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# Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*

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1 Title:

2 Evidence for long term change in length, weight and migration phenology of anadromous  
3 spawners in French Atlantic salmon *Salmo salar*

4

5

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15

16 Running headline:

17 Changing salmon size and phenology in France

18

19 Abstract

20 We provide new data on Atlantic salmon *Salmo salar* life history traits across France, using a  
21 recreational angling database coming from fed by a mandatory catch declaration scheme over  
22 a large temporal (1987-2013) and spatial (n = 34 rivers) scale including three regions (genetic  
23 units). We reported new insights on changes in *S. salar* life history traits, with a decline in  
24 individual length, weight and a delay in the migration phenology of adult *S. salar* returning to  
25 French rivers. Similarities in time trends between regions may be attributable to common  
26 changes in environmental conditions at sea. Results also revealed different rates of change  
27 between early maturing fish (1SW fish) and late maturing fish (2SW fish), phenotypic traits  
28 being less variable and less impacted by environmental variations in freshwater returning  
29 2SW fish than in 1SW ones. This study highlights the necessity to account for the variability  
30 in life history strategies when exploring mechanisms of phenotypic change in *S. salar*.  
31 Detailed data on *S. salar* in France have long been missing from the literature. This large  
32 scale study on French populations contributes to reduce the gap in knowledge by providing  
33 further empirical evidence of a global pattern in *S. salar* life history shared by all populations  
34 across the Atlantic Ocean, which is consistent with the widespread hypothesis of global  
35 response of populations to a major ecological mechanism during the marine phase of the life  
36 cycle.

37

38

39 Keywords

40 body size, environmental buffering, environmental variability, life history strategy, *Salmo*  
41 *salar*

42

43 Introduction

44

45

46 Global climate warming in the Atlantic Ocean is responsible for rising sea surface  
47 temperature since the 1970's ([Levitus et al., 2000](#); [Polyakov et al., 2009](#)). There is also strong  
48 evidence that climate change is altering ecosystem functioning, which is driving a major shift,  
49 observable across multiple trophic levels, in the North Atlantic ([Durant et al., 2004](#);  
50 [Beaugrand et al., 2008](#)). Concomitantly, Atlantic salmon *Salmo salar* L. 1758 populations  
51 have suffered a tremendous decline in abundance across their distribution range ([Jonsson &](#)  
52 [Jonsson, 2004](#); [Chaput, 2012](#); [ICES, 2016](#)), together with marked changes in life history traits  
53 and population structure. In particular, a decline in the proportion of late maturing fish has  
54 been reported for many European and North American stocks ([Baglinière et al., 2004](#); [ICES,](#)  
55 [2016](#); [Jonsson et al. 2016](#); [Otero et al. 2012](#)). Those changes have been accompanied by  
56 declines in age-specific length and weight of fish ([Aprahamian et al., 2008](#); [Bacon et al.,](#)  
57 [2009](#); [Jonsson et al. 2016](#)), together with a delay in adult migration timing ([Todd et al., 2012](#);  
58 [Valiente et al., 2011](#)). Such changes are expected to affect population growth rate, raising  
59 concerns about the viability of this species of great patrimonial and economical value.

60

61

62 Identifying the causal link between latent driving factors and those phenotypic changes is  
63 difficult and may consist in one of the greatest challenges for fisheries ecology, and for *S.*  
64 *salar* in particular ([Crozier & Hutchings, 2014](#)). Due to a complex life cycle shared between  
65 freshwater and the marine environment, diadromous fishes are vulnerable to various factors of  
66 stress in a hierarchy of spatial scales ([Armstrong et al., 1998](#); [Mather et al., 1998](#); [Lindburg &](#)  
67 [Waldman, 2009](#)). Evidence now accumulates for a major impact of changes in the marine

68 environment encountered by *S. salar* (Jonsson & Jonsson, 2004; ICES, 2016; Jonsson *et al.*,  
69 2016). Both direct and indirect effects of rising sea surface temperature have been proposed.  
70 Temperature increase would impede post-smolt growth (Friedland *et al.*, 2000, 2005). In  
71 addition, temperature increase would decrease the productivity of North Atlantic pelagic food  
72 web, thus indirectly affecting feeding opportunities for salmon at sea (Friedland *et al.*, 2000;  
73 Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008; Jensen *et al.*, 2011). In particular, the  
74 abundance and/or energy content of key pelagic crustaceans and small pelagic fish, on which  
75 *S. salar* largely prey, may have declined (Beaugrand & Reid, 2012; Friedland *et al.*, 2013;  
76 Mills *et al.*, 2013; Miller *et al.*, 2014). Recent stock rebuilding in some pelagic fish competing  
77 for similar resource as *S. salar* may further amplify this process (Jonsson *et al.* 2016;  
78 Mäntyniemi *et al.*, 2012).

79

80

81 Simultaneous temporal trends in growth, length, weight and/or phenology variations have  
82 been observed in Norway (Jensen *et al.*, 2011), Ireland (Quinn *et al.*, 2006), and Scotland  
83 (Summers, 1995; Todd *et al.*, 2008; Bacon *et al.*, 2011). Given that those populations breed in  
84 very distant rivers, the existence of a large-scale mechanism taking at sea has been suggested.  
85 To go further, large scale data for Southern populations is required to confirm the influence  
86 and the extent of such global change. Yet, precise ecological and demographic mechanisms  
87 that underline those changes are still not clear (Crozier and Hutchings, 2014). Despite elusive  
88 causes, there is a need to better understand the factors regulating *S. salar* response to ongoing  
89 environmental change, for management and policy purposes.

90

91

92 In *S. salar*, anadromous adults mature after one winter at sea (1SW) or more than one winter  
93 at sea (MSW, i.e. up to five years) (Hutchings & Jones, 1998; Aas *et al.*, 2011). The  
94 differences in their respective life history traits (e.g. body size, growth rate, age at maturity,  
95 fecundity or migration timing) reflect the strategy of resource allocation to growth, survival  
96 and reproduction (Cody, 1966; Williams, 1966; Schaffer, 1983; Stearns, 1976). Under this  
97 strategy, alternative tactics seem to be partially determined by sex and genes (Fleming, 1996;  
98 Barson *et al.*, 2015). Females, whose breeding success is strongly related to body size  
99 (Fleming, 1996), are more abundant among MSW, while males tend to mature earlier i.e.  
100 most of them are 1SW (Hutchings & Jones, 1998; Aas *et al.*, 2011). Thus, any change in  
101 resource availability or more generally in environmental conditions at sea is likely to induce  
102 contrasted response in 1SW and MSW, because of difference in their resource allocation  
103 (Stearns, 1976; Gaillard *et al.*, 1989; Reznick *et al.*, 1996). In Southern Europe, growing areas  
104 at sea used by MSW are farther away than in 1SW, resulting in an even greater contrast in  
105 mortality during sea migration between tactics. For instance, somatic growth might be more  
106 impacted by poor environmental condition at sea in 1SW, as energy allocation might be  
107 primarily dedicated to maturation in this group. Also, differences in age and sex-ratio between  
108 sea-age classes may confer different ability in buffering external forcing in 1SW and MSW,  
109 as already observed in mammals for instance (Coulson *et al.*, 2001). Monitoring life history  
110 traits by sea age class is essential to better understand and predict species response to ongoing  
111 global changes and provide sound insights for the management of *S. salar* across its  
112 distribution range (Armstrong *et al.*, 1998; Mather *et al.*, 1998).

113

114

115 In this study we investigated the long term change in length, weight and migration phenology  
116 of French *S. salar* populations over the last three decades, using a recreational angling

117 database coming from fed by a mandatory catch declaration scheme over a large spatial (n =  
118 34 rivers) scale. Although the available literature accumulates evidence of temporal changes  
119 in life history traits in a high number of *S. salar* populations, only few results concern  
120 Southern Europe rivers (Valiente et al., 2011) and no results have been published for France  
121 so far. Extending the geographical range for which evidence of changes are documented is a  
122 prerequisite to test for the hypothesis of a common response of *S. salar* to environmental  
123 conditions at sea, and then refine our understanding of the factors driving those reported  
124 changes. We described how *S. salar* length, weight, body condition factor and annual  
125 migration timing have changed over the period 1987-2013 in French rivers. We investigated  
126 whether common patterns could be detected in geographically distant populations. We then  
127 tested the hypothesis of a tactic-dependent response to environmental variation in *S. salar*.  
128 Finally, we assessed the difference in individual response in 1SW and MSW, by analyzing the  
129 relative rate of change in key life history traits between 1SW and MSW over the study period.  
130 Overall, results brought new contributions to the understanding of the demographic and  
131 evolutionary forces that control *S. salar* response to environmental change in the Southern  
132 part of the species distribution range.

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135

## 136 MATERIALS & METHODS

137

138 Recreational fishery data

139

140

141 Analyses are based on the French recreational angling database fed by a mandatory catch  
142 declaration scheme over a large temporal (1987-2013) and spatial (n = 34 rivers) scale. In  
143 France, *S. salar* recreational rod and line fishery takes place in more than 40 rivers of the  
144 Atlantic and Channel coasts, which are characterized by uneven spatial distribution and river  
145 profiles. These rivers are mainly localized in three regions that represent more than 90% of  
146 French *S. salar* abundance: Normandy, Brittany and Aquitaine (Fig. 1). This regional  
147 stratification results from previous analyses of both the genetic structure of French *S. salar*  
148 populations and based on their demographic and morphometric characteristics (Prévost, 1987;  
149 Perrier *et al.*, 2011). In addition to recreational fishery, a small commercial fishery takes place  
150 in the Adour River, Aquitaine region (on average 10.5 % of the annual salmon catches). The  
151 fishing season extends from the beginning of March to the end of October for rod fishing and  
152 to the end of July for commercial fishing. Since 1987, *S. salar* fishery rely on a national  
153 compulsory catch declaration scheme which offers a national sampling survey of adult *S.*  
154 *salar* and feed one of the largest dataset for salmonid fishery in Europe. Catch data are  
155 collected by anglers and centralized by the National Center for the Interpretation of Salmonid  
156 Catches. For each fish caught, the recorded data are date (D, day of the year), river, size (L,  
157 total length in mm), weight (W, in g) and a sample of scales. All scales are analyzed  
158 following a standardized protocol (Baglinière *et al.*, 1985) to estimate both the time spent in  
159 freshwater during the juvenile phase (freshwater age) and the time spent at sea during the  
160 adult phase of the life cycle, i.e. (sea-age). Current French populations are mainly composed  
161 of one sea winter (1SW), two sea winters (2SW) and rarely three sea winters (3SW) salmon.  
162 However, because of the unbalanced fishing effort between sea-age classes (being historically  
163 more intense on large 2SW fish than on 1SW ones), the data do not allow us to draw any  
164 inference on the relative abundance of the two tactics and its variation over time.

165



166

167 The ordinal date of capture (D) was considered as an index for the date of river entry. Indeed,  
168 as already discussed in Bacon et al. (2009), the rod capture data mostly concerns newly  
169 arrived fresh-run fish, often caught in lower parts of rivers just after their entry in freshwater.  
170 Several studies have shown that the movements and capture rates of *S. salar* decline rapidly  
171 after river entry (e.g., Thorley et al., 2005), suggesting that *S. salar* may be harder to catch by  
172 rod after several days in freshwater.

173

174

175 Because salmonids are considered to have a standard body shape, we used the condition  
176 coefficient of Fulton (K) as a proxy for *S. salar* body condition. It is calculated for each fish  
177 as  $K = W/L^3$  (Bolger & Connolly, 1989; Nash *et al.*, 2006).

178

179

180 Quality control and data processing

181

182

183 Fish spending three winters at sea became scarce in French populations while repeat spawners  
184 are very rare (Baglinière & Porcher, 1994). Data from those fish were too few to allow  
185 reliable statistical analysis. They were thus removed from the study. Unrealistic combination  
186 of length and weight (i.e., K outside the range [0.4, 1.6]) coming from erroneous records,  
187 were discarded. The date of capture was also used as a filter criterion on the dataset. In  
188 France, *S. salar* migration is depending on sea age and hydrological conditions, with a MSW  
189 early run and a 1SW summer run (Baglinière & Porcher, 1994). Some years, late records are  
190 observed in the dataset, which correspond to a late upstream migration from the estuary as no

191 late run of “silver fish” are recorded on index rivers with fish trap facilities in France (e.g.  
192 Scorff River, E. Prévost, pers. com.). Also, the recorded length and weight of fish caught late  
193 in the season may be a biased proxy of the phenotypic traits of those fish at the time of their  
194 return. Indeed, fish caught late in the season often stayed several weeks in river waiting for  
195 favorable river discharge conditions to migrate upstream to spawning grounds. During this  
196 waiting period, fish may lose weight and the length of males may start to increase with the  
197 development of secondary sexual characters, such as the elongation of the upper jaw in the  
198 male salmon ([Maise & Baglinière, 1986](#); Baglinière & Porcher, 1994). Because sexual  
199 dimorphism is large enough to allow sex determination in salmon from September, we  
200 decided to only consider fish caught until the end of August for our analysis. Furthermore,  
201 fishery management could interfere with fish sampling, with late running fish being more  
202 likely to be under-represented in the dataset. Indeed, since 1994, *S. salar* recreational fishery  
203 in French rivers closes to preserve the targeted stock of spawners as soon as the allocated  
204 river-specific quota is reached (catch release is not implemented in France; Porcher & Prévost  
205 (1996)). Fishing closure often took place early in the season, leading to an uneven sampling of  
206 fish in fall.

207

208

209 In total, our analysis included 27,709 individual records (11,466 1SW fish and 16,243 2SW  
210 fish) collected over the period 1987-2013 on 34 rivers. Sample size per river was too small,  
211 thus records from single rivers were pooled into three study regions (Normandy, Brittany, and  
212 Aquitaine) to reduce sampling noise (Table I, Fig. 1). Despite an unbalanced number of river  
213 per regions and contrasted river profiles, this regionalization of the catch data reflects the  
214 spatial distribution of *S. salar* abundance in France. Populations from the Loire River and  
215 from Northern France, which represent less than 5% of the records, were excluded from the

216 dataset for three main reasons: i) salmon fishing in the Loire River has been forbidden since  
217 1994; ii) salmon catches in Northern France are low; iii) stocking practice takes place on all  
218 these rivers, which may mask ecological signals ([Le Cam \*et al.\*, 2015](#)).

219

220

221 Statistical analyses

222

223 Characterizing temporal trends and the impact of covariates

224

225

226 Temporal trends in D, L, W and K (see Supporting Information A1 and A2) were analyzed  
227 using Generalized Additive Models (GAM) as implemented in the R package *mgcv*, V. 1.8-6  
228 ([Wood, 2011](#)) to capture the non-linearity in the data. Independent models were built for each  
229 of the four response variables, here denoted Z for genericity. The effects of the sea-age class  
230 (1SW or 2SW), and regions (Normandy, Brittany, Aquitaine) were introduced as categorical  
231 effects, and the Year was considered as a continuous variable in the non-parametric smooth  
232 trend. The most complex model considered was:

$$233 Z_{Y,A,R,i} \sim A \times R + s(Y, A \times R) + \epsilon_i,$$

234 where  $Z_{Y,A,R,i}$  is the variable D, L, W or K for any fish  $i$  of sea-age A, caught at year Y in  
235 region R, 'A×R' is a sea-age by region interaction,  $s(Y, A \times R)$  is a sea-age by region specific  
236 smooth time trend, and  $\epsilon_i$  are independent and identically distributed residuals  $\sim N(0, \sigma^2)$  for  
237 any individual fish  $i$ . To test for the existence of trends specific to sea-age and region, simpler  
238 nested models without time trend, or with identical time trend for each region and/or sea-age  
239 were considered. Competing models were compared using the Akaike Information Criterion  
240 (AIC; Burnham & Anderson, 2002). The reduction of the model deviance as the models get

241 more parameters (i.e. increase in complexity) was also used to comment on the relative  
242 importance of the covariates in explaining the data variability. No data transformation was  
243 needed as the residuals from the models did not reveal any departure from the assumptions of  
244 normality and homogeneity of variance.

245

246

247 Common fluctuations among regions

248

249

250 Time trends in each life history trait were then examined to test for common temporal  
251 fluctuations among regions (for any sea-age strategy). To ensure that two regions would not  
252 appear to be correlated simply because both showed comparable long-term trends, any long  
253 term trend (low frequency) in the data was first removed by fitting a spline a priori forced to  
254 be very smoothed by fixing the degree of freedom to 5 in the GAM procedure. Correlations  
255 across years between any two regions were then analysed on the de-trended time series by  
256 calculating the Pearson correlation coefficient. Following the methodology developed in  
257 Pyper and Peterman (1998), the significance of the correlation was tested using modified  
258 Student t-tests with a reduced degree of freedom to correct for any remaining autocorrelation  
259 in the de-trended time series.

260

261

262 Comparing rates of change between strategies

263

264

265 We investigated the relative rate of change in life history traits (L, W and K) over the study  
266 period to test for potential difference in the intensity of the response between strategies (1SW  
267 or 2SW). The average rate of change (in % per year) of each life history trait was directly  
268 estimated as the slope of a linear model over time, based on standardized data. The effects of  
269 the sea-age and region on the rate of change were introduced as categorical effects, and the  
270 year was considered as a continuous variable. Nested models without time trend or with time  
271 trends identical for each region and/or sea-age (additive models) were also considered. The  
272 best models were selected using the Akaike Information Criterion (AIC; Burnham &  
273 Anderson, 2002). Then for each region, the difference in the rate of change (i.e. slope) in the  
274 1SW and 2SW strategies were tested using the Wald test using the ‘*glht*’ function of the  
275 ‘*multcomp*’ R package that automatically corrects for multiple comparison.

276

277 RESULTS

278

279 Differences in mean life history traits between regions and sea-ages

280

281

282 For each trait (L, W, K and D), the data was best explained by a GAM including both an  
283 average term and a smoothed temporal trend specific to each combination of region and sea-  
284 age (Table II). The average interaction term (region by sea-age) explained most of the  
285 observed variability in the data, revealing high differences in the average level of life history  
286 traits across sea-age classes and regions. The strongest difference occurred between the North  
287 West (Normandy and Brittany) and the South West (Aquitaine) regions. Fish from Aquitaine  
288 were noticeably larger and heavier than fish from Normandy and Brittany for both 1SW and  
289 2SW fish. 1SW fish from Normandy were also heavier than in Brittany, but no clear  
290 difference was detected in 2SW fish between the two regions. 2SW fish from Aquitaine were  
291 caught later than fish from Normandy and Brittany, the average difference in the date of river  
292 entry between the three regions being much weaker for 1SW. Comparatively, the smoothed  
293 time trends explained a much lower part of the deviance, even when considering an  
294 interaction with sea-age and/or region (Table II).

295

296

297 Time trends in life history traits and common fluctuations between regions

298

299

300 Overall, the nonlinear smoothed temporal trends on the 1987-2013 period revealed a general  
301 delay in the date of river entry and a decrease in fish weight and length (Figure 2). However,

302 time trend were specific for each region and sea-age. In particular, the coefficient of condition  
303 of fish was more contrasted between sea ages than the other life history traits. K exhibited a  
304 clear downward trend in 1SW fish but remained rather stable in 2SW fish. Changes in the date  
305 of capture also exhibited differences between regions and sea age. 1SW fish from Normandy  
306 and Brittany showed the most important delays of return migration, with a lag of up to 40  
307 days throughout the study period. Meanwhile, the observed delays for 2SW fish and 1SW fish  
308 in Aquitaine were only 20 days. Besides, smoothed time trends also suggested synchronous  
309 fluctuations across regions with a 7-8 years period, with high similarity between Brittany and  
310 Normandy (Figure 2). Variations in size and weight suggested a common temporal pattern  
311 across regions, characterized by repeated declines in both phenotypic traits around years  
312 1990, 1998 and 2007.

313

314

315 The analysis of correlations between de-trended time series further support the hypothesis of a  
316 synchronous change in L, W, K or D across regions (Table III). Indeed, for each trait, most of  
317 the correlations between regions were positive and significant, even after accounting for  
318 autocorrelation. The strongest correlations between regions were found for L and W. The  
319 strongest correlations were also found between Brittany and Normandy, which are  
320 geographically close. Correlations between more distant regions (i.e. Brittany and Aquitaine,  
321 Normandy and Aquitaine) were generally weaker. Also, with the exception of D, between-  
322 region correlations seemed stronger in 2SW fish than in 1SW fish.

323

324

325 In general, the date of river entry showed opposite trends to length and weight, a later date of  
326 river entry being associated with a decline in the length and weight of fish. Interestingly, those

327 opposite smoothed time trends were also associated with negative correlations at a shorter  
328 time scale, with 7-8 years periodicity in the date of river entry being in antiphase with those of  
329 length and weight (Figure 2).

330

331

332 Rate of change over the study period (1987-2013)

333

334

335 Consistently with the analyses of non-linear trends, average rates of change in traits were  
336 almost all negative (Figure 3) and depended upon both region and sea-age (based on AIC and  
337 explained deviance, not shown). Overall, pairwise comparison tests of the difference between  
338 rate of change in traits (per sea-age and per region) revealed a stronger decline in W, L and K  
339 for 1SW fish than for 2SW fish. The largest rates of change were found for weight, with an  
340 average rate of -1.00% per year for 1SW fish and -0.32% per year for 2SW in Brittany. The  
341 body condition of 1SW fish declined by 0.20 % (Aquitaine) to 0.51 % (Normandy) per year  
342 while the rate of change in K was close to zero for 2SW and could even be positive in some  
343 regions. The relative rate of change in L was not different in 1SW and 2SW (p-value > 0.05),  
344 fish having lost on average 0.10% (Brittany) to 0.20% (Aquitaine) of their initial body length  
345 per year between 1987 and 2013.

346

347

348 DISCUSSION

349

350



351 Our analysis provides new insights on temporal changes in *S. salar* life history traits across  
352 France over the last three decades, and contributes to reduce the gap in knowledge by  
353 providing further empirical evidence of a long suspected change in life history of *S. salar*  
354 throughout its entire distribution area. Using a large dataset from rod and line and commercial  
355 catches, we describe a decline in individual length, weight, together with a delay in the  
356 migration phenology of adult *S. salar* returning to French rivers. Our analysis highlighted  
357 similarities in time trends between regions, but the rate of change in life history traits clearly  
358 depends upon the tactic at sea.

359

360

361 Strength and limitation of the data

362

363

364 Time trends in *S. salar* life history traits were analyzed using catch data from recreational and  
365 commercial salmonid fishery. This unique dataset provides a large scale observatory of wild  
366 French *S. salar* populations. Commercial fisheries of *S. salar* are almost all closed since the  
367 early 1990's (ICES, 2016), and scientific data are only available for a few rivers and generally  
368 cover only short periods of time. By contrast, recreational hook and line fishery are operating  
369 in almost all rivers across the species distribution range. Thus, when available catch data  
370 provides to date the broadest spatio-temporal sampling of *S. salar* populations across several  
371 countries (Bacon *et al.*, 2009; Valiente *et al.*, 2011; Fjørtoft *et al.*, 2014).

372

373

374 The advantages offered by the large spatial and temporal coverage of this fishery dataset are  
375 balanced by the difficulty to control the sampling effort. Recreational fishery data might

376 indeed suffer from non-random sampling caused by fishery management rules and intrinsic  
377 variability in fishing effort (Bacon *et al.*, 2009). Although catch data virtually come from  
378 newly arrived fresh-run fish only (Thorley *et al.*, 2005; Bacon *et al.*, 2009), the date of capture  
379 may still provide a biased estimate of the date of river entry, and this bias may differ between  
380 regions. For instance, fish from Aquitaine generally undertake a longer journey in freshwater  
381 before being caught (longer rivers) than fish from Brittany and Normandy (smaller and  
382 shorter rivers). Hence, the late migration timing reported for Aquitaine (2SW) may be partly  
383 explained by a specific spatial setting compared to the other regions rather than by a latter  
384 return to coastal waters. This late migration can also reflect a distinct flow regime in early  
385 spring, that is driven by melting snow on the Adour - Gaves rivers (where most catches come  
386 from). By contrast, we assume that our results on the relative variability and the rate of  
387 change in this trait within a given region are robust.

388

389

390 By removing catches made in the end of fishing season, our analysis might miss key  
391 ecological signal. In particular, we would not be able to detect any potential compensatory  
392 mechanism that would occur between early and late migrating fish. For instance one can  
393 hypothesize that a decline in body size among studied fish might be balanced by an increasing  
394 number of large fish in a potential late run. Although we cannot rule out such a process, the  
395 late captures represented only a small proportion of fish in France, which may thus have a  
396 limited impact on our results. Migration monitoring using a fish trap on the Scorff River  
397 shows that less than 10% of all 1SW and 2SW fish were trapped in fall, with no evidence of  
398 growth compensation (E. Prévost, pers. com.).

399

400 Lastly, although raw data were available at the scale of single rivers, samples were pooled at  
401 the regional scale to dampen the effect of uncontrolled sampling variability and local  
402 heterogeneity. Indeed, the low signal-to-noise ratio due to low sample size or uncontrolled  
403 variation of the fishing effort in space and time for single rivers (e.g., due to alleged report of  
404 the fishing effort from one river to the other within the fishing season) would impede the  
405 detection of time trends. Aggregating data on several rivers of the same region helped  
406 disentangling the temporal variation attributable to large scale environmental change, from  
407 local factors.

408

409

410 Evidence for change in phenotypic traits

411

412

413 In France, differences in average phenotypic traits and migration date were detected between  
414 regions. Interestingly, those patterns have already been described in previous analyses on  
415 older data (Prévost, 1987), thus highlighting the stability of the regional contrast over several  
416 decades. As discussed previously, the date of river entry may be overestimated in Aquitaine  
417 due to uneven sampling design across regions. Genetic drivers of the migration timing may  
418 also be considered (Hansen & Jonsson 1991). But this effect is unlikely to explain weight and  
419 length differences. Such phenotypic differences are likely to reflect distinct genetic pools  
420 (Perrier at al., 2011).

421

422

423 Overall, this study highlighted important change in phenotypic traits in French *S. salar*  
424 populations over the period 1987-2013. In all regions, we detected a significant decline in fish

425 length and weight, as well as a delay in the date of river entry. Results are consistent with  
426 patterns already reported in several other rivers in Northern Europe. Similar declines in *S.*  
427 *salar* length (about 1 cm per decade), weight (200-400 g per decade) or 1SW body condition  
428 have been observed in Scotland (Bacon *et al.*, 2009; [Todd \*et al.\*, 2011](#)), Ireland (Quinn *et al.*,  
429 2006), Norway ([Jonsson \*et al.\*, 2016](#)) or North America ([Friedland \*et al.\*, 2005](#)). The observed  
430 delay in migration timing (about 5-10 days per decade) is also congruent with previous  
431 findings in Scotland (Youngson *et al.*, 2002; Todd *et al.*, 2012), England (Aprahamian *et al.*,  
432 2008) or Spain (Valiente *et al.*, 2011).

433

434

435 Moreover, our correlation analysis highlighted common inter-annual fluctuations in  
436 phenotypic traits across all three French regions. Interestingly, we detected more similarities  
437 in the temporal variability of those traits between neighboring French Northern regions  
438 (Brittany and Normandy) than between these two Northern regions and the more distant  
439 Aquitaine. These results support the hypothesis of a segregation of populations by distance  
440 (Jensen *et al.*, 2011; [Juanes \*et al.\*, 2004](#); [Perrier \*et al.\*, 2011](#)), which may be driven by spatial  
441 or temporal segregation in post-smolt migration route and feeding zone at sea (Bacon *et al.*,  
442 2009; Jensen *et al.*, 2011) or to a difference in river profiles ([Juanes \*et al.\*, 2004](#); Valiente *et*  
443 *al.*, 2011). French *S. salar* populations face environmental conditions that differ in many ways  
444 from the conditions encountered by Northern Europe populations (e.g. longer migration  
445 routes, higher freshwater temperature, high anthropic pressure ...). However, the impact of a  
446 large scale phenomenon in the marine environment, initially described in Northern Europe,  
447 seemed to prevail in France as well. Therefore, by providing empirical evidence for Southern  
448 populations, our study nicely complements existing literature to better describe the “big  
449 picture”.

450

451

452 A response to marine environmental change

453

454

455 Taken together, results suggest a globally coherent response across French populations and

456 beyond, in Northern Europe. They strongly support the hypothesis of a common

457 environmental mechanism affecting *S. salar* population throughout its distribution area.

458 Temporal similarities across regional patterns, e.g. time series varying in phase or antiphase,

459 strongly suggest a response to common environmental drivers jointly impacting the marine

460 phase of the life cycle of different populations spawning in distant rivers. Several studies

461 suggested that a major decline in growth condition would be responsible for the decrease in *S.*

462 *salar* length and weight ([Friedland \*et al.\*, 2000](#); [Peyronnet \*et al.\*, 2007](#); [McCarthy \*et al.\*, 2008](#);

463 [Jensen \*et al.\*, 2011](#)), while within river migration timing increased. As a mechanism, it has

464 been suggested that bottom-up control on food resources during the early marine phase of

465 post-smolts may have negatively impacted both growth and survival ([Friedland \*et al.\*, 2009](#);

466 [Jensen \*et al.\*, 2011](#); [Beaugrand & Reid, 2012](#)). Triggered by ocean warming, a major trophic

467 shift in the North Atlantic Ocean has been documented in the 1990s, with reported changes in

468 zooplankton communities up to seabird population dynamics ([Durant \*et al.\*, 2004](#); [Beaugrand](#)

469 [et al., 2008\). As a result, decrease in prey abundance and energetic quality may have altered](#)

470 *S. salar* growth potential at sea ([Otero \*et al.\*, 2012](#), [Mills \*et al.\*, 2013](#)). [Jonsson \*et al.\* \(2016\)](#)

471 further noted that direct effect of temperature are unlikely to explain observed changes but

472 argued in favor of an impact of stock rebuilding in the Herring *Clupea harengus* L. 1758, or

473 in other Clupeides species, which may compete for resources with salmon smolt, as observed

474 in the Baltic Sea.

475

476

477 It has been demonstrated that the mortality of fish at sea is size dependent (Lorenzen, 1996;  
478 Gislason *et al.*, 2010). In particular, *S. salar* marine mortality is believed to be mostly caused  
479 by predation and will then be size- and growth-dependent ([Friedland \*et al.\*, 1993](#); [Friedland \*et al.\*, 2000](#)), i.e. larger and more robust fish have a higher probability to escape predation. As a  
480 consequence, decreasing growth rate at sea may also be responsible for a decline in marine  
481 survival, as also suggested by synchronous patterns across Northern Europe reported by  
482 several authors ([Friedland \*et al.\*, 1993](#); [Friedland \*et al.\*, 2000](#); [Peyronnet \*et al.\*, 2007](#); [Chaput  
483 2012](#)). However, our catch data do not inform about survival in French populations.  
484 Nevertheless, *S. salar* monitoring using a fish trap on the Scorff river showed substantial  
485 change in marine survival, the average return rate decreasing from 10,3 % (1997-2003) in the  
486 2000's to 4,8 % in recent years (2009-2013) (ICES, 2016).

488

489

490 The temporal coherence (i.e. direct anti-phase) in declining length/weight and delaying run  
491 migration observed in our populations appeared compatible with such a degradation of  
492 feeding conditions at sea. Within a given sea-age class, the spawning run lasts several weeks,  
493 and its seasonal timing is expected to be driven by the tradeoff between reproduction and  
494 survival. The reproductive benefit associated with extra feeding opportunities at sea would be  
495 balanced against the risk of mortality during an extra time at sea ([Clark, 1994](#)). As a  
496 consequence, decreasing growth rate may call for an extra time at sea, aiming at maximizing  
497 growth potential, as observed in some Scottish rivers ([Todd \*et al.\*, 2012](#)). However, if  
498 resource conditions turn out to be so degraded, the decline in growth rate would be too large  
499 to be compensated by a mere delay in the date of river entry. Such a mechanism may generate

500 opposite patterns of temporal variability in migration timing and length or weight (using de-  
501 trended data), as observed in French populations. Interestingly, Valiente *et al.* (2011) also  
502 reported negative correlations between medium term fluctuations of length/ weight and the  
503 date of river entry.

504

505

506 Different responses between 1SW and 2SW

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508

509 Our results stressed that the relative change in weight and condition of returning *S. salar* was  
510 weaker and less variable in 2SW than in 1SW. Similar differences between 1SW and 2SW  
511 seemed to be present in Scottish (Bacon *et al.*, 2009) and Norwegian populations (Jonsson &  
512 Jonsson, 2004) as well. Thus, there is a need to better account for differences in *S. salar*  
513 anadromous tactics to better understand the demographic and ecological mechanisms  
514 underlining population changes.

515

516

517 1SW and 2SW *S. salar* have first similar migration routes at the beginning of their journey at  
518 sea and then separated migration routes where they may encounter different growth condition  
519 at sea. One cannot exclude that change in the feeding condition experienced by 1SW has been  
520 more stringent than in 2SW fish, thus explaining a weaker decline in 2SW weight. A  
521 proportionally lower decrease in the length of 2SW fish may also point at some compensatory  
522 mechanism. For instance, 2SW may move toward more favorable feeding grounds which  
523 would then support a higher growth rate over the second year at sea (Auer *et al.*, 2010; Hogan  
524 & Friedland, 2010). However, this hypothesis appears poorly supported by recent studies that

525 analyzed growth patterns on fish scales for Northern populations, showing that growth  
526 increment in 2SW during the second year at sea was not significantly higher than growth rate  
527 over their first year at sea ([Hogan & Friedland, 2010](#); *Jensen et al.*, 2011; *Jonsson et al.*,  
528 2016).

529

530

531 In *S. salar*, the duration of the marine phase of the life cycle may reflect different strategy of  
532 resource allocation between key fitness components (e.g. survival, growth, reproduction).

533 Intrinsic difference in allocation rule may generate contrasted response to a given change in

534 resource availability between 1SW and 2SW fish. Females are largely dominant among 2SW

535 fish ([Baglinière & Porcher, 1994](#); [Fleming, 1996](#); [Barson et al. 2015](#)), thus suggesting that

536 difference in allocation rule between 1SW and 2SW could emerge from difference in

537 allocation rules between males and females. Noteworthy, males and females have specific

538 physiological and behavioral constraints over the reproduction period; they are also

539 characterized by distinct tactics at sea. In *S. salar*, female's fitness is more strongly driven by

540 body size than male's one because sexual maturation process requires greater energetic needs

541 in females than in males (i.e. to maximize fecundity). The tight dependence between sex and

542 sea age classes might explain the difference in individual's response to changes in

543 environmental conditions between sea age classes. As a result, 1SW fish (preferentially

544 males) might have favored activities related to survival at the expense of mass gain, and 2SW

545 fish (preferentially females) might have favored a large body size as a way to maximize

546 fecundity in surviving individuals, as suggested by our data.

547

548



549 In more details, the rate of change was not uniform for all life history traits in 1SW and 2SW.  
550 Actually, we highlighted a similar response in 1SW and 2SW across regions for body length.  
551 In *S. salar*, growth and body size are considered as key drivers of marine survival and female  
552 fecundity (Thorpe *et al.*, 1984; [Fleming, 1996](#); [Jonsson \*et al.\*, 1996](#)). But a large body size is  
553 also a key feature of reproduction success in anadromous males, as it confers an advantage in  
554 terms of intra-sexual competition for mate ([Fleming, 1996](#)). Therefore fish length appears as  
555 an important fitness component (Marschall *et al.*, 1998) in both males and females, i.e. in both  
556 1SW and 2SW fish. Not surprisingly, length happened to be the most preserved life history  
557 trait in our analysis: low variability and weak decline. Similarly Todd *et al.* (2008) reported a  
558 disproportional decline in body weight compared with length in Scottish 1SW fish (22% vs.  
559 4% declines, respectively). This pattern seems consistent with the life history theory, which  
560 states that phenotypic traits the more strongly connected to fitness are expected to be the more  
561 preserved - or canalized - against environmental stochasticity ([Stearns & Kawecki, 1994](#);  
562 [Pfister, 1998](#); [Caswell, 2001](#); [Gaillard & Yoccoz, 2003](#)). At the population level, the relative  
563 conservatism in body length, compared to other traits, can be perceived as a positive signal for  
564 population viability.

565

566

567 Conclusion

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569

570 This large scale study on French populations contributes to reduce the gap in knowledge by  
571 providing further empirical evidence of a long suspected change in life history of *S. salar*  
572 throughout its North East distribution area. Results also revealed different rates of change  
573 between 1SW and 2SW fish, thus pointing out the importance of considering the complexity

574 of life history strategies when exploring mechanisms of changes in *S. salar* phenotypic traits.

575 We hope that this long due analysis for France would encourage other authors to make their

576 dataset available to the scientific community, which is a prerequisite to improve our

577 understanding of major cross-border ecological mechanisms.

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579

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814

815 Tables

816 Table I. Sample size: number of 1SW and 2SW *S. salar* per region considered in the study.

Age	Normandy	Brittany	Aquitaine
1SW	3716	12053	959
2SW	3110	9577	3870

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818

819 Table II. Modelling date of river entry, length, weight and condition in *S. salar* caught in  
 820 France as a function of sea age (A), region (R) or year (Y). Deviance explained, F-test p-  
 821 values and delta AIC are presented for each model. s() indicated GAM smoothing.  
 822

Covariates	Date of river entry		Length		Weight		Condition	
	Dev exp	$\Delta$ AIC	Dev exp	$\Delta$ AIC	Dev exp	$\Delta$ AIC	Dev exp	$\Delta$ AIC
A×R	61.26	-91970	71.94	-153634	68.68	-91117	3.34	-11314
A×R+s(Y)	63.7	-1790	72.84	-889	70.17	-1335	5.24	-533
A×R + s(Y,by=A)	64.47	-572	72.95	-95	70.29	-96	6.26	-283
A×R+s(Y,by=A×R)	64.95	-313	73.17	-161	70.55	-177	6.65	-61

823

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825 Table III. Cross-correlations in date of river entry, length, weight and condition between  
 826 regions for each sea-age class. The significance of the tests is presented as follow: “\*\*\*”,  
 827 “\*\*”, “\*” and “.” correspond to p-values inferior or equal to 0.001, 0.01, 0.05 and 0.1,  
 828 respectively. The p-values are corrected to account for the autocorrelation in the times series.  
 829

	Normandy / Brittany	Normandy / Aquitaine	Brittany / Aquitaine
1SW Date	0.46*	0.38*	0.01
1SW Length	0.35.	0.56**	0.57**
1SW Weight	0.46*	0.44*	0.68***
1SW Condition	0.47*	0.34.	0.45*
2SW Date	0.32.	0.01	-0.02
2SW Length	0.75***	0.54**	0.52**
2SW Weight	0.86***	0.57**	0.42*
2SW Condition	0.66***	0.46*	0.25

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832 Figure captions

833 Figure 1. Description of the three regions considered in the analysis: Normandy, Brittany and  
834 Aquitaine. In each region, the name of the rivers that provided *S. salar* captures are presented.

835

836 Figure 2. Change in the date of river entry, length, weight and condition in 1SW and 2SW *S.*  
837 *salar* from Normandy, Brittany and Aquitaine.

838

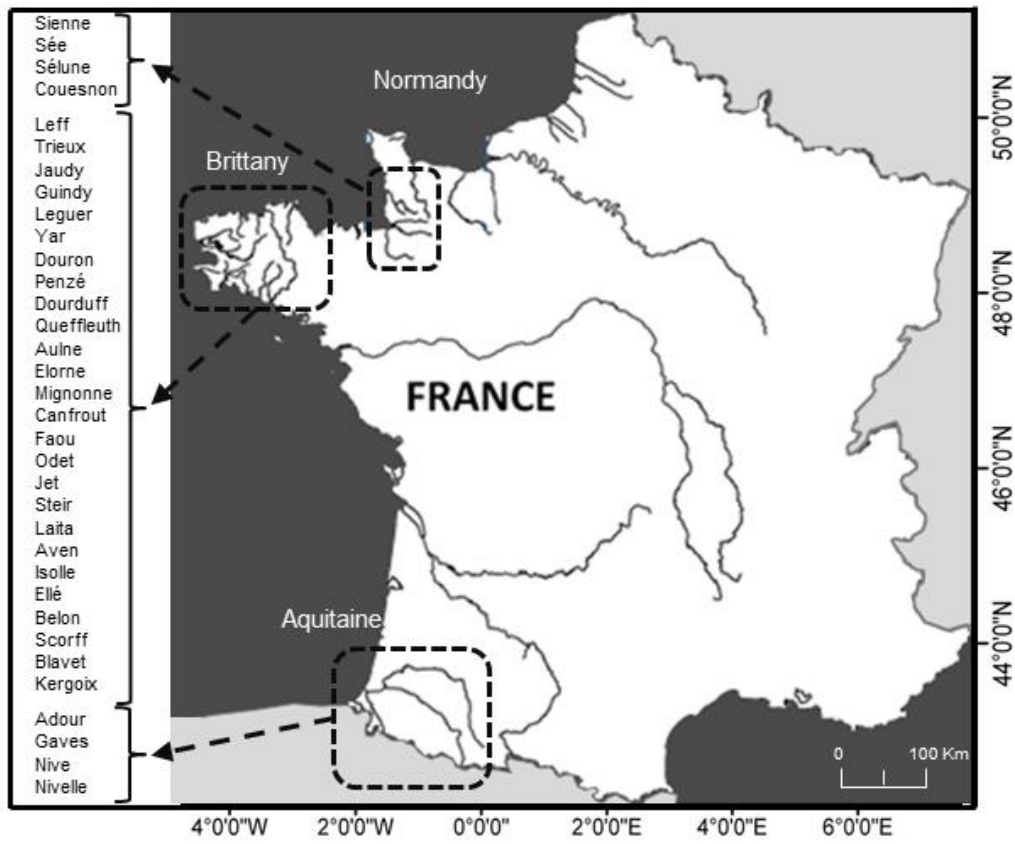
839 Figure 3. Linear rate of change in the date of river entry (D), length (L), weight (W) and  
840 condition (K) in 1SW and 2SW *S. salar* from Normandy (N), Brittany (B) and Aquitaine (A).  
841 The the difference in the rates of change between 1SW and 2SW was assessed with a Wald  
842 test. The significance of the test is presented as follow: “\*\*\*\*”, “\*\*\*”, “\*\*” and “.” correspond to  
843 p-values inferior or equal to 0.001, 0.01, 0.05 and 0.1, respectively.

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845



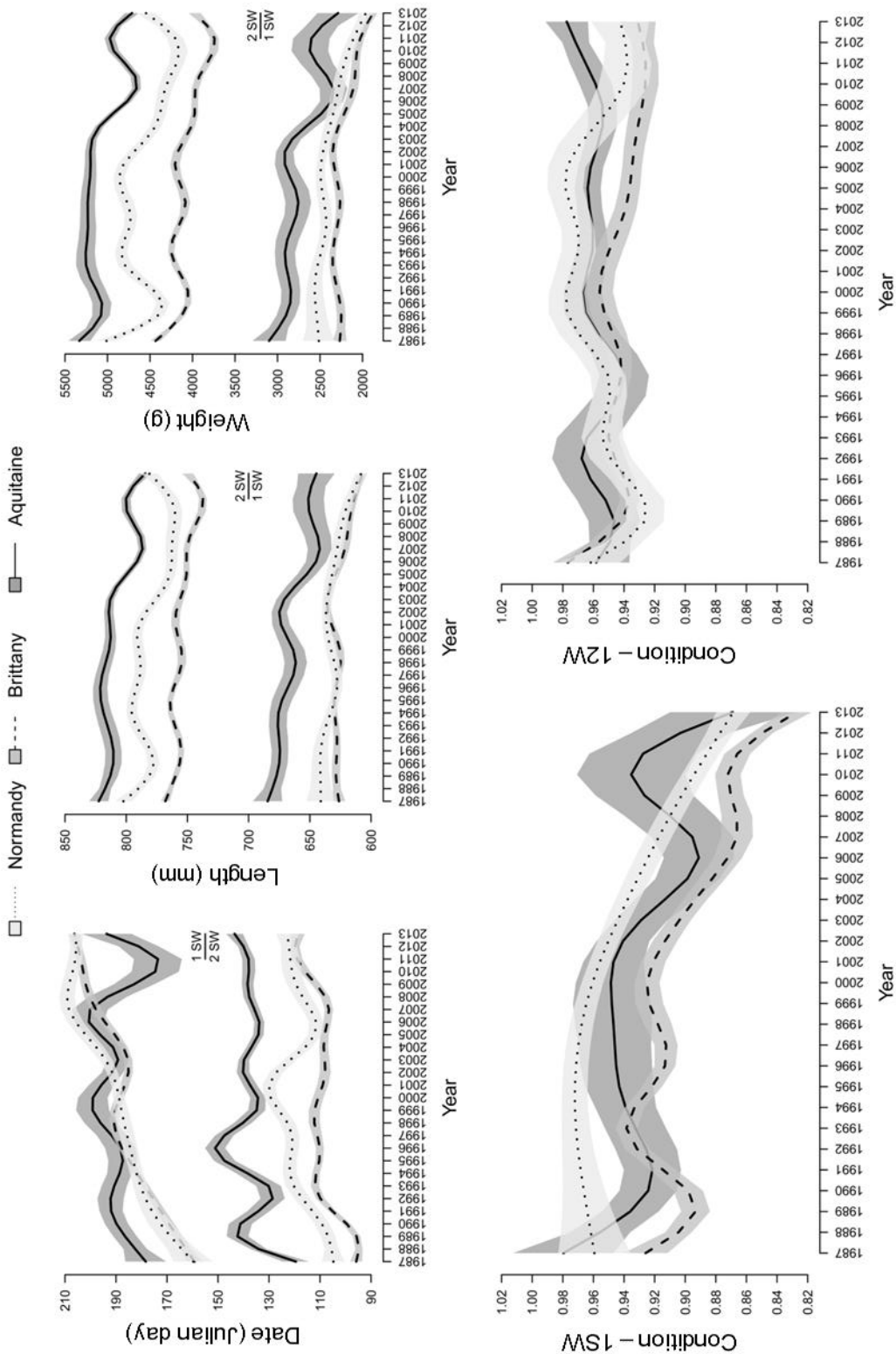
846 Figure 1



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849 Figure 2

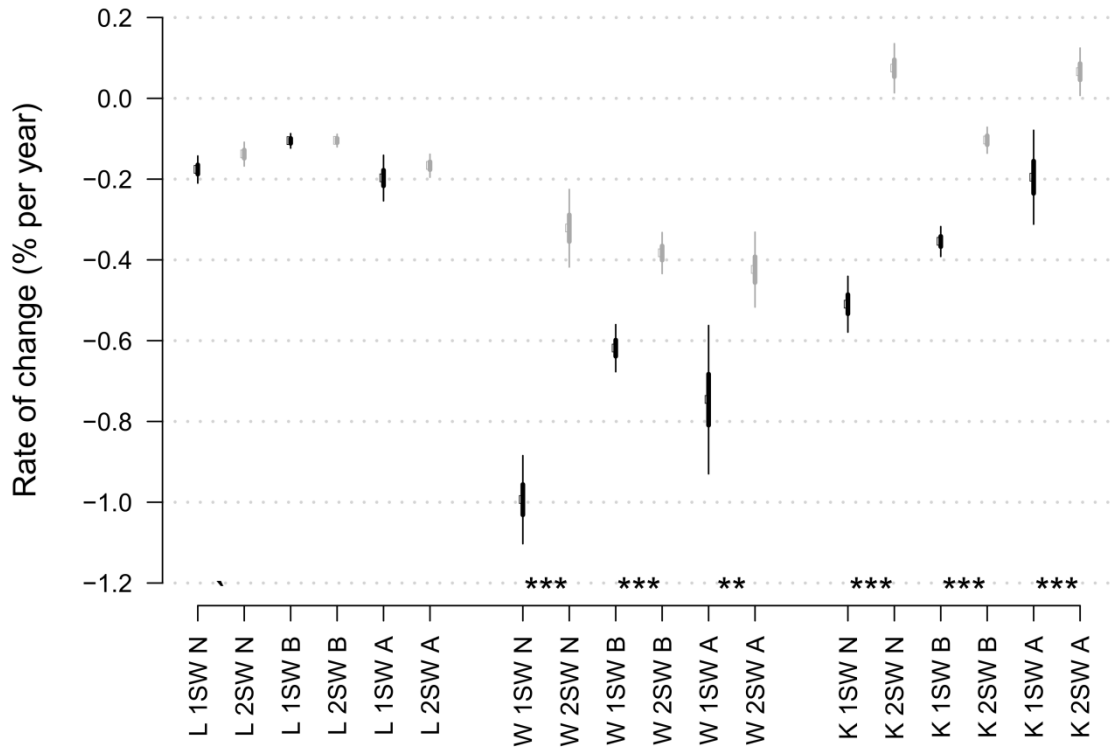


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853 Figure 3



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856 Supporting information

857 Figure captions

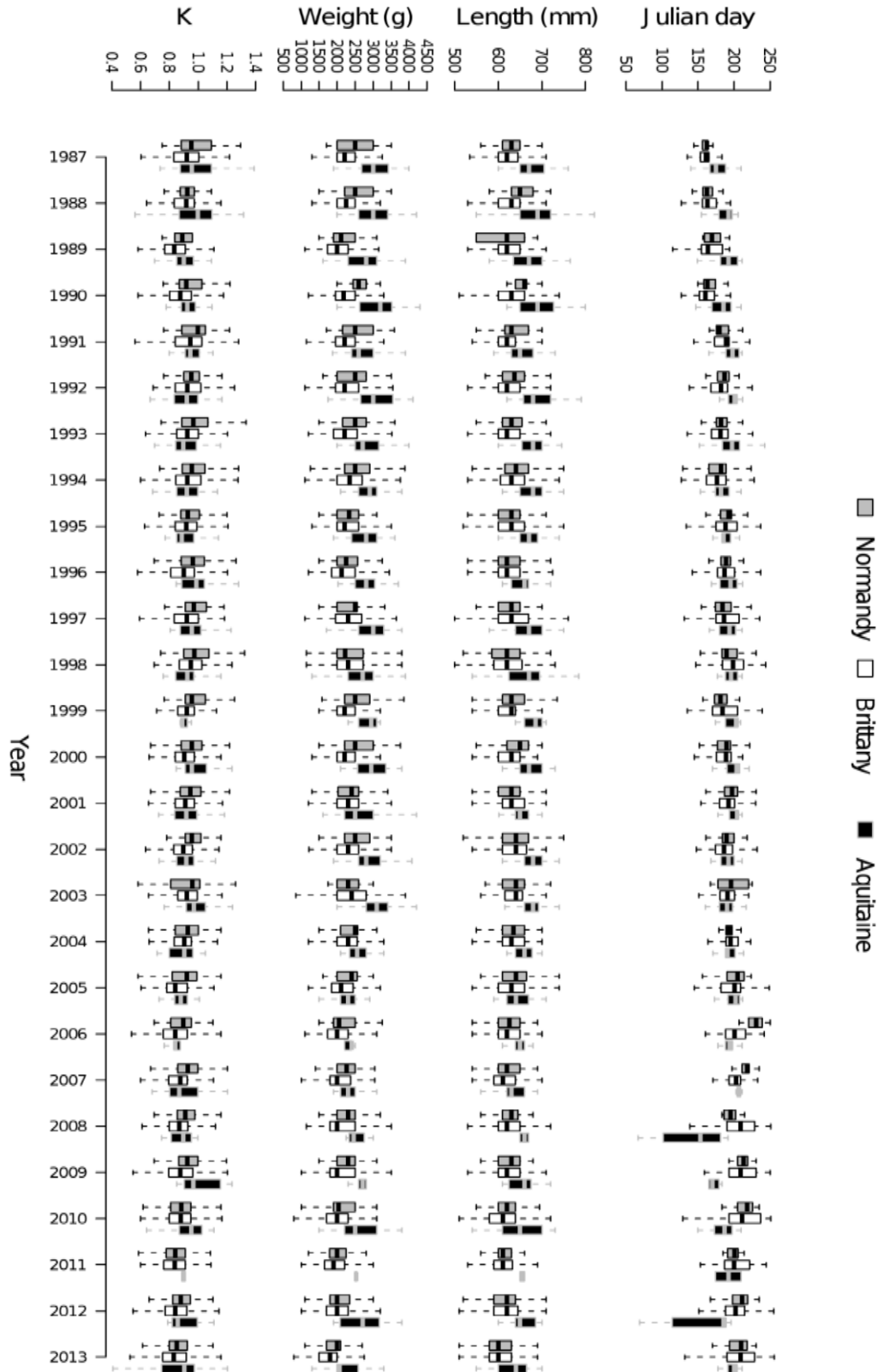
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859 Figure A1. Boxplots of raw data for the date of river entry, the length, the weight and the  
860 condition (K) of 1SW fish caught by the French hook and line recreational salmon fishery  
861 (spring and summer catches).

862

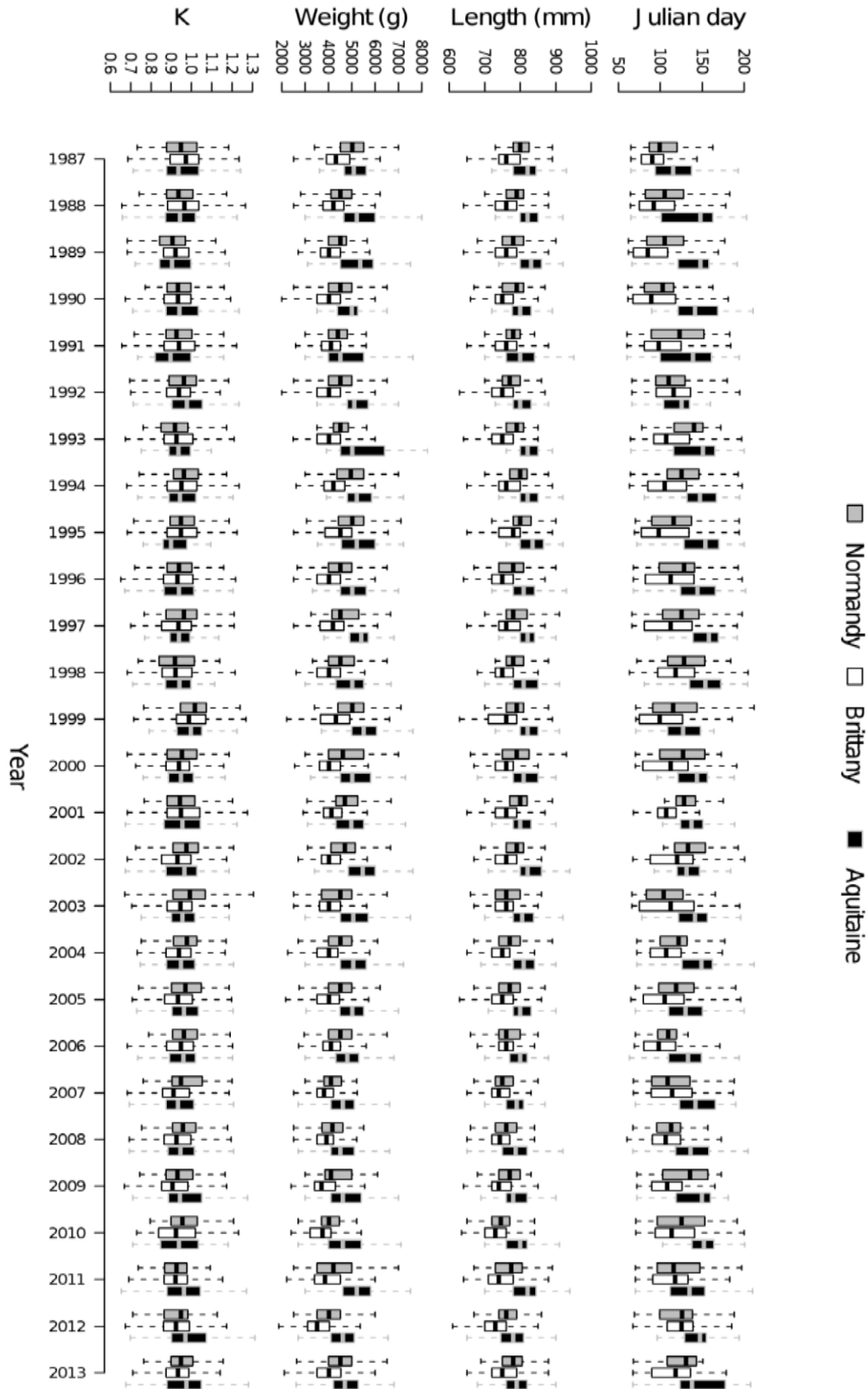
863 Figure A2. Boxplots of raw data for the date of river entry, the length, the weight and the  
864 condition (K) of 2SW fish caught by the French hook and line recreational salmon fishery  
865 (spring and summer catches).

866



867

868 Figure A1.



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870 Figure A2.