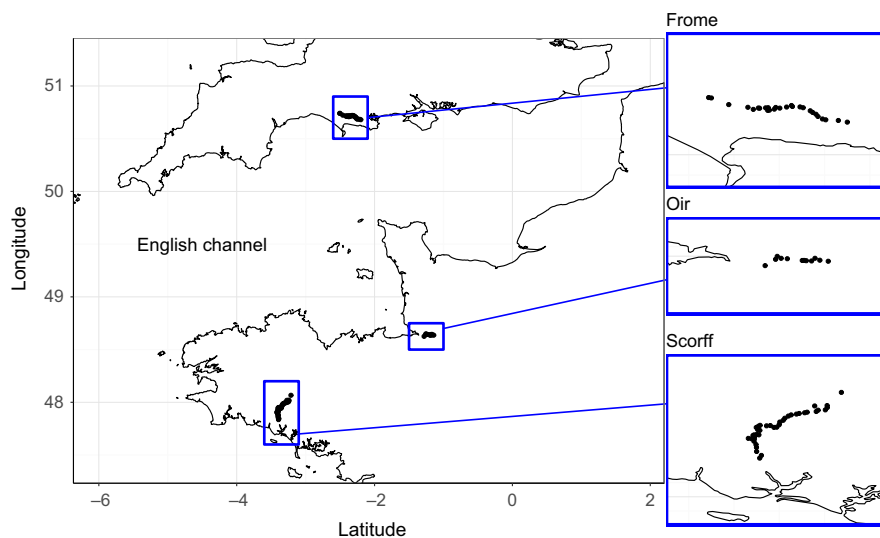

FIGURE 1 A map showing the locations of the three rivers included in this study: rivers Frome (Dorset, U.K.), Oir (Normandy, France) and Scorff (Brittany, France)

conspecific density. Although conspecific density was not a measure of true density in any particular year, inter-annual changes in conspecific density were assumed to correspond to inter-annual changes in true density. A more rigorous approach to using an index of parr density would be to estimate parr abundance using an explicit sampling (sub)model, as structured in *N*-mixture models, for example, Kanno et al. (2015). Other salmonids, for example, brown trout and European grayling (*Thymallus thymallus*, Family Salmonidae), were not included in the calculation of conspecific density because (1) they were not consistently recorded in salmon surveys, and (2) they were expected to occupy different niches, as suggested in other studies (e.g. Davidson et al., 2010).

A total of 94,497 individual parr were available for analysis: 61,515 captured at 27 locations on the Frome from 2004 to 2013; 5,797 captured at 12 locations on the Oir from 1994 to 2013; and 27,185 captured at 40 locations on the Scorff from 1993 to 2013. All sites yielded at least 10 parr in each year. Mean parr lengths (with standard errors) are presented in Figure 2.

2.3 | Age models

We limited our analysis to age 0 parr (i.e. parr that hatched from eggs in spring of the same year) for three reasons: (1) age 0 parr constitute a large majority of total parr numbers in these rivers and numbers of older parr were expected to be too small for statistical inference; (2) the effect of environmental conditions on older age >0 parr growth was expected to be weaker than in their first year (Parra et al., 2012) and (3) age >0 parr might have experienced unusual growth in their first year that was a factor in their decision to remain in the river for a second or more years (Baglinière & Maisse, 1985).

For the large majority of parr, age was estimated by visual assessment from length; scales were read only for parr whose age could not be estimated visually. However, aging parr from length for an analysis of temporal changes in parr length introduces circularity. To overcome this, we used mixture models to reclassify—objectively—parr *i* as age 0 or age >0 based on its length *l*. We estimated parr ages for the Oir and Scorff separately; we did not estimate ages for Frome parr because overlap in length densities was considered
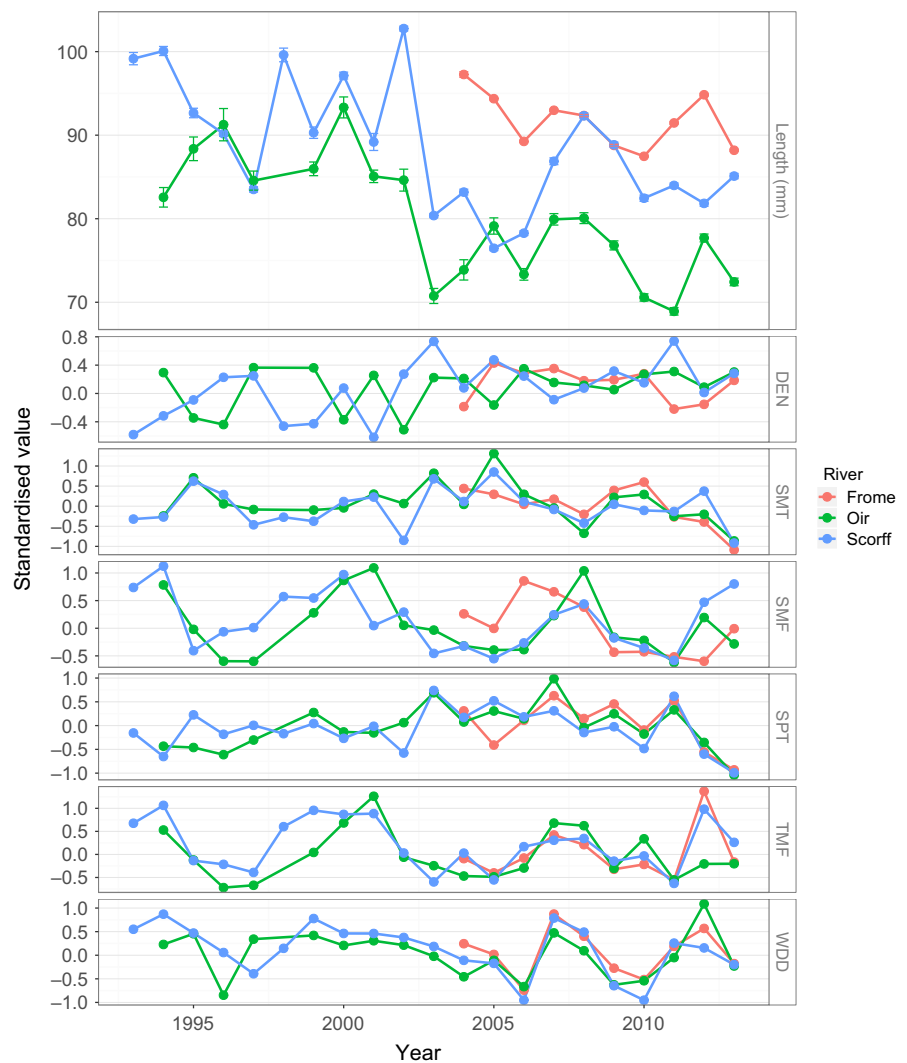

FIGURE 2 Line plots showing the mean and standard error (error bars) of unstandardised juvenile salmon length and standardised environmental variables plotted separately for each river over time. Value on the y-axis is the value of the variable in the units used in model fitting. DEN = conspecific density, SMT = summer maximum temperature, SMF = summer minimum discharge = SPT spring mean temperature, TMF total mean discharge, and WDD = winter degree days

negligible and age assignment from length reliable (Figures S2 and S3). The age model was given by

$$l_i \sim \sum_{j=1}^{J} \pi_j \mathrm{Normal}\left(l_i | \mu_j, \sigma^2\right)$$
$$\mu_{j=1} = \alpha + \beta_1 \mathrm{Maturity} + \beta_2 \mathrm{Day\ of\ Year} + \beta_3 \mathrm{Site} + \beta_4 \mathrm{Year}$$
$$\mu_{j=2} = \mu_{j=1} + I\delta$$

(1)

where α is a constant representing the mean length of age 0 parr adjusted by a coefficient representing the effect of parr maturity (β_1), a coefficient representing the effect of Day of Year (DoY) that parr i was captured (β_2) and coefficients representing the effects of Site (β_3) and Year (β_4), π_j is the proportion of individuals in age class j and

$$\pi_j \geq 0, \sum_{j=1}^{J} \pi_j = 1$$
$$\delta \sim \mathrm{half\text{-}Normal}(0, \tau)$$

We recognised $J = 2$ components: $j = 1$ for age 0 parr and $j = 2$ for age >0 parr. Note that we assumed a time-invariant π_j because we felt that the annual parr length distributions were similar between years within rivers (Figure S2). All parameters were constant across components except for δ that measured the difference ($\delta \geq 0$ mm) in length of age >0 parr compared to age 0 parr as a consequence of spending an additional year(s) in the river. We multiplied δ by an indicator variable I indicating whether or not the parr was estimated as age >0 where $I \in \{0, 1\}$ so that $I_{=0}\delta = 0$ and $I_{=1}\delta = \delta$.

All age models included all effects because we were striving for accurate age estimates rather than a parsimonious model. We included *Maturity* because mature parr tend to be larger than immature parr, especially when age 0; *Day of Year* because parr caught later in the year could be larger due to their longer growing period; and *Site* and *Year* to account for observed spatio-temporal variations in parr length distributions (Figures S2 and S3) and because we included these as random effects in subsequent models. We omitted interactions because mixture model convergence is often slow and less likely for complex models (Congdon, 2007).

We used Monte Carlo Markov Chain (MCMC) for inference because it produces more accurate mixture model parameter estimates than maximum likelihood. It is also, however, prone to label switching (Jasra, Holmes, & Stephens, 2005). To overcome this, we created a vector of observed ages that was missing data everywhere except for the shortest parr at each site, which was fixed at age 0, and the largest parr anywhere, which was fixed at age >0 (Chung, Loken, & Schafer, 2004). This assumption was justified because age >0 parr were present in each river in each year.

Each parr was assigned age 0 with probability $p0$ calculated as the marginal probability that the individual was assigned age 0. Parr assigned age >0 were discarded from subsequent analyses.

2.4 | Length model

We developed a model accounting for differences in sampling protocols and biological factors to investigate the influence of environmental variables on inter-annual age 0 parr lengths, and whether their effect was apparent at a local or a regional geographical scale. The model was of the form

$$l_{i,s,y} \sim \mathrm{Normal}\left(l_i | \mu_{s,y}, \sigma^2\right)$$
$$\mu_{s,y} = \alpha + \theta X + \upsilon_s + \nu_y$$

(2)

where $\theta = \beta_1, \beta_2, \ldots, \beta_k$ is a vector of K parameters relating explanatory variables $X = x_1, x_2, \ldots, x_k$ to the mean parr length at site s in year y, accounting for a Site within River random effect υ_s with a zero mean and variance τ_s from a half-Normal distribution and a Year within River random effect ν_y with a zero mean and variance τ_y from a half-Normal distribution. We considered two types of explanatory variables: (1) *baseline variables* describing the effect of river-specific parr sampling protocols and maturity on individual length, and (2) *environmental variables* summarising variables hypothesised to drive the observed changes in age 0 parr lengths (Table 1). Baseline variables included the effect of River, Maturity and DoY, and were in the model to explain variations in parr length due to differences in river-specific processes and sampling protocols. A Site within River random effect was included because samples were taken at the site level rather than the river level. A Year within River random effect was included to account for inter-annual variability in age 0 parr length unexplained by the explanatory variables.

We parameterised a saturated model including information from all three rivers and all environmental variables (Table 1). Environmental variables entered the model as a linear and/or a nonlinear main effect, which assumes an identical effect on all three rivers, and as a linear and/or nonlinear effect in interaction with river, which allows the strength of the effect to be different for each river (Table 1). The saturated model was simplified by dropping those effects judged to be "unimportant." The importance of each effect was judged by Bayesian variable selection (see Hooten & Hobbs, 2015). Specifically, we multiplied the coefficient representing the effect of the kth environmental variable β_k by a stochastic Bernoulli indicator variable I_k that evaluates to $I_k \in \{0, 1\}$ so that $I_{k=1}\beta_k \sim \beta_k$ and $I_{k=0}\beta_k = 0$ (Kuo & Mallick, 1998). For interaction effects, a coefficient representing the effect of the kth environmental variable on the rth river $\beta_{k,r}$ was multiplied by a single stochastic Bernoulli indicator variable I_k^{int} with inclusion probability $p_{k,r}$ representing the importance of the whole interaction term. The same approach was taken for the main effects except that the inclusion probability of the main effect p_k was conditional on the probability of inclusion of the interaction term according to $p_k = I_k^{\mathrm{int}} + \left(1 - I_k^{\mathrm{int}}\right)0.5$. This ensured that the main effect was retained if the corresponding interaction term was retained (Ntzoufras, 2002).

A nonlinear effect was represented as a second-order polynomial and its probability of inclusion was conditional on retention of the first-order polynomial, that is, the linear effect, in both the main and interaction effects. We tested all temperature-related variables as linear and nonlinear effects because several studies have shown a negative effect of high temperatures (e.g. Crozier et al., 2010; Table 1). Interactions among explanatory variables were investigated by calculating the product of the two variables and entering this new environmental variable into the model as an independent

explanatory variable. In this way, their inclusion was not conditional on the inclusion of their constituent variables. We considered interactions between conspecific density and both spring mean temperature and total mean discharge because both have been shown to ameliorate the negative influence of competition for limited resources at high conspecific density (e.g. Crozier et al., 2010; Table 1).

The Bayesian variable selection procedure retained coefficients that were estimated to be substantially more or less than zero, that is, did not intercept zero, overcoming problems associated with unrealistic *p* values when modelling many cases (Ellison, Gotelli, Inouye, & Strong, 2014).

2.5 | Model fitting

To compare the effect of environmental variables on age 0 parr length between rivers, they were standardised within river by subtracting the mean and dividing by 2 standard deviations (Gelman, 2008). This allowed the statistical effect size to be compared between rivers although the biological effect size could be different, that is, the actual change in parr length due to a unit change in a standardised environmental variable could be different between rivers. We took this decision to allow for local adaptation in growth at the different location (Hutchings, 2011).

To account for any possible collinearity among explanatory variables, we took the *Absolute value of correlation coefficients* (|*r*|) approach (*sensu* Dormann et al., 2013) because it avoids spurious estimation of regression coefficients and thus misinterpretation. Pearson's correlations among the standardised environmental variables (excluding NAO) were all $r \leq |.61|$ (Dormann et al., 2013; Table S2). (Indeed, only 1 and 2 pairs of standardised environmental variables were correlated $r \leq |.61|$ and $r \leq |.48|$, respectively; the other 8 pairwise comparisons were all ($r \leq |.44|$). The correlations between winter NAO (NAO, average NOAA NAO index from December to March, www.cpc.ncep.noaa.gov; Hallett et al., 2004) and all other environmental variables, including conspecific density, were similar to those for (WDD; Table S3). The correlation between WDD and NAO was $r = .70$.

To ensure identifiability, we applied constraints to variables represented as factors. For age models, we constrained coefficients for levels representing the first site and the last survey year to zero. For the length model, we applied a zero-sum constraint to interaction coefficients so that coefficients for all levels of the interaction term summed to zero. Coefficient estimates for interaction terms were therefore the estimated main effect coefficient modified by the estimated river-specific interaction coefficient.

The model coefficients were estimated using jags (version 4.2.0) called from R (version 3.3.2) using packages base, stats, ggplot2, stringr, lubridate, rrcovNA, data.table, dclone and rjags. We placed weakly informative priors on regression coefficients, $\beta \sim$ Normal (0, 0.001), and on the model error term, $\sigma^2 \sim$ Gamma^{-1} (0.001, 0.001). Random effect variances took weakly informative half-Normal priors, $\tau \sim$ half-Normal (0, 0.01), to improve estimation

behaviour where the random effect variance was close to zero (Gelman, 2006). Stochastic Bernoulli indicator variables were given a vague prior, that is, Bernoulli (0.5), which assumes values 0 and 1 occur with probability .5 (e.g. Tenan, O'Hara, Hendriks, & Tavecchia, 2014). All coefficient estimates are presented with their 95% Bayesian credible interval (CrI).

Parameters were estimated from three parallel MCMC chains run for 10^5 iterations together with an adaptive period of 20^3 iterations and burnin period of 10^4 iterations (20^4 iterations for the age models) that were discarded and parameter values were saved from every 20th iteration for inferences.

To assess model adequacy, we simulated a replicate dataset in each MCMC iteration and calculated the discrepancy of the replicate dataset X from the expected values E given model θ as

$$D(x|\theta) = \sum_N X_n - E_n$$

and then calculated the probability p (also known as the Bayesian p value) that the discrepancy from the replicate dataset X_{rep} exceeded the discrepancy calculated for the observed data X_{obs} as

$$p = \Pr[D(X_{rep}|\theta) > D(X_{obs}|\theta)]$$

A p value of .5 indicates that the model is adequate, that is, the evidence for a lack of fit to the observed data is weak.

3 | RESULTS

3.1 | Age results

An estimated 86.9% ($\pi_0 = 0.869$, CrI: 0.860–0.878) of parr captured in the Oir were age 0 and they were—on average—52.0 mm (CrI: 51.0–53.0) shorter than age >0 parr. The estimated proportion of age 0 parr was similar in the Scorff ($\pi_0 = 0.878$, CrI: 0.874–0.882) and they were an estimated 49.5 mm (CrI: 49.0–49.9) shorter than age >0 parr. Maturity had a positive effect on mean age 0 and age >0 parr lengths, as expected, but DoY had a negative (albeit, small) effect on mean age 0 and age >0 parr lengths on the Scorff (but not on the Oir; Table 2a).

Age models correctly classified 99.4% and 94.9% of scale-read age 0 and age >0 parr from the Oir, respectively (Table S4). (The misclassification rate was higher for Scorff scale-read parr but are not reported here because of small sample sizes [Figure S4]). Furthermore, we consider this misclassification rate to be biased high because scales were read only for parr that could not be aged reliably by visual assessment from length. Length frequency histograms coloured by model-assigned age reveal good separation for both rivers (Figure S5).

Gelman's diagnostic statistics suggest that the age model MCMC chains were stationary and mixed well (Table S5).

3.2 | Length results

On average, parr were longest on the Frome and shortest on the Oir (Table 2b). Sexually mature parr were longer on all three rivers, but

TABLE 2 (a) Coefficient estimates (and 95% Bayesian credible intervals) for variables included in the *age* models (used to estimate individual juvenile salmon ages) and (b) the *length* model (used to describe inter-annual changes in mean juvenile salmon length and test whether effects are "regional" or "local," respectively)

(a)

Variable	River[a]	
	Oir	Scorff
Overall mean	68.02 (66.38, 69.67)	84.69 (83.39, 85.99)
Maturity	5.48 (4.11, 6.89)	10.36 (9.68, 11.07)
DoY	0.02 (−0.05, 0.09)	−0.10 (−0.13, −0.07)
Delta	52.00 (50.96, 53.04)	49.47 (49.04, 49.92)
Proportion age 0	86.9 (86.0, 87.8)	87.8 (87.4, 88.2)

(b)

Variable	River		
	Frome	Oir	Scorff
Overall mean	92.013 (89.632, 94.406)	79.234 (75.154, 83.371)	87.540 (84.347, 90.865)
Maturity	6.409 (6.050, 6.770)	5.932 (4.175, 7.690)	14.365 (13.654, 15.071)
DoY[b]		−0.032 (−0.043, −0.021)	
Site|River variance	0.067 (0.038, 0.109)	0.031 (0.012, 0.064)	0.026 (0.016, 0.039)
Year|River variance	0.136 (0.043, 0.327)	0.047 (0.022, 0.089)	0.032 (0.016, 0.056)

[a]Age models were not fitted for the Frome.
[b]Day of Year (DoY) was fitted as a single parameter in the length model because its effect on parr lengths was negligible.

the effect of maturity on Scorff parr length was over twice that estimated for the Frome or Oir (Table 2b). The effect of DoY was small and counter-intuitive: it suggested that parr were shorter each day after the start of the sampling season (Table 2b).

Only five of the eight environmental variables hypothesised to influence age 0 parr length changes were retained in the length model (Figure 3). Conspecific density (DEN) was important and had a negative influence on age 0 parr lengths on all three rivers suggesting that parr were shorter when there were more competitors for limited resources and the strength of this effect was river-specific (Figures 3 and 4a). The interaction between conspecific density and total mean discharge (DENTMF) was also retained and differed between rivers. Its effect was negative on all rivers but was generally weaker than the negative effect of conspecific density (Figures 3 and 4b). Summer minimum discharge (SMF), spring mean temperature (SPT), its square (SPT2) and WDD were also all retained and had a positive effect on mean age 0 parr length: SMF had a similar positive effect on all three rivers suggesting parr were longer in years when summer drought was less severe (Figures 3 and 4c); the effect of SPT was best described together with SPT2 as a similar quadratic curve on all three rivers with the strongest positive effect at intermediate temperatures (Figures 3 and 4d); WDD had a similar positive effect on all three rivers suggesting that parr were longer in years when winter was milder (Figures 3 and 4e). The estimated indicator variable values are given in Table S6 and all had a mean value ≥0.5 and median value of 1. We repeated our analysis using the winter NAO (NAO) index in place of WDD; the results were qualitatively and quantitatively

similar to the results with WDD, except that the effect of SPT was not retained (Figure S6).

Gelman's diagnostic statistics suggested that the MCMC chains were stationary and mixed well (Table S7). Neither the Site within River nor the Year within River random effect estimates diverged substantially from a theoretical normal distribution, supporting the assumption that they were normally distributed (Figure S7). Residuals did not show any systematic patterns for the length model. The Bayesian *p* value was .48, indicating that the model fitted the data well (Figure S8).

4 | DISCUSSION

Our study demonstrates that environmental variables affect biological processes at different but predictable geographical scales. Actions to protect threatened populations from, for example, the impacts of climate change must therefore be formulated at a scale appropriate to the biological process being affected (Armstrong et al., 1998). We predicted and found that temperature-related environmental variables influence inter-annual changes in wild Atlantic salmon parr lengths at a regional scale, whereas non-temperature environmental variables, such as biotic interactions, influence them at a local scale (Poff & Huryn, 1998). Specifically, we found that conspecific density and the interaction between conspecific density and total mean discharge (but not summer minimum flow) had "local" effects on parr lengths specific to each river, whereas WDD and spring mean temperature had "regional" effects that were similar on all three
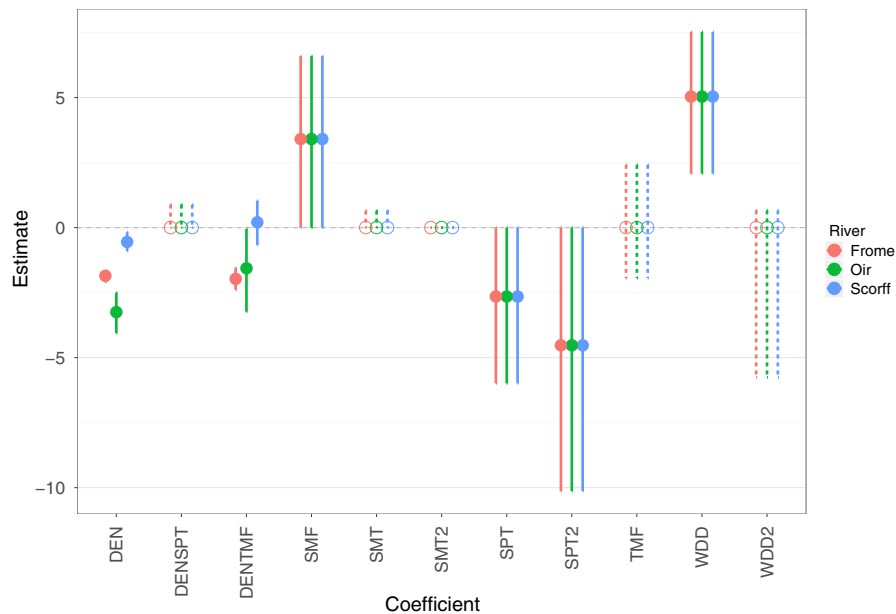
FIGURE 3 Caterpillar plot showing the coefficient estimates (and 95% Bayesian credible intervals) for each of the environmental variables included in the length model. Filled circles with solid bars identify coefficients retained in the model; hollow circles with dashed bars identify coefficients that were dropped. Where coefficient estimates are the same, the river-interaction effect has been dropped suggesting that the effect of that environmental variable can be represented as a single coefficient applicable to all three rivers, that is, its effect is "regional" rather than "local" (see text). DEN = conspecific density, DENSPT = conspecific density × spring mean temperature, DENTMF = conspecific density × total mean discharge, SMF = summer minimum discharge, SMT = summer maximum temperature, SMT2 = summer maximum temperature^2, SPT = spring mean temperature, SPT2 spring mean temperature^2, TMF = total mean discharge, WDD = winter degree days, and WDD2 = winter degree days^2

geographically independent rivers. Furthermore, these effects were in the same direction as those generally reported from other salmon populations of the U.K. and France, and throughout their geographical range (see reviews by Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Milner et al., 2003; Jonsson & Jonsson, 2009; and Warren, Dunbar, & Smith, 2015).

Winter degree days and spring mean temperature (standardised within river) had a "regional" positive influence on age 0 parr lengths that was best represented as a single linear and quadratic main effect, respectively. We argue that as temperature-related variables, WDD and spring mean temperature affect physiological processes, such as individual metabolic rate, so their effects are expected to be similar between populations inhabiting independent rivers (Atkinson, 1994). Mechanistically, we hypothesise that the effect of WDD characterises faster development and earlier emergence of parr from their gravel nests in spring, which affords them a longer growing period (Jonsson & Jonsson, 2009). Saltveit and Brabrand (2013) showed that salmon egg development and emergence occurred up to 40 days earlier in egg boxes situated nearest to warm groundwater seepages. Moreover, a semi-natural emergence experiment by Skoglund, Einum, and Robertsen (2011) found that eggs incubated at a higher temperature produced larger and better surviving parr compared to those incubated at lower ambient temperatures. We note that a positive effect of WDD suggests that parr are shorter after harsh, cold winters, perhaps because their development or emergence is retarded, and resources available post-emergence are scarce

due to lower in-river productivity or higher competition (Skoglund, Einum, Forseth, & Barlaup, 2012). The effect of spring mean temperature was best characterised as a quadratic effect, with a maximum positive effect at intermediate temperatures, after which its effect was detrimental. Crozier et al. (2010) reported a quadratic effect of temperature on juvenile salmon length across 13 populations in Idaho, U.S.A. although their measure represented summer temperature. Swansburg, Chaput, Moore, Caissie, and El-Jabi (2002) describe how the mean length of juvenile salmon in the Northwest and Southwest Miramichi rivers is negatively related to spring mean temperature, presumably due to an increased metabolic cost of living at higher temperatures and limiting the energy available to devote to growth. Note that the infection point in length for these rivers occurred at a lower than the average river temperature (approximately −0.25), suggesting that cooler temperatures encouraged better growth, presumably through higher productivity.

The effect of winter North Atlantic Oscillation index (NAO; Hallett et al., 2004) on parr length was qualitatively and quantitatively similar to the effect of WDD, that is, a single coefficient representing a "regional" effect was retained (Figure S6). We suggest that NAO is related to WDD and is capturing the same effect on individual metabolic rates, as supported by their high correlation (Pearson's $r = .70$). Consequently, NAO could be used in the absence of any direct measure of water temperature (Ottersen et al., 2001). Interestingly, however, spring mean temperature was not retained in the NAO length model, suggesting that winter NAO captures some of
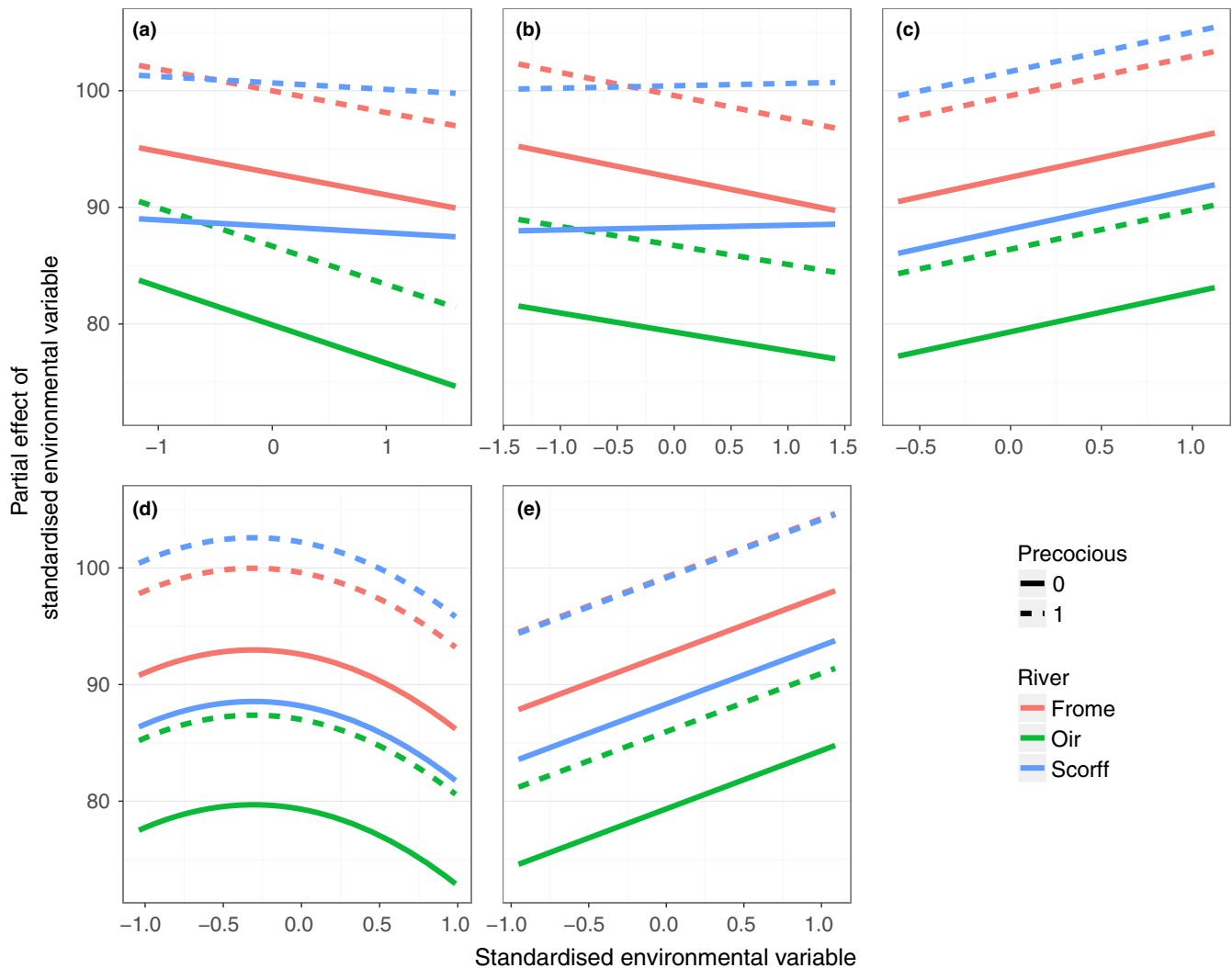
FIGURE 4 Partial effect plots for each of the environmental variables retained in the length model. Lines are plotted for immature and mature (Precocious = 1) parr separately for each river. Variables are plotted on their standardised scale. Panels are: (a) conspecific density (DEN) (b) conspecific density × total mean discharge (DENTMF) (c) summer minimum discharge (SMF) (d) spring mean temperature (SPT) and (e) winter degree days (WDD)

the variation in parr length otherwise explained by spring mean temperature. The relationship between WDD, spring mean temperature and winter NAO merits further investigation.

As predicted, the effects of conspecific density and its interaction with total mean discharge differed in strength (but not direction) between the three rivers, as indicated by the separation in their estimated CrIs (Figure 3). The effect of conspecific density (standardised within river) was negative and differed strongly in strength on all three rivers. We hypothesise that the difference in the strength of the effect is due to river-specific influences on parr condition or density, which could be due to a number of factors and their interactions. For example, the rivers might differ in their productivity causing a difference in the amount or replenishment rate of a limiting resource (Armstrong et al., 2003). Or habitat available to the spawning stock might differ from one site to another, within and between rivers, perhaps due to different levels of

exploitation. Although the mechanism(s) remain speculative, the direction and strength of these conspecific density effects are consistent with other studies. For example, Richard, Cattaneo, and Rubin (2015) found a strong negative influence of density on brown trout length at nine locations along the river Boiron, Switzerland, which differed in strength between locations. The negative effect of density is supported by mean parr lengths trends that decrease over time, particularly since 2006 when parr density was consistently high (Figure 2). Compared to the strength of the conspecific density effect, its effect in interaction with total mean discharge was somewhat weaker although it also differed in strength on all three rivers (Figure 3). This suggests that total mean discharge affects mean age 0 parr lengths on these rivers indirectly through its effect on conspecific density (Figure 4b). We speculate that total mean discharge dampens the negative effect of conspecific density by delivering more resources, whether available habitat

or food, to lessen the *per capita* effect on inter-cohort competition (e.g. Davidson et al., 2010).

The effect of SMF (standardised within river) was positive but—contrary to our predictions—its strength was similar on all three rivers. We hypothesised that the effects of discharge would differ between rivers due to river-specific processes, perhaps related to geology or human activity (Warren et al., 2015). We speculate that the effect of SMF was similar between rivers because it represents a strong but acute effect that might overshadow weaker river-specific processes. The positive effect of higher SMF (i.e. less severe droughts) is supported by other studies. For example, Davidson et al. (2010) and Xu, Letcher, and Nislow (2010) both describe how juvenile salmonid growth increased with increasing summer discharge. Whether this effect is due to discharge directly or indirectly is not clear. Harvey, Nakamoto, and White (2006) showed that high (compared to low) discharge delivered more invertebrate food that boosted rainbow trout (*Oncorhynchus mykiss*, Family Salmonidae) growth rates. Although the effect of SMF was similar across rivers, we note that the effect of total mean discharge, albeit in interaction with conspecific density, was river-specific.

None of the remaining environmental variables (conspecific density interacting with spring mean temperature, summer maximum temperature and total mean discharge) were found to influence age 0 parr lengths despite reported findings to the contrary (Table 1). Possible explanations for this disparity include lack of a strong effect, as supported by conflicting effects for the same variables outlined in Table 2 in Jonsson and Jonsson (2009); different variable representations compared to other studies (e.g. Hallett et al., 2004); and our statistical methods differed from more conventional methods and did not rely on *p* values that are more likely to find "significant," but negligible effects by chance or due to a large number of cases (Ellison et al., 2014). Alternatively, these differences could be due to limitations in our own study. We might have omitted potentially important variables, for example, macrophyte cover and primary productivity which could affect the estimated effects of all other variables in the model. For example, although the effect of DoY was small (<0.04 mm per day; equivalent to a maximum of 1.1, 0.9 and 0.67 mm during the longest annual survey on the Frome, Oir and Scorff, respectively), it suggested that parr measured later in the season are shorter than those measured earlier, which was counterintuitive and could be explained by an omitted variable. Also, we draw conclusions about the spatial scale of effects from just three geographically independent rivers although we feel that the geographical area encompassing these rivers is large enough to justify our conclusions.

Using a large and long-term database of Atlantic salmon parr length observations, we show that temperature-related environmental variables affect the body sizes of exothermic animals at a regional scale, whereas non-temperature environmental variables, such as precipitation and local human activities, exert their influence at a more local scale (Poff & Huryn, 1998). This highlights the importance of integrating local and regional management plans to better manage ecosystems and their constituent species, particularly for salmon

(Armstrong et al., 1998): if the negative impact of these environmental variables intensifies under forecast climate change, or the balance between the environmental variables shifts to drive a shrinking trend in juvenile salmon parr, as has been observed on these three rivers (Figures 1 and S9), then the migrating smolt are likely to suffer greater marine mortality (e.g. Jutila, Jokikokko, & Julkunen, 2006; Otero et al., 2014), resulting in a net decrease in the number of adult salmon returning to their natal rivers to spawn (Russell et al., 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supporting Information

16

Supporting methods

Study sites and sampling

Rivers included in this study were the Frome (Dorset, UK), Oir (Normandy, France) and Scorff (Brittany, France). Table S presents basic summary statistics of the river and their catchments. In addition to these statistics, it is interesting to note the following differences:

- The Frome is a chalk stream river, fed largely from aquifers. The Scorff and Oir have a harder, less permeable granite bedrock and are largely rain-fed;
- The Scorff discharges into the ocean directly; the Frome discharges into Poole Harbour, the world's second largest natural harbour; and the Oir is a tributary of the larger Selune river;
- The Oir has a minor flow when compared with the Frome and Scorff.

Table S1. [Catchment descriptions] A table presenting river and catchment descriptions of the three rivers included in this study.

	River		
	Frome	**Oir**	**Scorff**
Tidal limit lat. / long.	50.677 / -2.117	NA	47.742 / -3.348
Catchment area: km²	454	87	480
Length: km	69.8	19.5	75
Mean flow: m3 s-1	6.7	0.92	5.0
Q95: m3 s-1	102	14	97
Gradient: mean %	2.5	1.1	1.8

Atlantic salmon parr were captured by electrofishing from September to October on each river in each year, when they are large enough to be electro-fished and marked. Electrofishing surveys were part of long-term monitoring programmes on each river and followed consistent protocols with standardised effort. A brief description of each sampling protocol is outlined below:

Frome

Throughout the sampling period, fish capture was carried out using pulsed DC electric fishing. Two types of output waveforms were used, a half-wave rectified waveform and a square-wave waveform. Both were fished at 50 Hz and approximately 200 volts and the square-waveform was fished at 25-30% duty cycle. Fishing was normally carried out using a single anode (380 mm diameter and a 3000 mm cathode) but on occasions twin anode fishing was used. Two nets were used to capture salmon: one primary net held by the operator and one "back up" net. Specific conductivity of the river Frome is around 460 μScm^{-1}, being a groundwater fed river this conductivity shows little variation (±50 μScm^{-1}).

Oir & Scorff

Throughout the study, a single electro-fishing unit was used (Martin Pêcheur, DREAM Electronique) delivering pulsed DC square-wave waveform fished at 400 Hz frequency, 200-350 volts and a 4-10% duty cycle. The anode diameter was 250 mm. Three nets were used to capture salmon: one of 600 mm width and one of 400 mm width used to catch salmon within the 4-5 m zone electified by the anode, and one of 250 mm width used to catch salmon missed by those nets. Surveys were 5 mins effective fishing time, i.e., 5 mins with the anode in the water and electrified.

River water temperature and discharge data imputation

River water temperature and discharge data had missing values. To overcome this limitation, we imputed missing values using measured and interpolated air temperature and precipitation records (see article methods).

Here, we present the details of a small experiment we did to help decide the best imputation algorithm to use.

Based on this experiment, we decided to use `impSeqRob`.

To account for the possibility that the missing river water temperature and flow values might not be "Missing At Random" (MAR) but are "Missing Not At Random" (MNAR), we repeat an experiment with MAR and MNAR data using the `impSeqRob` and `irmi` algorithms.

```r
## bootstrap function
impute.boot <- function(dat, miss.col = 'mean', n, n.missing = 100, missingness =
'MAR'){

  ## check missingness
  if(!missingness %in% c('MAR', 'MNAR')) stop('missingness must be MAR or MNAR')

  ## back up missing col data
  d <- dat[, miss.col]

  ## holding list
  df.irmi <- df.impSeqRob <- list()

  ## repeat in loop
  for(i in 1:n){

    ## reset dat
    dat[, miss.col] <- d

    ## add NAs to dataset
    if(missingness == 'MAR'){
      nas <- sample(x = 1:nrow(dat), size = n.missing, replace = FALSE)
      dat[, miss.col][nas] <- NA
    }else{
      ff <- factor(sort(sample(1:5, n.missing, replace = TRUE, prob = c(0.1, 0.1,
0.5, 0.2, 0.1))))
      splt <- split(1:n.missing, f = ff)
      nas.strt <- sample(x = 1:nrow(dat), size = 5, replace = TRUE)
      nas <- unlist(lapply(1:length(nas.strt), function(v) nas.strt[v] +
1:length(splt[[v]])))
      dat[, miss.col][nas] <- NA
    }

    ## fit models
    # irmi
    sink('NUL'); foo <- irmi(dat, trace = FALSE); sink()
    # impSeqRob
    fii <- impSeqRob(dat)
    fii <- data.frame(fii$x)
    fii$Date <- dat$Date

    ## add imputation indicator
    foo$Imp <- fii$Imp <- 0
    foo[nas, 'Imp'] <- 1
    fii[nas, 'Imp'] <- 1

    ## add residuals
    foo$Res <- foo[, miss.col] - d
    fii$Res <- fii[, miss.col] - d
```

```r
110
111      ## add to holding lists
112      df.irmi[[i]] <- foo
113      df.impSeqRob[[i]] <- fii
114
115      }
116
117    ## aggregate dfs
118    df.irmi <- do.call('rbind', df.irmi)
119    df.impSeqRob <- do.call('rbind', df.impSeqRob)
120
121    ## add index of iterations
122    df.irmi$Iter <- rep(1:n, each = nrow(dat))
123    df.impSeqRob$Iter <- rep(1:n, each = nrow(dat))
124
125    ## return imputed data
126    return(list('irmi' = df.irmi, 'impSeqRob' = df.impSeqRob))
127
128    }
129
130  ## use the EObs mean, minimum and maximum temperatures
131  foo.df <- df[, c('Date', 'dailymeantemperature', 'dailymaximumtemperature',
132  'dailyminimumtemperature')]
133  colnames(foo.df)[2:4] <- c('mean', 'max', 'min')
134  head(foo.df)
135  ##               Date mean    max   min
136  ## 18629 2001-01-01 6.79 10.86 2.09
137  ## 18630 2001-01-02 9.10 10.22 7.51
138  ## 18631 2001-01-03 5.97  9.42 1.97
139  ## 18632 2001-01-04 6.94  7.61 4.48
140  ## 18633 2001-01-05 6.02  8.76 4.94
141  ## 18634 2001-01-06 5.43  7.64 1.52
142
143  ## do MAR analysis
144  mar.res <- impute.boot(foo.df, miss.col = 'mean', n = 10, n.missing = 100,
145  missingness = 'MAR')
146
147  ## make data.frame
148  mar.df <- do.call('rbind', mar.res)
149  mar.df$Method <- factor(gsub('\\.[0-9]*$', '', rownames(mar.df)))
150
151  ## print sums of squares by method for each iteration and overall
152  ss.mar.iter <- aggregate(Res ~ Method + Iter, mar.df, function(v) sum(v^2))
153  ss.mar.all <- aggregate(Res ~ Method, mar.df, function(v) sum(v^2))
154  print(ss.mar.iter)
155  ##       Method Iter   Res
156  ## 1  impSeqRob    1 25.18
157  ## 2       irmi    1 48.19
158  ## 3  impSeqRob    2 28.62
159  ## 4       irmi    2 64.07
160  ## 5  impSeqRob    3 40.38
161  ## 6       irmi    3 75.27
162  ## 7  impSeqRob    4 25.82
163  ## 8       irmi    4 58.82
164  ## 9  impSeqRob    5 34.17
165  ## 10      irmi    5 53.79
166  ## 11 impSeqRob    6 23.83
167  ## 12      irmi    6 49.61
168  ## 13 impSeqRob    7 28.97
169  ## 14      irmi    7 61.33
170  ## 15 impSeqRob    8 17.13
171  ## 16      irmi    8 43.77
172  ## 17 impSeqRob    9 17.67
173  ## 18      irmi    9 52.07
174  ## 19 impSeqRob   10 21.89
175  ## 20      irmi   10 51.06
176  print(ss.mar.all)
```

```
177   ##       Method   Res
178   ## 1 impSeqRob 263.7
179   ## 2      irmi 558.0
180
181   ## do MNAR analysis
182   mnar.res <- impute.boot(foo.df, miss.col = 'mean', n = 10, n.missing = 100,
183   missingness = 'MNAR')
184
185   ## make data.frame
186   mnar.df <- do.call('rbind', mnar.res)
187   mnar.df$Method <- factor(gsub('\\.[0-9]*$', '', rownames(mnar.df)))
188
189   ## print sums of squares by method for each iteration and overall
190   ss.mnar.iter <- aggregate(Res ~ Method + Iter, mnar.df, function(v) sum(v^2))
191   ss.mnar.all <- aggregate(Res ~ Method, mnar.df, function(v) sum(v^2))
192   print(ss.mnar.iter)
193   ##       Method Iter    Res
194   ## 1  impSeqRob    1 24.945
195   ## 2       irmi    1 52.964
196   ## 3  impSeqRob    2  5.036
197   ## 4       irmi    2 31.049
198   ## 5  impSeqRob    3 26.587
199   ## 6       irmi    3 53.975
200   ## 7  impSeqRob    4  7.337
201   ## 8       irmi    4 40.687
202   ## 9  impSeqRob    5 13.313
203   ## 10      irmi    5 46.326
204   ## 11 impSeqRob    6 19.088
205   ## 12      irmi    6 52.490
206   ## 13 impSeqRob    7  6.240
207   ## 14      irmi    7 29.475
208   ## 15 impSeqRob    8  8.222
209   ## 16      irmi    8 30.158
210   ## 17 impSeqRob    9 42.835
211   ## 18      irmi    9 75.828
212   ## 19 impSeqRob   10  9.420
213   ## 20      irmi   10 39.248
214   print(ss.mnar.all)
215   ##       Method   Res
216   ## 1 impSeqRob 163.0
217   ## 2      irmi 452.2
218
```
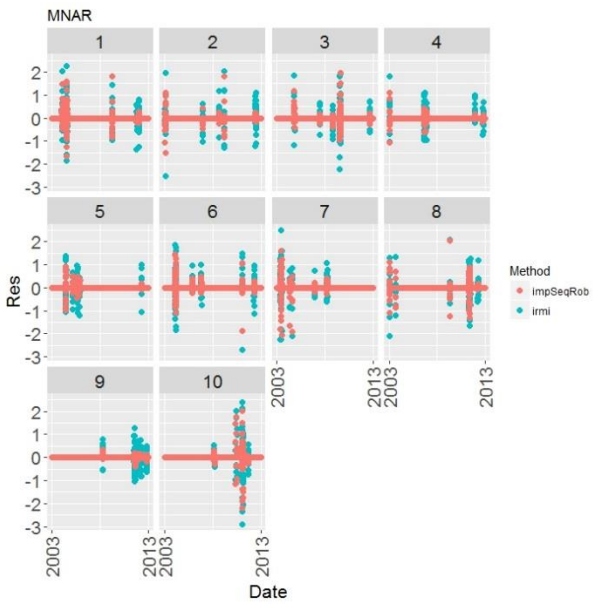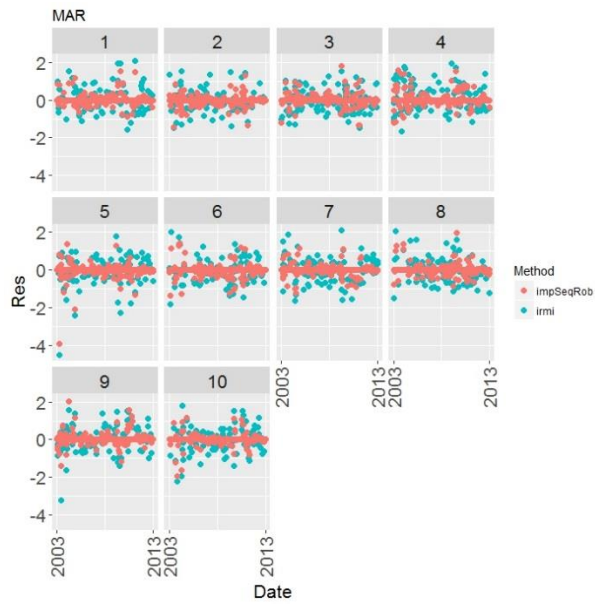
219
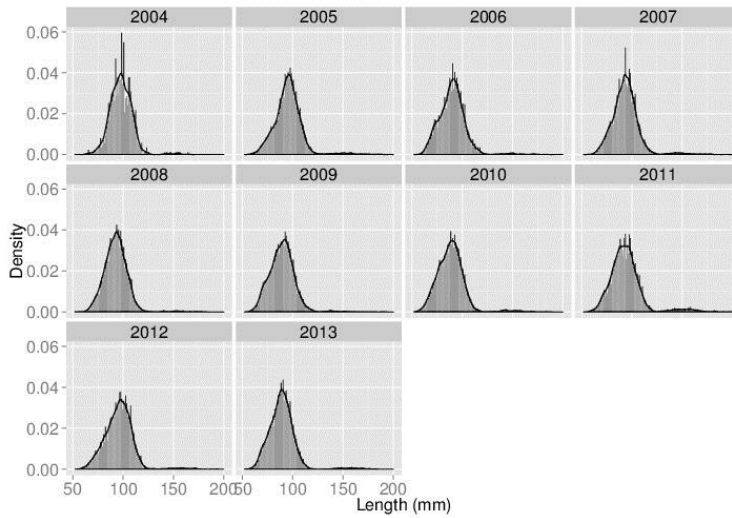
220   (a)   (b)

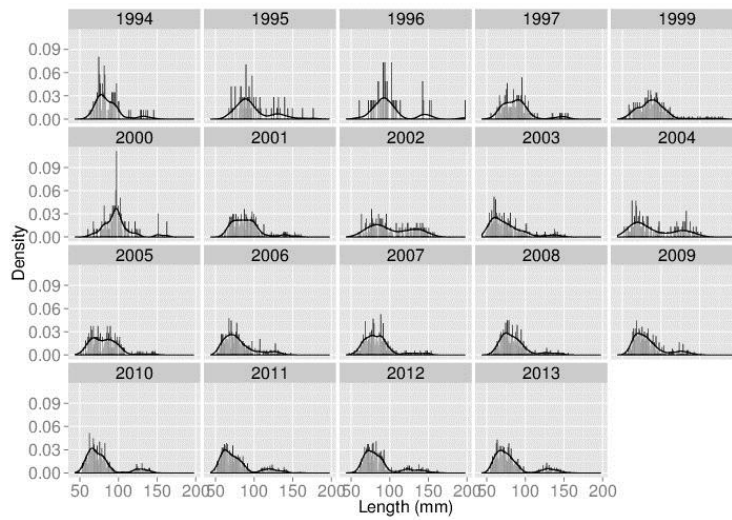221   **Figure S1.** [Imputation residual plots] Residuals (imputed – actual value) for each of 10 bootstrap
222   datasets with values (a) Missing at Random (MAR) and (b) Missing Not at Random (MNAR).

223

Age models

(a)

(b)

(c)
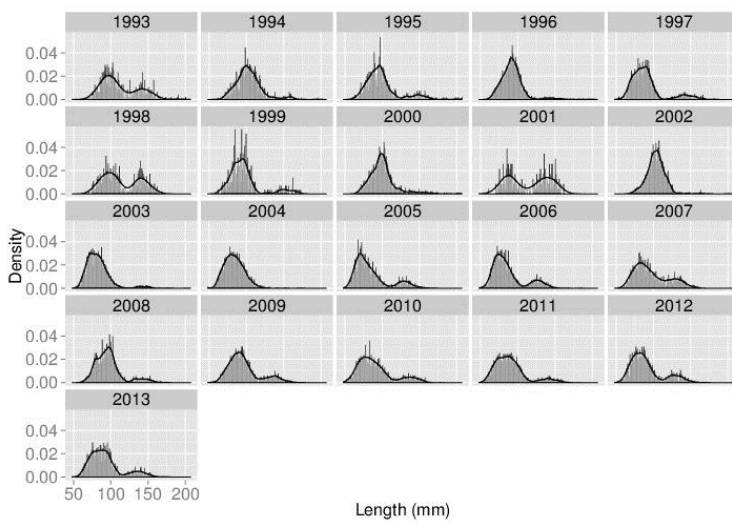
Figure S2. [Juvenile salmon length density plots by year] Density plots showing the overlap in parr lengths in each year on the rivers (a) Frome, (b) Oir and (c) Scorff.
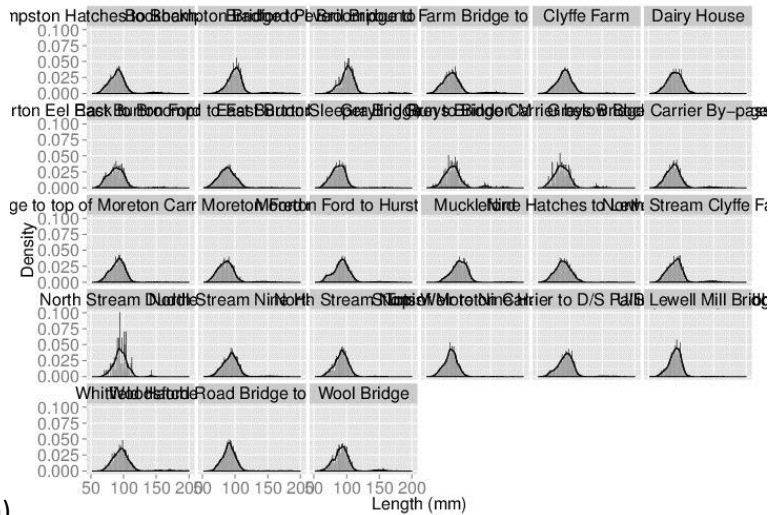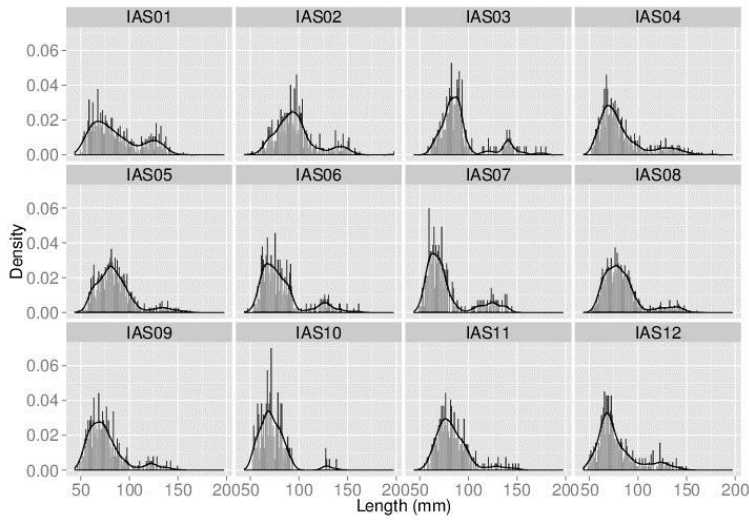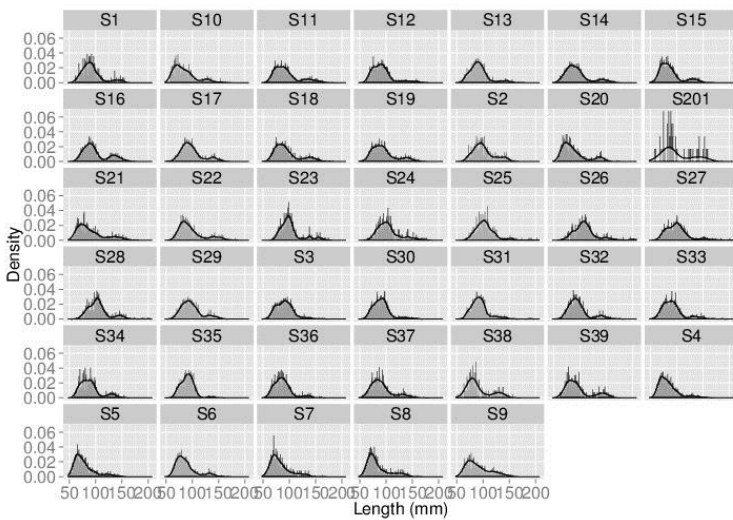
230   (a)

231   (b)

232   (c)

Figure S3. [Juvenile salmon length density plots by site] Density plots showing the overlap in parr lengths in each site on the rivers (a) Frome, (b) Oir and (c) Scorff.

8

Length model

Explanatory variable correlation matrix

Table S2. [Explanatory variable correlation matrix] A correlation matrix between the environmental
explanatory variables. Abbreviations are: DEN, conspecific density; WDD, winter degree days; SPT,
spring mean temperature; SMT, summer maximum temperature; TMF, total mean discharge; SMF,
summer minimum discharge; DENSPT, conspecific density and spring mean temperature product,
and DENTMF, conspecific density and total mean discharge product.

	DEN	WDD	SPT	SMT	TMF	SMF	DENSPT	DENTMF
DEN	1.000	-0.102	0.102	0.155	-0.232	0.021	0.120	-0.035
WDD	-0.102	1.000	0.167	-0.165	0.480	0.206	0.187	0.035
SPT	0.102	0.167	1.000	0.601	-0.277	-0.060	0.444	0.038
SMT	0.155	-0.165	0.601	1.000	-0.245	-0.203	0.281	-0.083
TMF	-0.232	0.480	-0.277	-0.245	1.000	0.324	0.039	0.073
SMF	0.021	0.206	-0.060	-0.203	0.324	1.000	-0.048	0.232
DENSPT	0.120	0.187	0.444	0.281	0.039	-0.048	1.000	-0.373
DENTMF	-0.035	0.035	0.038	-0.083	0.073	0.232	-0.373	1.000

NAO correlation matrix

Table S3. [Winter North Atlantic Oscillation index correlation matrix] A correlation matrix showing correlation between Winter North Atlantic Oscillation index (WNTNAO) and the other environmental variables. Abbreviations are: DEN, conspecific density; WDD, winter degree days; SPT, spring mean temperature; SMT, summer maximum temperature; TMF, total mean discharge; SMF, summer minimum discharge; DENSPT, conspecific density and spring mean temperature product, and DENTMF, conspecific density and total mean discharge product.

```
                 DEN       WDD        SPT        SMT        TMF
WDD       -0.1023995 1.0000000 0.16726624 -0.1646876 0.4796696
WNTNAO    -0.1358511 0.7024501 0.06490442 -0.1579133 0.5896265

                 SMF     DENSPT      DENTMF     WNTNAO
WDD        0.2063852 0.1866084  0.03475113 0.7024501
WNTNAO     0.2743359 0.1589354 -0.01795812 1.0000000
```

Supporting results

Age results

Table S4. [Age model misclassification rates] Validation of the parr aging model predictions (misclassified ages are in italics). Note that the Scorff misclassification rates are considered unreliable because of possible scale-read aging errors.

| River	Scale-read age	Model-assigned age		Misclassification rate (%)
		0	**1**	
Oir	**0**	672	*4*	0.59
	1	*17*	316	5.11
Scorff	**0**	217	*23*	9.58
	1	*26*	100	20.64

Table S5. [Age model convergence statistics] Gelman statistic estimates for all estimated parameters in the age models. Note: an estimate of 1 suggested converged, stationary and well mixing chains.

Estimate	River	Point estimate	Upper Confidence Interval
delta	Oir	1.00	1.00
	Scorff	1.00	1.00
deviance	Oir	1.00	1.00
	Scorff	1.00	1.00
alpha	Oir	1.00	1.00
	Scorff	1.00	1.00
beta_d	Oir	1.00	1.00
	Scorff	1.00	1.00
beta_p	Oir	1.00	1.00
	Scorff	1.00	1.00
beta_s	Oir	all 1.00	all 1.00
	Scorff	all 1.00	all 1.00
beta_y	Oir	all 1.00	all 1.00
	Scorff	all 1.00	all 1.00
pAges[1]	Oir	1.00	1.00
	Scorff	1.00	1.00
pAges[2]	Oir	1.00	1.00
	Scorff	1.00	1.00
sigma	Oir	1.00	1.00
	Scorff	1.00	1.00
tau	Oir	1.00	1.00
	Scorff	1.00	1.00

269
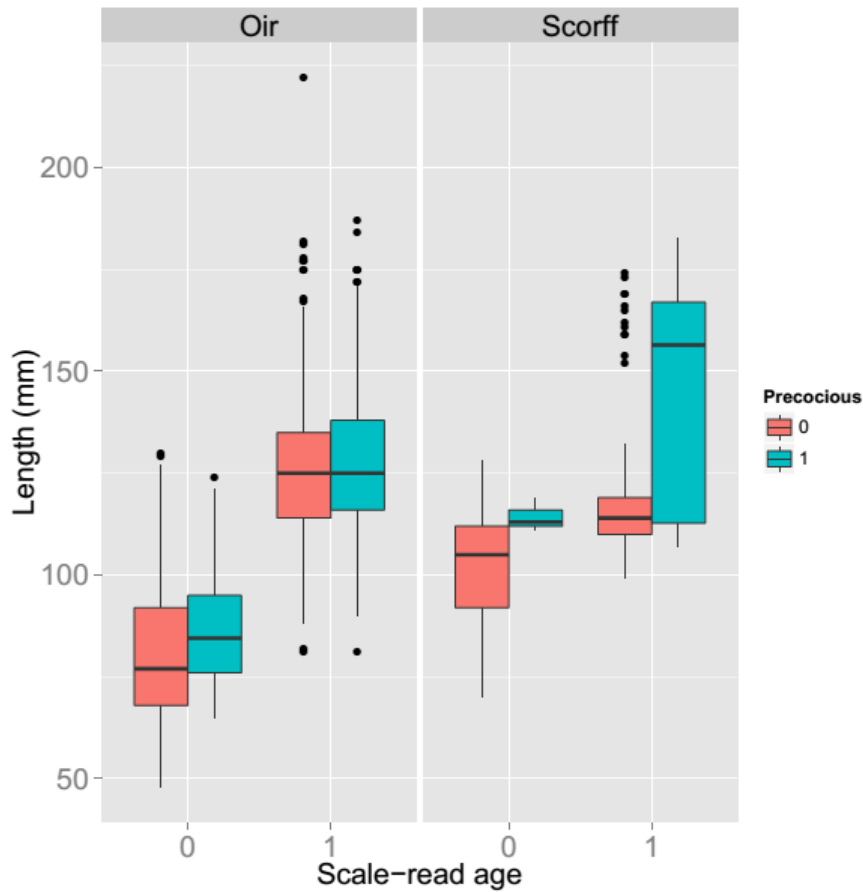
Figure S4. [Boxplots of scale-aged juvenile salmon lengths] Lengths of scale-read aged non-precocious (0) and precocious (1) parr for the rivers Oir (n = 3214) and Scorff (n = 381). Note that (1) the Scorff plot is based on approximately 10% of the amount of data as the Oir plot, and (2) there were only 3 and 28 age 0 and age >0 parr judged to be precocious in the Scorff sample. Based on the small sample sizes the Scorff scale-read parr ages were not used to assess model accuracy.
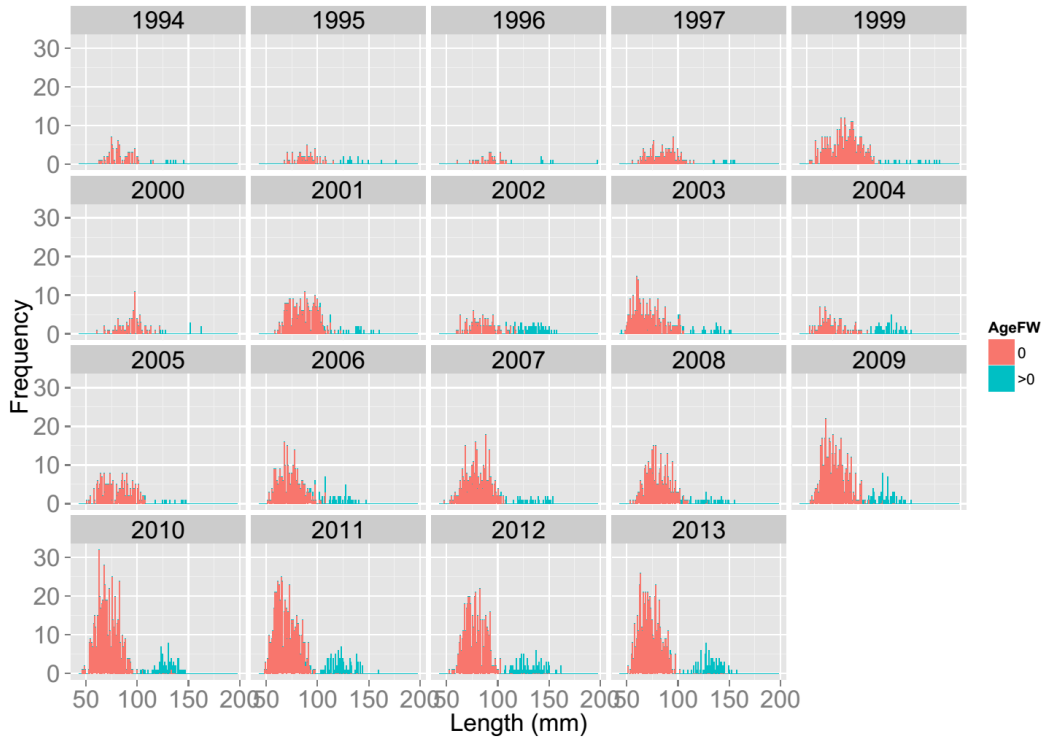
275 (a)
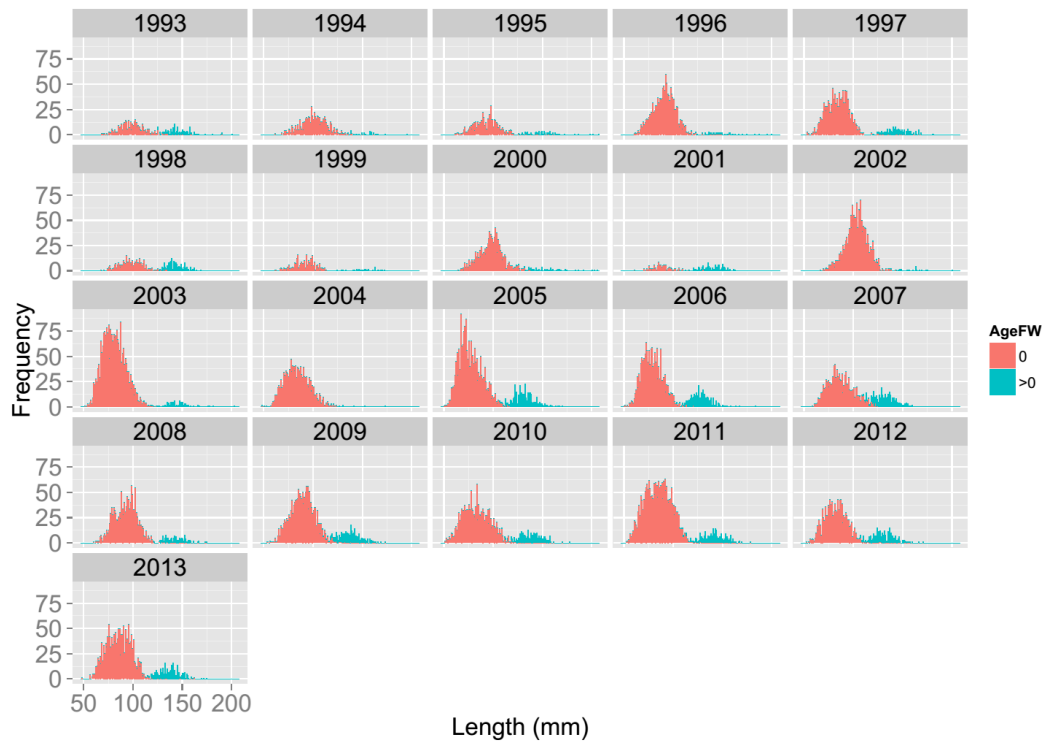
276 (b)

Figure S5. [Juvenile salmon length histograms by estimated age] Histograms for the (a) Oir and (b)
Scorff showing separation between the lengths of model-estimated freshwater age (AgeFW) age 0
and age >0 parr.

13

Length results

Table S6. [Length model indicator variable estimates] A table presenting the mean and standard deviation, together with the 2.5, 25, 50, 75 and 97.5% quantiles of the estimates for each indicator variable retained in the length model. All other environmental variables had a mean estimate <0.5 and 50% quantile estimate of 0 and were dropped from the final model.

Indicator variable	Mean	Standard Deviation	Quantiles				
			2.5%	25%	50%	75%	97.5%
I_{den}	1.00	0.00	1	1	1	1	1
$I_{den \times river}$	1.00	0.00	1	1	1	1	1
$I_{den \times tmf}$	1.00	0.00	1	1	1	1	1
$I_{den \times tmf \times river}$	1.00	0.00	1	1	1	1	1
I_{smf}	0.92	0.27	0	1	1	1	1
I_{spt}	0.77	0.42	0	1	1	1	1
I_{spt^2}	0.71	0.45	0	0	1	1	1
I_{wdd}	1.00	0.00	1	1	1	1	1

Table S7. [Length model convergence statistics] Gelman statistic estimates for all estimated parameters in the age models. Note: an estimate of 1 suggested converged, stationary and well mixing chains.

| Estimate	Point estimate	Upper Confidence Interval
a	1.01	1.02
b_den	1.01	1.04
b_denr[1]	1.02	1.08
b_denr[2]	1.02	1.06
b_denr[3]	1.00	1.01
b_dentmf	1.00	1.01
b_dentmfr[1]	1.01	1.05
b_dentmfr[2]	1.01	1.02
b_dentmfr[3]	1.01	1.01
b_smf	1.01	1.01
b_spt	1.12	1.40
b_sptq	1.15	1.42
b_wdd	1.01	1.01

291
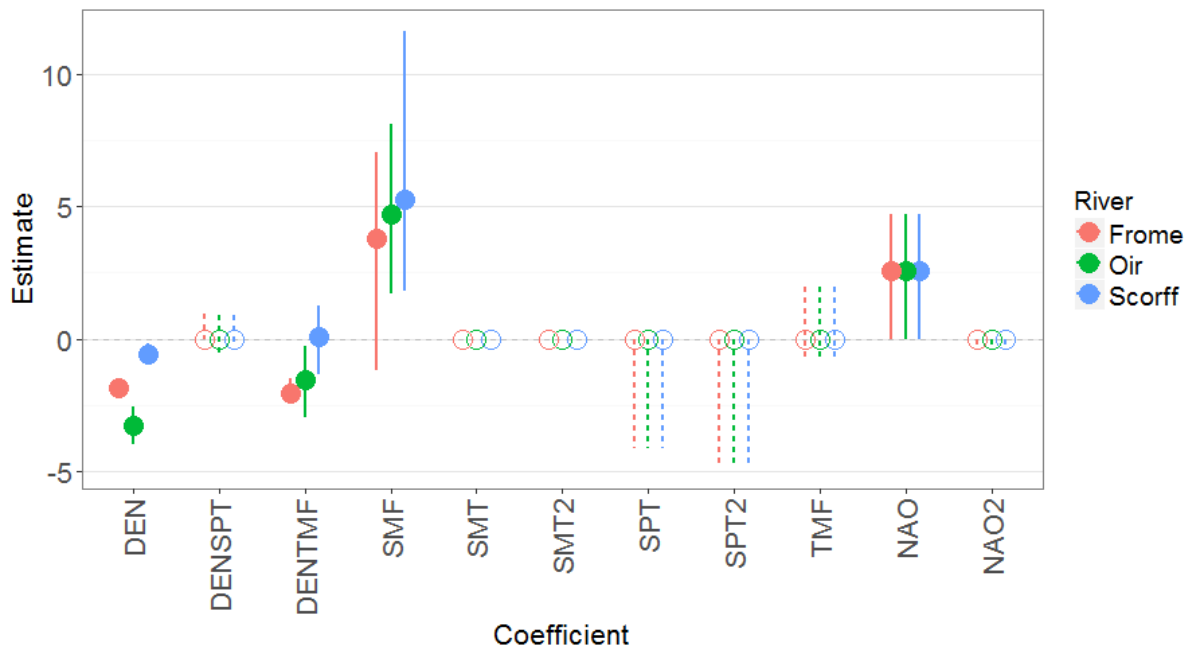
Figure S6. [NAO coefficients] Caterpillar plot showing the coefficient estimates (and 95% Bayesian credible intervals) for each of the environmental variables included in the length model with a measure of winter North Atlantic Oscillation (NAO) in place of Winter Degree Days (WDD). Filled circles with solid bars identify coefficients retained in the model; hollow circles with dashed bars identify coefficients that were dropped. Where coefficient estimates are the same, the river-interaction effect has been dropped suggesting that the effect of that environmental variable can be represented as a single coefficient applicable to all three rivers, i.e., its effect is "regional" rather than "local" (see text). Abbreviations are: DEN, conspecific density; DENSPT, conspecific density x spring mean temperature; DENTMF, conspecific density x total mean discharge; SMF, summer minimum discharge, SMT, summer maximum temperature; SMT2, summer maximum temperature ^2; SPT spring mean temperature; SPT2 spring mean temperature ^2; TMF total mean discharge; NAO, winter NAO; and NAO2, winter NAO ^2.

304

305
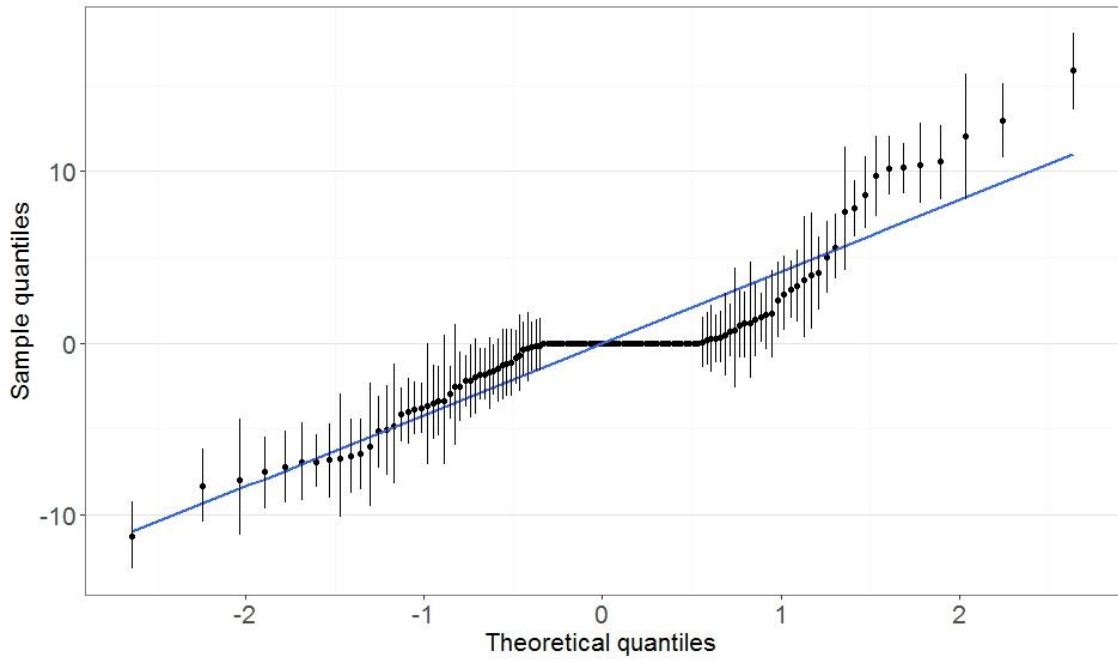
306   (a)
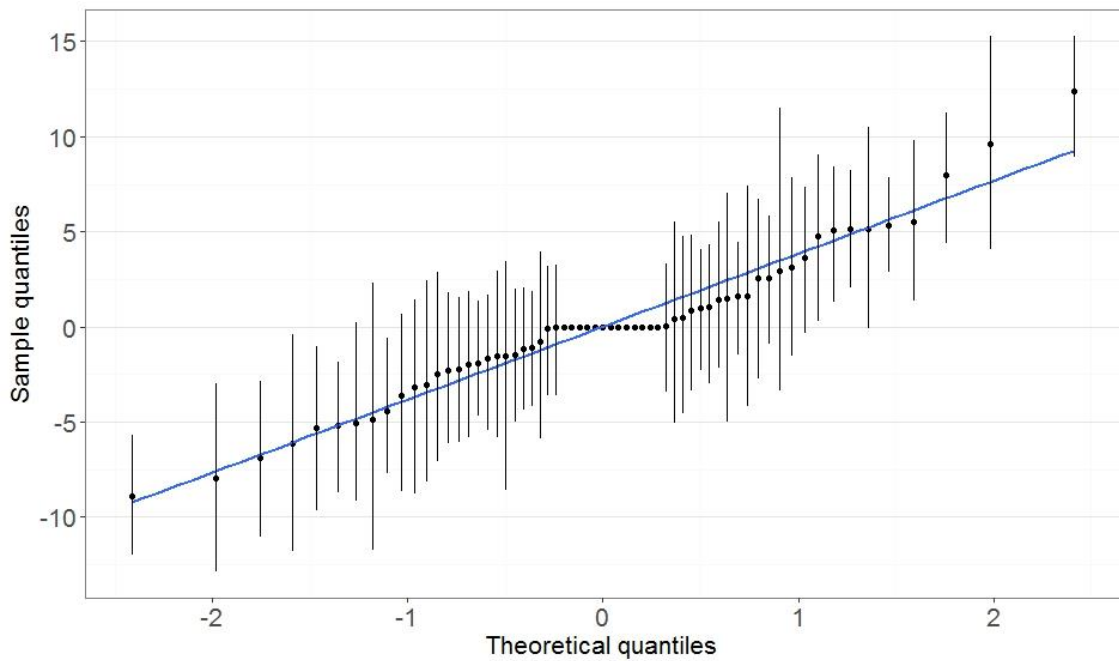
307   (b)

308   **Figure S7.** [Random effect QQ-plots] Quantile-quantile plots showing that the (a) Site within River
309   and (b) Year within River random effects empirical distributions did not differ substantially from a
310   theoretical normal distribution for the length model. Note: several effects are equal to 0 and have
311   no variance because they represent sites or years that were not surveyed in some rivers.

312

313
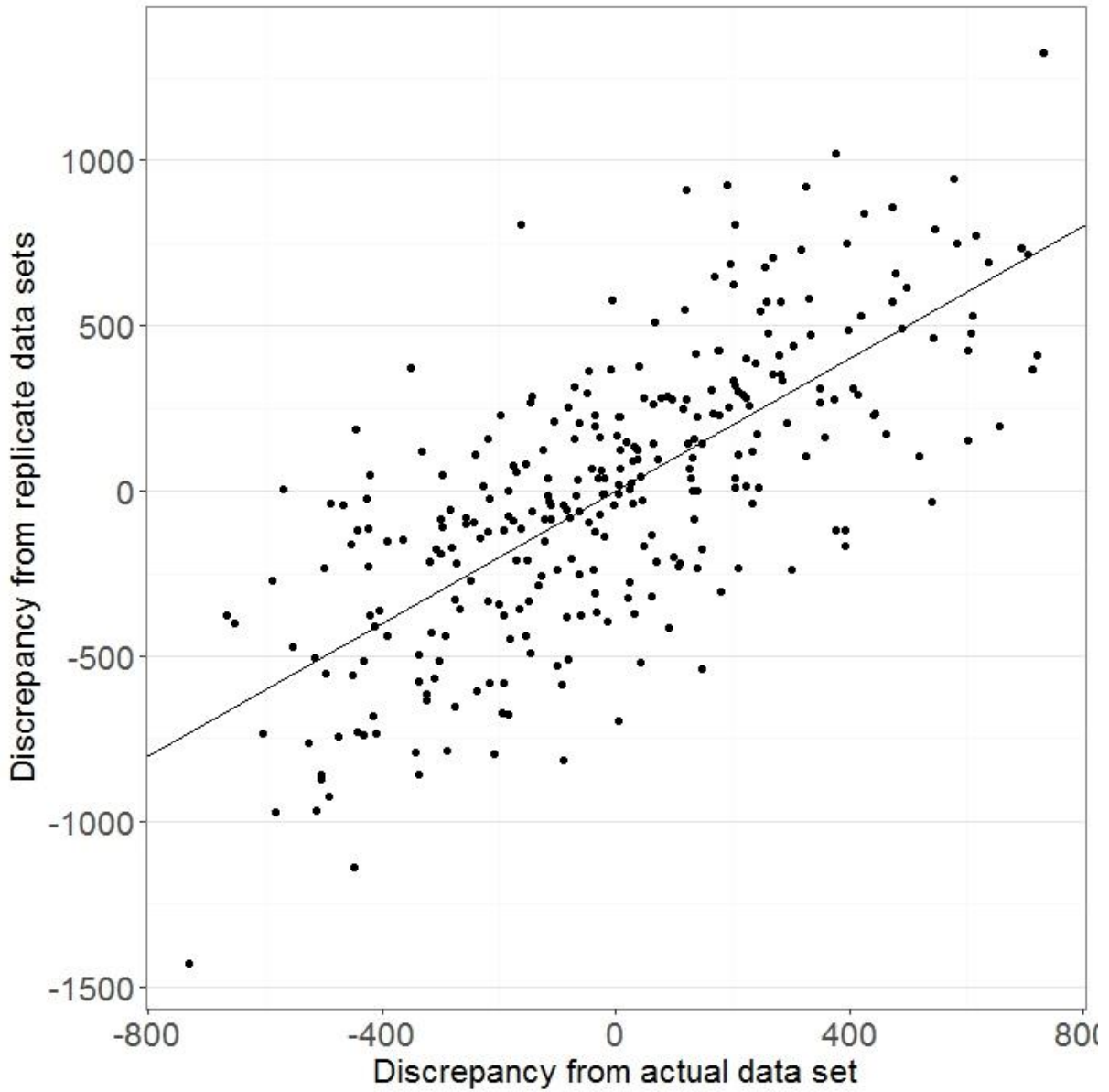
Figure S8. [Length model adequacy plot] Plot showing the performance of the length model for replicate datasets. The Bayesian P value was 0.48, indicating that this model provided an adequate fit to the data.

317

318
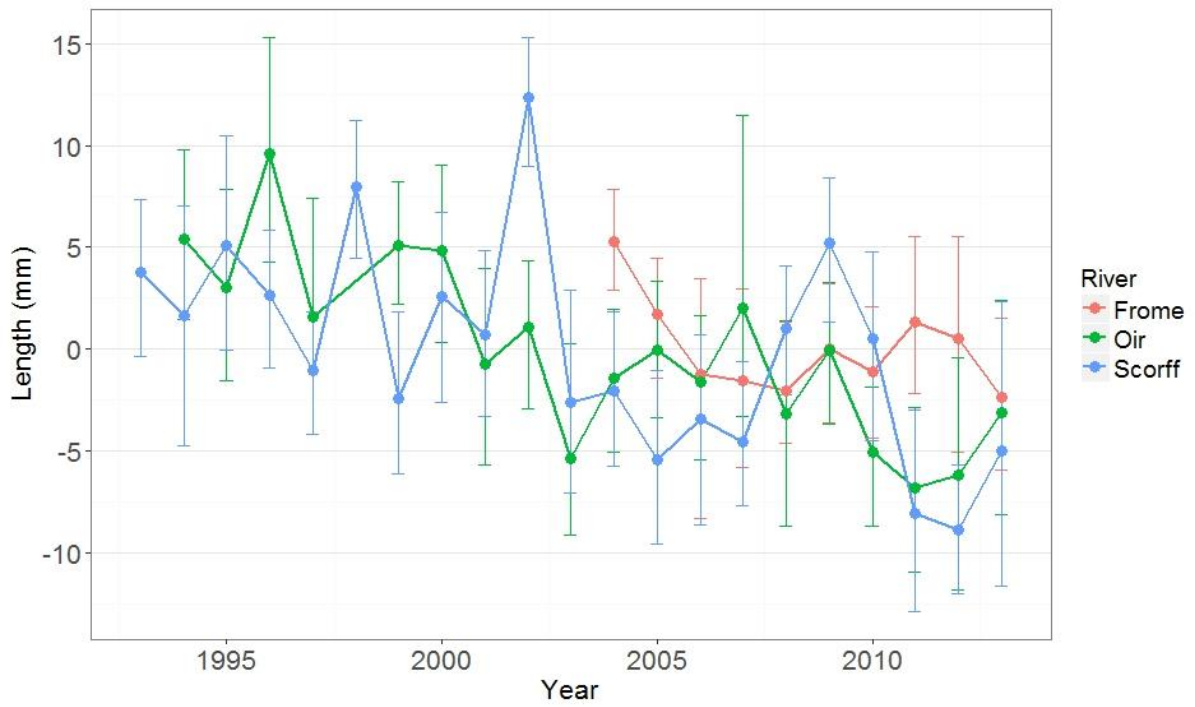
Figure S9. [Year random effect plot] Plot showing the year-specific random effect estimates plotted
by year for the Frome (Dorset, UK), Oir (Normandy, France) and Scorff (Brittany, France). Note: there
appears to be a residual declining trend in all three rivers that was not explained by the
environmental explanatory variables used in this study.

323

324   (a)
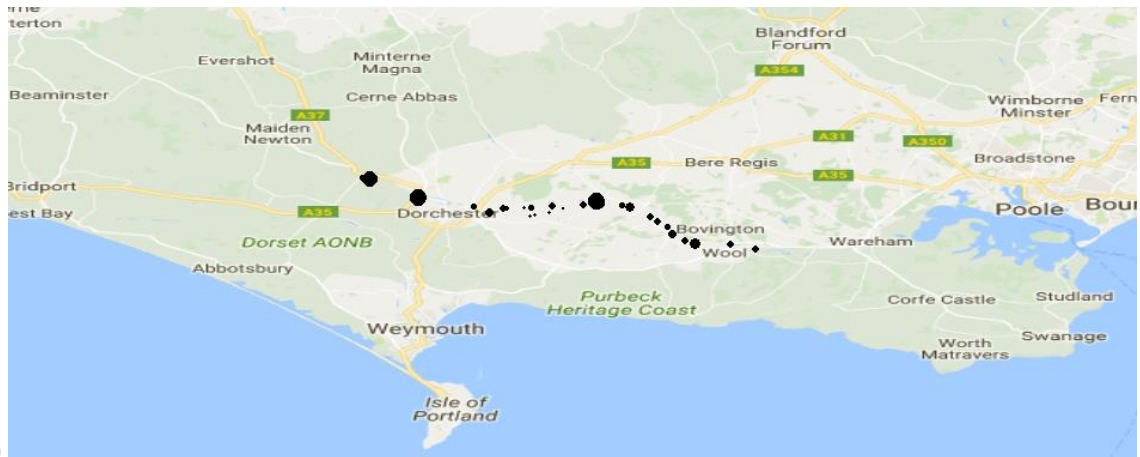
325   (b)

326   (c)

327   **Figure S10.** [Site random effect maps] Maps showing the relative size of site-specific random effect
328   estimates for the (a) Frome (Dorset, UK), (b) Oir (Normandy, France) and (c) Scorff (Brittany, France).
329   Note: there does not appear to be any relationship to distance from tidal limit.

330

Annotated JAGS code for the Age model

```
331   {
332
333
334           ## notes
335           ## parameter code in parentheses, e.g., B_1, correspond with the explanatory variable in
336           ## eqn 1.
337           ## pAges is written as pi in eqn 1
338
339           ## intercept
340           alpha ~ dnorm(0, 0.001)
341
342           ## precocious fixed effect (B_1)
343           beta_p ~ dnorm(0, 0.001)
344
345           ## day of Year fixed effect (B_2)
346           l_beta_d ~ dnorm(0, 0.001)
347
348           ## site fixed effect (B_3)
349           beta_s[1] <- 0
350           for(i in 2:n_sites){
351                   l_beta_s[i] ~ dnorm(0, 0.001)
352           }
353
354           ## year fixed effect (B_4)
355           for(i in 1:(n_years - 1)){
356                   l_beta_y[i] ~ dnorm(0, 0.001)
357           }
358           l_beta_y[n_years] <- 0
359
360           ### error model
361           ## tau
362           tau ~ dgamma(0.001, 0.001)
363           sigma <- 1 / sqrt(tau)
364
365           ## delta
366           delta ~ dnorm(0, 0.001);T(0, )
367
368           ## proportional age split
369           pAges[1:2] ~ ddirch(Ps[])
370
371           ## model fitting
372           for(i in 1:n_fishes){
373
374                   ## length error estimate
375                   Length_mm[i] ~ dnorm(mu[i], tau)
376
377                   ## average length estimate
378                   mu_prime[i] <- l_alpha + (l_beta_p * Precocious[i]) + (l_beta_d * DoY[i]) +
379           l_beta_s[Site[i]] + l_beta_y[Year[i]]\nmu[i] <- mu_prime[i] + ((Age[i] - 1) * delta)
380
```

```
381                # Estimate age
382                Age[i] ~ dcat(pAges[])
383
384                } # end of fish loop
385
386        }
387
388
```

Annotated JAGS code for the Length model

```
{

        ## notes
        ## #####
        ## - parameter names correspond with the environmental explanatory variable
        ##      abbreviations used in the main text. For example, "b_den" is the coefficient
        ##      capturing the strength of the effect of conspecific density or DEN on mean age 0
        ##      parr lengths. Parameters ending with "_p" or "_p_tmp" are related to indicator
        ##      variables. Parameters ending with "r" are river interactions, those ending with "q"
        ##      are quadratic terms and those ending with "rq" are quadratic terms in interaction
        ##      with river.
        ## - main effects are given the weakly informative prior dnorm(0, 0.001)
        ## - variance terms are given the weakly informative prior dgamma(1, 0.001)
        ## - terms are included conditional upon other terms, according to the following rules:
        ##      + a main effect is included with probability 1.0 if the river interaction effect is
        ##              included, otherwise it is included with probability 0.5
        ##      + a quadratic main term is included with probability 0.5 if the linear main term is
        ##              included, otherwise it is not included
        ##      + a quadratic river interaction term is included with probability 0.5 if the linear
        ##              river interaction term is included, otherwise it is not included
        ## - model adequacy is measured using simulated datasets to calculate the Bayesian P value

        ## intercept
        a ~ dnorm(0, 0.01)

        ## river main effect
        for (r in 1:n_rivers) {
          b_r[r] ~ dnorm(0, tau_b_r)
        }
        tau_b_r ~ dgamma(1, 0.01)

        ## precocious main effect and precocious * river interaction effect
        b_precocious ~ dnorm(0, 0.01)
        for(r in 1:(n_rivers - 1)){
          b_precociousr[r] ~ dnorm(0, 0.01)
        }
        b_precociousr[n_rivers] <- -sum(b_precociousr[1:(n_rivers - 1)])

        ## doy main effect
        b_doy ~ dnorm(0, 0.01)

        ## den effects
        ### den linear main effect conditional on linear interaction term
        b_den_tmp ~ dnorm(0, 0.01)
        b_den_p_tmp <- b_denr_p + ((1 - b_denr_p) * 0.5)
        b_den_p ~ dbern(b_den_p_tmp)
        b_den <- b_den_p * b_den_tmp
        ### den * river interaction term
        for(r in 1:n_rivers){
```

```
439          b_denr_p_tmp[r] ~ dbern(0.5)
440          }
441          b_denr_p ~ dbern(sum(b_denr_p_tmp) / n_rivers)
442          for(r in 1:(n_rivers - 1)){
443            b_denr_tmp[r] ~ dnorm(0, 0.01)
444          }
445          b_denr_tmp[n_rivers] <- -sum(b_denr_tmp[1:(n_rivers - 1)])
446          for(r in 1:n_rivers){
447            b_denr[r] <- b_denr_p * b_denr_tmp[r]
448          }
449
450          ## wdd effects
451          ### wdd linear main effect conditional on linear interaction term
452          b_wdd_tmp ~ dnorm(0, 0.01)
453          b_wdd_p_tmp <- b_wddr_p + ((1 - b_wddr_p) * 0.5)
454          b_wdd_p ~ dbern(b_wdd_p_tmp)
455          b_wdd <- b_wdd_p * b_wdd_tmp
456          ### wdd quadratic main effect conditional on linear main effect term
457          b_wddq_tmp ~ dnorm(0, 0.01)
458          b_wddq_p_tmp <- b_wdd_p * 0.5
459          b_wddq_p ~ dbern(b_wddq_p_tmp)
460          b_wddq <- b_wddq_p * b_wddq_tmp
461          ### wdd * river interaction term
462          for(r in 1:n_rivers){
463            b_wddr_p_tmp[r] ~ dbern(0.5)
464          }
465          b_wddr_p ~ dbern(sum(b_wddr_p_tmp) / n_rivers)
466          for(r in 1:(n_rivers - 1)){
467            b_wddr_tmp[r] ~ dnorm(0, 0.01)
468          }
469          b_wddr_tmp[n_rivers] <- -sum(b_wddr_tmp[1:(n_rivers - 1)])
470          for(r in 1:n_rivers){
471            b_wddr[r] <- b_wddr_p * b_wddr_tmp[r]
472          }
473          ### wdd * river interaction term conditional on linear interaction term
474          p_wddrq <- b_wddr_p * 0.5
475          for(r in 1:n_rivers){
476            b_wddrq_p_tmp[r] ~ dbern(p_wddrq)
477          }
478          b_wddrq_p ~ dbern(sum(b_wddrq_p_tmp) / n_rivers)
479          for(r in 1:(n_rivers - 1)){
480            b_wddrq_tmp[r] ~ dnorm(0, 0.01)
481          }
482          b_wddrq_tmp[n_rivers] <- -sum(b_wddrq_tmp[1:(n_rivers - 1)])
483          for(r in 1:n_rivers){
484            b_wddrq[r] <- b_wddrq_p * b_wddrq_tmp[r]
485          }
486
487          ## spt effects
488          ### spt linear main effect conditional on linear interaction term
489          b_spt_tmp ~ dnorm(0, 0.01)
```

```
490        b_spt_p_tmp <- b_sptr_p + ((1 - b_sptr_p) * 0.5)
491        b_spt_p ~ dbern(b_spt_p_tmp)
492        b_spt <- b_spt_p * b_spt_tmp
493        ### spt quadratic main effect conditional on linear main effect term
494        b_sptq_tmp ~ dnorm(0, 0.01)
495        b_sptq_p_tmp <- b_spt_p * 0.5
496        b_sptq_p ~ dbern(b_sptq_p_tmp)
497        b_sptq <- b_sptq_p * b_sptq_tmp
498        ### spt * river interaction term
499        for(r in 1:n_rivers){
500          b_sptr_p_tmp[r] ~ dbern(0.5)
501        }
502        b_sptr_p ~ dbern(sum(b_sptr_p_tmp) / n_rivers)
503        for(r in 1:(n_rivers - 1)){
504          b_sptr_tmp[r] ~ dnorm(0, 0.01)
505        }
506        b_sptr_tmp[n_rivers] <- -sum(b_sptr_tmp[1:(n_rivers - 1)])
507        for(r in 1:n_rivers){
508          b_sptr[r] <- b_sptr_p * b_sptr_tmp[r]
509        }
510        ### spt * river interaction term conditional on linear interaction term
511        p_sptrq <- b_sptr_p * 0.5
512        for(r in 1:n_rivers){
513          b_sptrq_p_tmp[r] ~ dbern(p_sptrq)
514        }
515        b_sptrq_p ~ dbern(sum(b_sptrq_p_tmp) / n_rivers)
516        for(r in 1:(n_rivers - 1)){
517          b_sptrq_tmp[r] ~ dnorm(0, 0.01)
518        }
519        b_sptrq_tmp[n_rivers] <- -sum(b_sptrq_tmp[1:(n_rivers - 1)])
520        for(r in 1:n_rivers){
521          b_sptrq[r] <- b_sptrq_p * b_sptrq_tmp[r]
522        }
523
524        ## smt effects
525        ### smt linear main effect conditional on linear interaction term
526        b_smt_tmp ~ dnorm(0, 0.01)
527        b_smt_p_tmp <- b_smtr_p + ((1 - b_smtr_p) * 0.5)
528        b_smt_p ~ dbern(b_smt_p_tmp)
529        b_smt <- b_smt_p * b_smt_tmp
530        ### smt quadratic main effect conditional on linear main effect term
531        b_smtq_tmp ~ dnorm(0, 0.01)
532        b_smtq_p_tmp <- b_smt_p * 0.5
533        b_smtq_p ~ dbern(b_smtq_p_tmp)
534        b_smtq <- b_smtq_p * b_smtq_tmp
535        ### smt * river interaction term
536        for(r in 1:n_rivers){
537          b_smtr_p_tmp[r] ~ dbern(0.5)
538        }
539        b_smtr_p ~ dbern(sum(b_smtr_p_tmp) / n_rivers)
540        for(r in 1:(n_rivers - 1)){
```

```
541        b_smtr_tmp[r] ~ dnorm(0, 0.01)
542      }
543      b_smtr_tmp[n_rivers] <- -sum(b_smtr_tmp[1:(n_rivers - 1)])
544      for(r in 1:n_rivers){
545        b_smtr[r] <- b_smtr_p * b_smtr_tmp[r]
546      }
547      ### smt * river interaction term conditional on linear interaction term
548      p_smtrq <- b_smtr_p * 0.5
549      for(r in 1:n_rivers){
550        b_smtrq_p_tmp[r] ~ dbern(p_smtrq)
551      }
552      b_smtrq_p ~ dbern(sum(b_smtrq_p_tmp) / n_rivers)
553      for(r in 1:(n_rivers - 1)){
554        b_smtrq_tmp[r] ~ dnorm(0, 0.01)
555      }
556      b_smtrq_tmp[n_rivers] <- -sum(b_smtrq_tmp[1:(n_rivers - 1)])
557      for(r in 1:n_rivers){
558        b_smtrq[r] <- b_smtrq_p * b_smtrq_tmp[r]
559      }
560
561      ## tmf effects
562      ### tmf linear main effect conditional on linear interaction term
563      b_tmf_tmp ~ dnorm(0, 0.01)
564      b_tmf_p_tmp <- b_tmfr_p + ((1 - b_tmfr_p) * 0.5)
565      b_tmf_p ~ dbern(b_tmf_p_tmp)
566      b_tmf <- b_tmf_p * b_tmf_tmp
567      ### tmf * river interaction term
568      for(r in 1:n_rivers){
569        b_tmfr_p_tmp[r] ~ dbern(0.5)
570      }
571      b_tmfr_p ~ dbern(sum(b_tmfr_p_tmp) / n_rivers)
572      for(r in 1:(n_rivers - 1)){
573        b_tmfr_tmp[r] ~ dnorm(0, 0.01)
574      }
575      b_tmfr_tmp[n_rivers] <- -sum(b_tmfr_tmp[1:(n_rivers - 1)])
576      for(r in 1:n_rivers){
577        b_tmfr[r] <- b_tmfr_p * b_tmfr_tmp[r]
578      }
579
580      ## smf effects
581      ### smf linear main effect conditional on linear interaction term
582      b_smf_tmp ~ dnorm(0, 0.01)
583      b_smf_p_tmp <- b_smfr_p + ((1 - b_smfr_p) * 0.5)
584      b_smf_p ~ dbern(b_smf_p_tmp)
585      b_smf <- b_smf_p * b_smf_tmp
586      ### smf * river interaction term
587      for(r in 1:n_rivers){
588        b_smfr_p_tmp[r] ~ dbern(0.5)
589      }
590      b_smfr_p ~ dbern(sum(b_smfr_p_tmp) / n_rivers)
591      for(r in 1:(n_rivers - 1)){
```

```
592        b_smfr_tmp[r] ~ dnorm(0, 0.01)
593        }
594        b_smfr_tmp[n_rivers] <- -sum(b_smfr_tmp[1:(n_rivers - 1)])
595        for(r in 1:n_rivers){
596          b_smfr[r] <- b_smfr_p * b_smfr_tmp[r]
597        }
598
599        ## den * spt interaction effects
600        ### denspt linear main effect conditional on linear interaction term
601        b_denspt_tmp ~ dnorm(0, 0.01)
602        b_denspt_p_tmp <- b_densptr_p + ((1 - b_densptr_p) * 0.5)
603        b_denspt_p ~ dbern(b_denspt_p_tmp)
604        b_denspt <- b_denspt_p * b_denspt_tmp
605        ### denspt * river interaction term
606        for(r in 1:n_rivers){
607          b_densptr_p_tmp[r] ~ dbern(0.5)
608        }
609        b_densptr_p ~ dbern(sum(b_densptr_p_tmp) / n_rivers)
610        for(r in 1:(n_rivers - 1)){
611          b_densptr_tmp[r] ~ dnorm(0, 0.01)
612        }
613        b_densptr_tmp[n_rivers] <- -sum(b_densptr_tmp[1:(n_rivers - 1)])
614        for(r in 1:n_rivers){
615          b_densptr[r] <- b_densptr_p * b_densptr_tmp[r]
616        }
617
618        ## den * tmf interaction effects
619        ### dentmf linear main effect conditional on linear interaction term
620        b_dentmf_tmp ~ dnorm(0, 0.01)
621        b_dentmf_p_tmp <- b_dentmfr_p + ((1 - b_dentmfr_p) * 0.5)
622        b_dentmf_p ~ dbern(b_dentmf_p_tmp)
623        b_dentmf <- b_dentmf_p * b_dentmf_tmp
624        ### dentmf * river interaction term
625        for(r in 1:n_rivers){
626          b_dentmfr_p_tmp[r] ~ dbern(0.5)
627        }
628        b_dentmfr_p ~ dbern(sum(b_dentmfr_p_tmp) / n_rivers)
629        for(r in 1:(n_rivers - 1)){
630          b_dentmfr_tmp[r] ~ dnorm(0, 0.01)
631        }
632        b_dentmfr_tmp[n_rivers] <- -sum(b_dentmfr_tmp[1:(n_rivers - 1)])
633        for(r in 1:n_rivers){
634          b_dentmfr[r] <- b_dentmfr_p * b_dentmfr_tmp[r]
635        }
636
637        ## site within river random effect with half-normal variance
638        for(r in 1:n_rivers){
639          mu_r_s[r] <- 0
640          sigma_r_s[r] ~ dnorm(0, 0.01);T(0, )
641          for(s in (n_sites[r] + 1):max(n_sites)){
642            u[r, s] <- 0
```

```
643                }
644               for(s in 1:n_sites[r]){
645                 u[r, s] ~ dnorm(mu_r_s[r], sigma_r_s[r])
646               }
647             }
648
649            ## year within river random effect with half-normal variance
650            for(r in 1:n_rivers){
651             mu_r_y[r] <- 0
652             sigma_r_y[r] ~ dnorm(0, 0.01);T(0, )
653             for(y in (n_years[r] + 1):max(n_years)){
654              v[r, y] <- 0
655             }
656             for(y in 1:n_years[r]){
657              v[r, y] ~ dnorm(mu_r_y[r], sigma_r_y[r])
658             }
659            }
660
661            ## model error
662            tau ~ dgamma(0.001, 0.001)
663            sigma <- 1/sqrt(tau)
664
665            ## model fitting
666            for (i in 1:n_fishes) {
667
668             Length_mm[i] ~ dnorm(mu[i], tau)
669
670             mu[i] <- a + b_r[River[i]] +
671              b_precocious * Precocious[i] + b_precociousr[River[i]] * Precocious[i] +
672              b_doy * DoY[i] +
673              b_den * deltaDens[i] + b_denr[River[i]] * deltaDens[i] +
674              b_wdd * WntDegD[i] + b_wddq * WntDegD[i]^2 + b_wddr[River[i]] * WntDegD[i] +
675    b_wddrq[River[i]] * WntDegD[i]^2 +
676                b_spt * SpgAvgT[i] + b_sptq * SpgAvgT[i]^2 + b_sptr[River[i]] * SpgAvgT[i] +
677    b_sptrq[River[i]] * SpgAvgT[i]^2 +
678                b_smt * SmrMaxT[i] + b_smtq * SmrMaxT[i]^2 + b_smtr[River[i]] * SmrMaxT[i] +
679    b_smtrq[River[i]] * SmrMaxT[i]^2 +
680                b_tmf * TotAvgF[i] + b_tmfr[River[i]] * TotAvgF[i] +
681                b_smf * SmrMinF[i] + b_smfr[River[i]] * SmrMinF[i] +
682                b_denspt * DensSpt[i] + b_densptr[River[i]] * DensSpt[i] +
683                b_dentmf * DensTmf[i] + b_dentmfr[River[i]] * DensTmf[i] +
684                u[River[i], Site[i]] + v[River[i], Year[i]]
685
686             }
687
688            ## model adequacy; Bayesian P value
689            for(i in 1:n_fishes){
690             res[i] <- (Length_mm[i] - mu[i]) / sigma
691             p.res[i] <- phi(res[i])
692             pred[i] ~ dnorm(mu[i], tau)
693             p.pred[i] <- step(Length_mm[i] - pred[i])
```

```
694              res.pred[i] <- (Length_mm[i] - pred[i]) / sigma
695            }
696          D.fit <- sum(res[])
697          D.fit.pred <- sum(res.pred[])
698
699        }
700
701
```