Changes in length-at-first return of a sea trout (*Salmo trutta*) population in northern France

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ABSTRACT

The resilience of sea trout populations is increasingly concerning, with evidence of major demographic changes in some populations. Based on trapping data and related scale collection, we analysed long-term changes in body length of a sea trout population in the Bresle River, France. From 1984-2022, the length of first-time returning individuals decreased by 1.18 mm.year-1 (SD = 0.03), which resulted in the loss of *c.* 8% of mean body length. This decrease results from a decrease in the age at first return, with a gradual loss of the oldest individuals and an increase in the proportion of the youngest. Timing of the return migration advanced drastically, although shorter sea sojourn had little influence on body length. We found little evidence of a decrease in length-at-age, to the exception of the oldest age class, suggesting that growth conditions at sea might not have deteriorated greatly during the study period.

Keywords: age structure, body length, life history, marine growth, migration, sea trout

Introduction

The environmental conditions that individuals experience, in conjunction with their genotype and epigenetic mechanisms (Ferguson et al., 2019), are susceptible to influence the expression of their phenotype and their life history trajectories (Walsh and Reznick, 2011). Migration decision, survival, growth, age at maturation or fecundity can thus be influenced by a series of intrinsic and extrinsic factors, such as environmental conditions (Crozier and Hutchings, 2014; Satterthwaite et al., 2012), genotype (McKinney et al., 2015), inter- and intra-specific competition (Helle et al., 2007), predator-prey relationships (Ohlberger et al., 2019), and anthropogenic activities (Hard et al., 2008; Law, 2000).

Recent environmental changes attributed to climate change and anthropogenic activities are assumed to be responsible for the widespread decline in salmonid abundance and distribution (Forseth et al., 2017; Kendall and Quinn, 2011; Kennedy and Crozier, 2010; Perrier et al., 2013). Ongoing changes, such as an increase in sea temperature, ocean acidification and stratification, rising sea levels, and eutrophication, are likely to influence marine trophic conditions (Möllmann and Diekmann, 2012). These changes could greatly modify the quality, quantity, and availability of trophic resources in the ocean (Bartolino et al., 2014; Brown et al., 2010; Niiranen et al., 2013) and thus impact growth opportunities for salmonid populations at sea.

Reduced growth opportunities can influence individuals' life history trajectories and fitness greatly by decreasing survival, fecundity, and competitive abilities (Perez and Munch, 2010; Quinn et al., 2016) or by delaying the age at maturation (Ishida et al., 1993). These changes can cause large variations in the length and age structure of populations. Such changes in population composition have been recorded for many salmon populations around the world (Bal et al., 2017; Jeffrey et al., 2017; Lewis et al., 2015; Morita and Fukuwaka, 2007; Ohlberger et al., 2018; Oke et al., 2020), but also sea trout (Milner et al., 2017), and could indicate a widespread decrease in marine growth and survival. In this context, identifying the ecological mechanisms that most likely influence these changes is crucial to better understand and predict population dynamics. This knowledge is also necessary to provide recommendations for effective management actions and to alleviate or compensate for pressures on sea trout populations when and where possible.

The anadromous form of the brown trout (*Salmo trutta,* L.) (hereafter, "sea trout") (ICES, 2020) exhibits an extreme diversity of life histories across its wide distribution range (Jonsson

and L'Abée-Lund, 1993), which makes it an appropriate model species to study variations in life histories in a changing environment. The age at seaward migration (*i.e.* smolt stage) ranges from 1-3 years in France to 5-7 years in northern Norway (Nevoux et al., 2019). First reproduction occurs after 0-2 or 2-4 years at sea in populations in the English Channel (Richard, 1981) and the Baltic Sea (Järvi, 1940), respectively.

In recent decades, alarming collapses in population abundance, as well as altered population structure, have been recorded in Europe, such as in the Burrishoole River, Ireland (Gargan et al., 2006), the Ewe River, Scotland (Butler and Walker, 2006), and the Vistula River, Poland (Dębowski, 2018). Damming of rivers forbidding the access to spawning sites, overfishing, or the development of offshore salmon aquaculture leading to sea lice epizootics, have been pointed as major factors of decline for some of these populations. Consequently, it is necessary to assess and understand possible changes in key life history traits, such as length at spawning, age at maturation, and length-at-age, which drive the dynamics of European sea trout populations.

In this study, we quantified the influence of key life history and phenological variables on the length of sea trout returning to the Bresle River, France, using 39 years of data from long-term population monitoring. Based on an intensive trapping protocol throughout the migration season, we obtained individual data on length, migration timing, and age, as inferred from scale reading. We first examined the temporal trend in the mean length of all fish captured in the trap to investigate a potential decrease in body length. We then focused on individuals returning for the first time to test four non-exclusive hypotheses: whether such a decrease was due to i) long-term effects of smaller length at seaward migration in smolts, ii) younger age at first

return, iii) a shorter growing season at sea and an advanced date of return, and vi) a decrease in the intrinsic growth rate at sea and a smaller length-at-age. The results provide insights into the ecology of sea trout in southern Europe and illustrate ongoing changes in life history strategies.

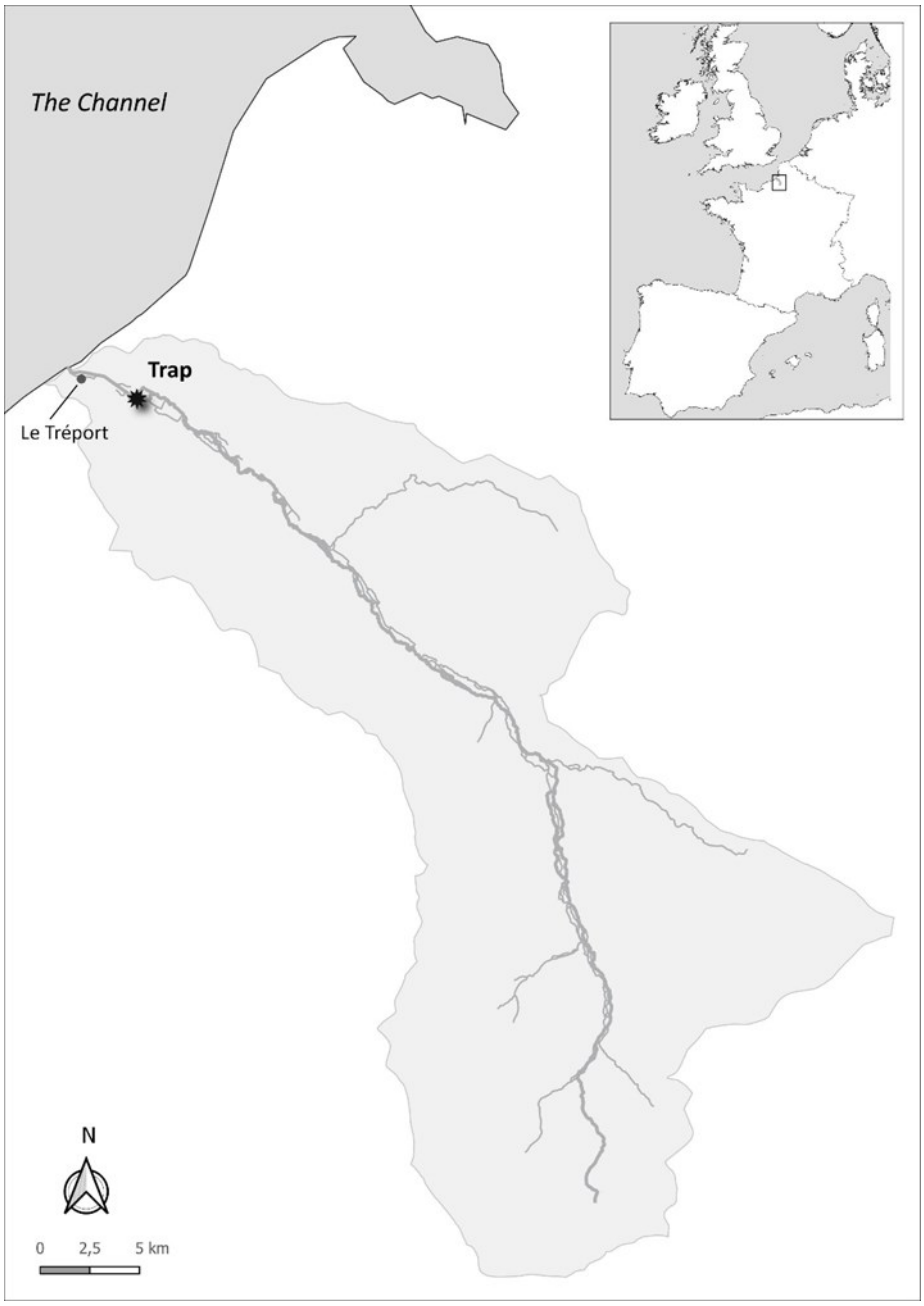

Figure 1 - Geographical location of the Bresle River, France, and its catchment

Materials and methods

Study site

The Bresle River, located in northern France, drains a 742 km² catchment into the English Channel at Le Tréport harbour (Figure 1). Mean annual discharge is 7.3 $m^3 s^{-1}$, and salmonids can access *c*. 2/3 of its total wetted length (137 km). Human activities strongly impact the Bresle estuary, and the Le Tréport harbour is the first obstacle to migration from the sea; however, the harbour is equipped with a fishway, which provides access to the main river (Euzenat et al., 2007). The Bresle River hosts a wild population of sea trout that has a life cycle of 1, 2, or 3 years in freshwater (hereafter, 1FW, 2FW, and 3FW, respectively) and 0, 1, or 2 years at sea until first return (hereafter, 0SW, 1SW, and 2SW, respectively).

Monitoring protocol

Since 1981, an intensive sea trout trapping protocol has been conducted throughout the up-stream migration season (March-December) each year at Eu, in the lower section of the Bresle River (Josset et al., 2023). It follows the ethical review from the committee C2EA-07, from the National Committee for Ethical Reflection on Animal Experimentation (permit number: APAFIS#26834-2020080615584492 v3). The trap is located on an obstacle 3 km upstream from the estuary and is checked twice a day for the presence of fish. Each year, a mean of 995 (SD = 511) sea trout are caught in the trap on their return from the sea. Each individual is measured to the nearest millimetre (total length from 1981-1983; fork length – from the tip of the snout to the fork of the tail – since 1984) using a manual or electronic measuring board. Examination of secondary sexual characteristics, which are visible mainly from September-December, indi-cates the sex of certain individuals. However, visual sexing is imperfect and relies mainly on

the presence of an elongated lower jaw (*i.e.* kype) on males. Scales are collected from a sub-sample of individuals to determine age, following (Baglinière et al., 2020)). Data on individual biometry, age, and scale samples are stored in the French COLISA archive (COLlection of Ichty-ological SAmples, (Marchand et al., 2019)), https://colisa.fr/) (in French) .

Data selection

For this analysis, we used data collected over a 39-year period (1984-2022). We focused only on individuals that returned to the river after their first marine sojourn (hereafter, "first re-turns"), to reduce heterogeneity between individuals as biological processes that influenced individuals returning for the first time may have differed from those that influenced individ-uals that had already returned to the river at least once. The returning status was defined based on i) the fish characteristics at capture and ii) on the examination of scales, which were available on a subset of 15,730 individuals out of the 41,412 individuals captured at the trap. Individuals with low relative weight (Wr < 90) (Blackwell et al., 2000) captured before April were considered late-running post-spawners migrating to the sea and were thus excluded from the analysis. Then, we defined a first return as a fish with no a spawning mark on its scales (n = 11844, 75.3% of available samples).

Data resampling

The subsample of fish which had their scales sampled, and age assessed, was unbalanced be-tween length classes, with individuals in the more abundant length classes being generally under-sampled. This bias skewed estimates of the mean length-at-age. To correct this bias, we randomly resampled within the subsample of fish which had their scales sampled, a subset of individuals with an even effort among length classes. We first calculated the proportion of

sampled individuals for each 50 mm length classes for a given year, determined the minimum proportion of sampling for each year, and then used this minimum proportion as a target for resampling individuals in each length classes for that given year. This resampling procedure was repeated 1000 times to ensure robustness and stability of the results. The following selection of first returns yielded datasets of varying lengths, with a mean sample size of 6060 individuals (SD = 23).

Statistical analyses

Long-term trend in the length of returning sea trout

To describe the long-term temporal trend in the length of returning sea trout, we modelled the mean yearly length of all individuals captured in the trap as a linear function of time and assessed the significance and direction of the trend. This was done using the “lm()” function of the “stats” package of R software (version 4.0.3) (R Core Team, 2020), using the year of return as a continuous variable.

Drivers of change in length-at-first return

We investigated the influence of key ecological variables on the length of first-time returning sea trout using Gaussian generalized linear models (McCullagh and Nelder, 1989) with a log link. The log-link function allows for multiplicative rather than additive effects, and the former are generally considered more appropriate for modelling ecological relations. The Gaussian distribution was selected because it is usually used when a linear relation between dependent and independent variables is expected, assuming a normal distribution of the residuals. Model selection followed stepwise inclusion of variables and relevant two-way interactions depending on the hypothesis selected.

Development of dimorphic sexual characteristics before reproduction, especially a kype at the end of the lower jaw (Witten and Hall, 2001), could bias length depending on the timing of return. This would be especially true in late-running males, although some females also have a small kype. To address this bias, we used the apparent sex recorded in the phenotypic data in the model as a corrective variable, with two levels: presence or absence of a kype.

Knowing that the longer the marine sojourn, the larger the trout is upon return (Thorstad et al., 2016), we included the "sea age" (*i.e.* the number of years spent at sea) as a categorical variable to explain length-at-first return. Similarly, we hypothesised that the number of years spent in the river influenced the length-at-first return, although less than the number of years spent at sea, due to substantial differences in growth potential in fresh and seawater (Gross et al., 1988; Nevoux et al., 2019). We thus used the "river age" (*i.e.* the number of years spent in freshwater before migrating to the sea) as another categorical variable in the model. We also considered an interaction between river age and sea age to capture effects of latent intrinsic differences among individuals depending on their life history (*e.g.* growth potential, metabolic rate, energy-use efficiency). Temporal variability in the effect of age on length was also tested by considering interactions between the year and river and sea ages.

The timing of migration can also influence the length of returning trout. Assuming that the timing of smolt migration to the sea remained unchanged, an early return in freshwater would mean shorter marine sojourn, reduced growth opportunities and potentially shorter bodies. Advanced migration timing can be driven by environmental conditions experienced by all individuals of a given sea-age class, as indicated by the mean day of year of return of each sea-

age class and year (ctrAvgDOY, centred on the inter-annual mean). Within a given sea-age class, differences in the timing of migration among individuals can also influence body length. This individual level was captured by the variable deltaDOY, which was calculated as an individual's return day minus the mean day of return of the corresponding sea-age class and year. We considered two-way interactions to test whether effects of phenology variables varied over time or among sea ages. The increase in length for each additional day at sea may have varied during the study period, and timing of return may have more influence on body length of young individuals returning after a short sojourn, due to their faster growth (Davaine et al., 1997).

Once the migration strategy and timing were considered, any remaining long-term trends in the length of returning sea trout would indicate a gradual change in the intrinsic growth rate at sea. To describe residual temporal variability in the length-at-first return, we used the year of return to the river (Year) as a continuous variable, which grouped sea trout that had experienced the same environmental conditions during their last months at sea.

Implementing and selecting the model

Collinearity among variables was tested using Pearson correlation coefficients, and only variables with $|r| \leq 0.7$ were kept (Dormann et al., 2013). A bootstrap procedure of the "boot" package (Canty and Ripley, 2021; Davison and Hinkley, 1997) was used to ensure stability of the results by reducing effects of sampling variability. One thousand datasets were generated using the bootstrap procedure, and candidate models were fitted to each dataset. Model selection aimed to minimise Akaike's information criterion (Akaike, 1974), following guidelines of Burnham et al. (2002). We identified the best model for each dataset and compared the

models' selection frequencies as a measure of support. Mean estimates and 95% confidence intervals of the best models' effects and interactions were then calculated from the 1000 iterations of the bootstrap procedure. In addition, to assess temporal changes in the age structure, yearly age-class percentages were recorded for each of the 1000 iterations. Similarly, slopes of a linear regression between the day of year and the year of return by sea age were extracted from each iterations to assess variations in the timing of return.

Results

Long-term decrease in the length of returning sea trout

The modelling of body length from 1984-2022 revealed that sea trout in the Bresle River lost in average 1.18 mm (SD = 0.03) per year, regardless of their age or the number of times they had reproduced, which represented a loss of 46.02 mm (SD = 1.17) (*i.e. c.* 8% of the mean body length from 1984-1988) over the 39 years studied (Figure 2).

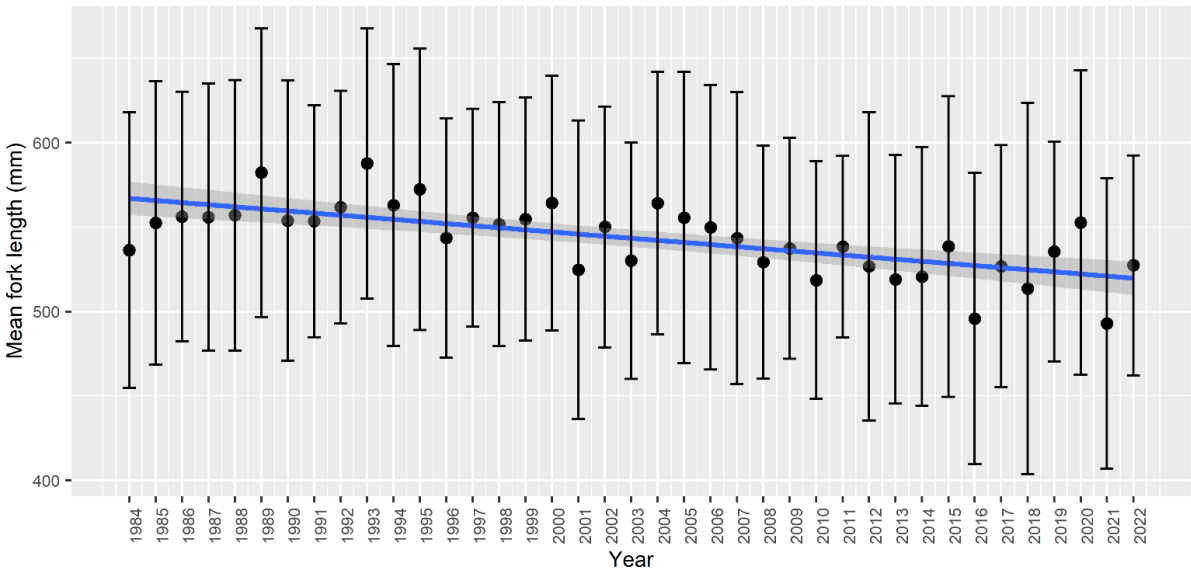

Figure 2 - Long-term temporal trend in the mean fork-length of sea trout captured in the Bresle River from 1984-2022. Error bars indicate 1 standard deviation. The shaded zone indicates the 95% confidence interval.

Model selection

Of the 1000 iterations of the bootstrap procedure and model selection, only two models (no. 21 and 19) were selected for having the lowest AIC (selected 77.3% and 22.7% of the time, respectively) (Table 1). The two models were similar, including all major variables, and thus had similar AIC and predictive power. They differed only in that model 21 included temporal interactions with the two phenology variables (*i.e.* ctrAvgDOY×Year and deltaDOY×Year). Although model selection based on the AIC balances likelihood and parsimony, two of the most complicated models were selected, which indicates overall complexity of the mechanisms that drive length-at-first return. The mean deviance calculated from the 1000 best models explained up to 66.00% (SD = 0.49) of the variability in the length-at-first return. Examination of the residuals showed slight deviation from the hypothesis of normality. As could be expected in a large dataset, wide tail distributions lead to the rejection of the normality hypothesis despite a quasi-normal distribution.

Decrease in the age of returning sea trout is a major driver of decrease in length-at-first return

We found that sea age influenced the length-at-first return the most. The more growth seasons an individual spent at sea, the greater was its length-at-first return. This result supports the hypothesis of a shift in the age structure, with a decrease in the number of growth seasons at sea, which would then drive the decrease in length. Indeed, the mean sea age structure of first returns changed greatly during the study period (Figure 3). In particular, 2SW individuals gradually disappeared and were not represented in 3 of the last 10 years of the study period.

Table 1 - The models tested to explain length-at-first return and their frequencies of selection (out of 1000 iterations) based on Akaike's information criterion. FL, fork length; Kype, presence/absence of a kype; Sea-age, number of years spent at sea; River-age, number of years spent in the river; ctrAvgDOY, mean day of year of return to the river by year and sea age (centred by sea age); deltaDOY, individual difference in the mean day of year of return; Year, year of return to the river.

Model number	Model	Selection frequency	Average explained deviance (%)	Standard deviation
1	Null	0	0	0
2	Kype	0	8.65	0.453
3	Kype + Sea-age	0	60.2	0.514
4	Kype + Sea-age + River-age	0	63.5	0.488
5	Kype + Sea-age + River-age + Sea-age×River-age	0	64.4	0.499
6	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY	0	64.6	0.498
7	Kype + Sea-age + River-age + Sea-age×River-age + deltaDOY	0	64.7	0.502
8	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY	0	64.9	0.501
9	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×Sea-age	0	65.0	0.501
10	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×River-age	0	64.9	0.500
11	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×Sea-age + Year×River-age	0	65.1	0.500
12	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Sea-age×ctrAvgDOY	0	65.2	0.497
13	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Sea-age×deltaDOY	0	65.5	0.498
14	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Sea-age×ctrAvgDOY + Sea-age×deltaDOY	0	65.7	0.494
15	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×ctrAvgDOY	0	64.9	0.502
16	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×deltaDOY	0	64.9	0.500
17	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×ctrAvgDOY + Year×deltaDOY	0	64.9	0.502
18	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×Sea-age + Year×River-age + Year×ctrAvgDOY + Year×deltaDOY	0	65.1	0.501
19	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×Sea-age + Year×River-age + Sea-age×ctrAvgDOY + Sea-age×deltaDOY	227	65.9	0.492
20	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×ctrAvgDOY + Year×deltaDOY + Sea-age×ctrAvgDOY + Sea-age×deltaDOY	0	65.8	0.493
21	Kype + Sea-age + River-age + Sea-age×River-age + ctrAvgDOY + deltaDOY + Year×Sea-age + Year×River-age + Year×ctrAvgDOY + Year×deltaDOY + Sea-age×ctrAvgDOY + Sea-age×deltaDOY	773	66.0	0.491

At the same time, the percentage of 0SW individuals increased in recent years to up to 60% (in 2018) of all first returning sea trout. The percentage of 1SW individuals in the population remained predominant and stable over time (mean = 82.3%; SD = 11.5%). This pattern indicates a decrease in the mean sea age at first return of the Bresle sea trout population: 1.06 years (SD = 0.4) from 1984-1988, but 0.80 years (SD = 0.4) from 2018-2022. The age structure differed greatly in 2001, when only 1SW individual was captured due to extreme flooding that disrupted trapping and thus decreased its efficiency greatly.

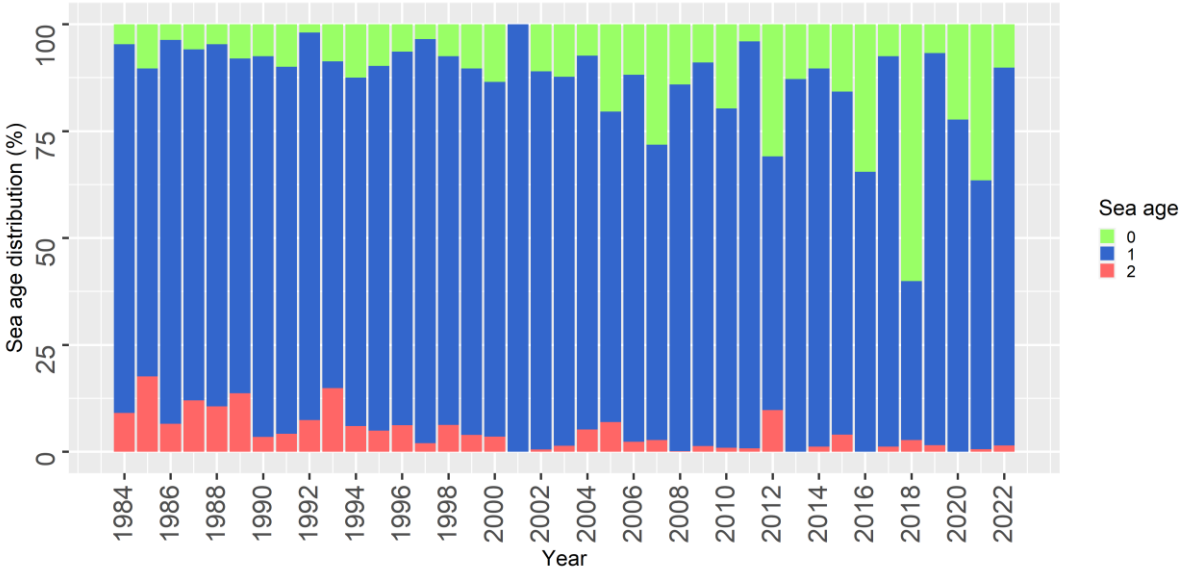

Figure 3 - Temporal variability in the age structure of first-time returning sea trout captured in the Bresle. Average proportions derived from the 1000 datasets.

Earlier life history determines the length of returning sea trout

River age had a long-term effect on the length-at-first return: individuals that smoltified after only 1 year in the river were shorter on their return than those that smoltified after 2-3 years (Figure 4). The younger the sea-age class the more pronounced this effect was, as indicated by the interaction between river age and sea age. For a 0SW individual smolting at age 2 or 3,

returns length was on average respectively 83.3 and 96.7 mm larger than in FW1 returns. River age was included in all of the best models, which highlights its high explanatory value.

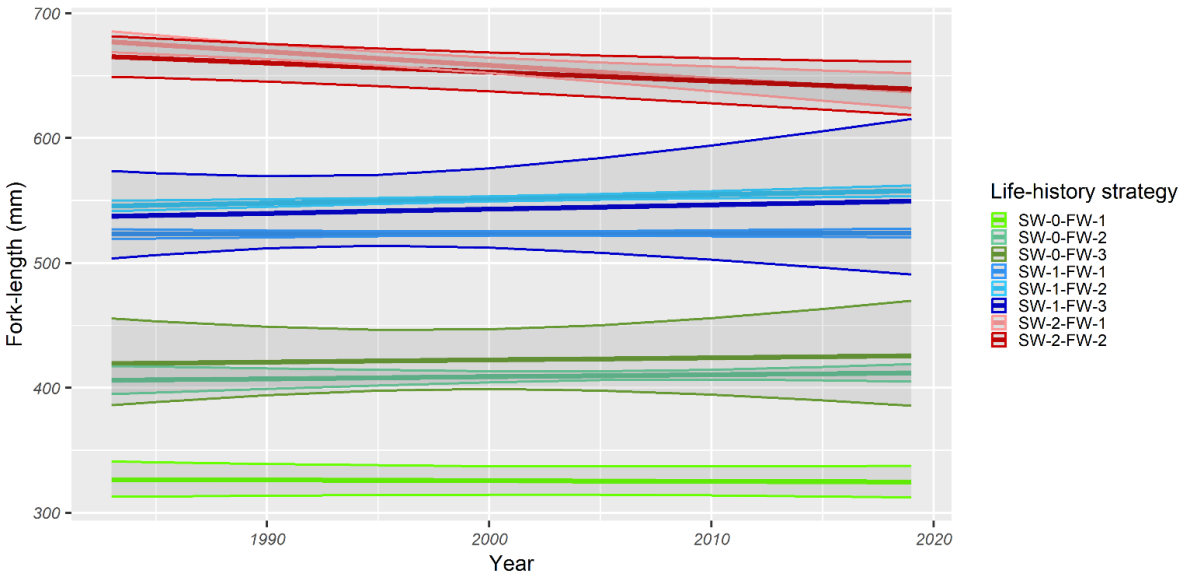

Figure 4 - Estimated changes in the length of sea trout at first return over time as a function of life history strategy. Mean fitted values in the 'response' scale derived from predictions on each best models. Shaded zones indicate 95% confidence interval. FW: number of years spent in river, SW: number of years spent at sea.

Length of returning sea trout is influenced by the migration timing

The two variables for migration timing (ctrAvgDOY and deltaDOY) explained some of the variability in the length-at-first return. Effects of return timing depended on the sea age, as indicated by the inclusion of the two-way interactions in the model. The effect of additional days at sea, measured at both inter-annual (ctrAvgDOY) and intra-annual (deltaDOY) scales, seemed to benefit 0SW individuals more than 1SW individuals. In contrast, this effect was negative for 2SW individuals, as late-returning individuals in this age class tended to be smaller than early-returning individuals. The inclusion of the temporal interaction indicated a potential change in effects of return timing over time, although support for it was weaker, as 22.7% of the best models did not include it.

Mean slopes of temporal linear regressions of the day of return indicated that the capture date of first returns advanced significantly ($p < 0.001$), with 0SW, 1SW, and 2SW being captured a mean of 1.38 (SD = 0.12), 1.21 (SD = 0.08), and 0.49 (SD = 0.26) days earlier each year, respectively. Over the 39-year period, the date of return thus advanced by 53, 47, and 19 days for 0SW, 1SW, and 2SW individuals, respectively. Despite this major change, the reduction in time spent at sea due to advanced seasonal migration timing had only a small effect on the length of sea trout at first return (Figure 5).

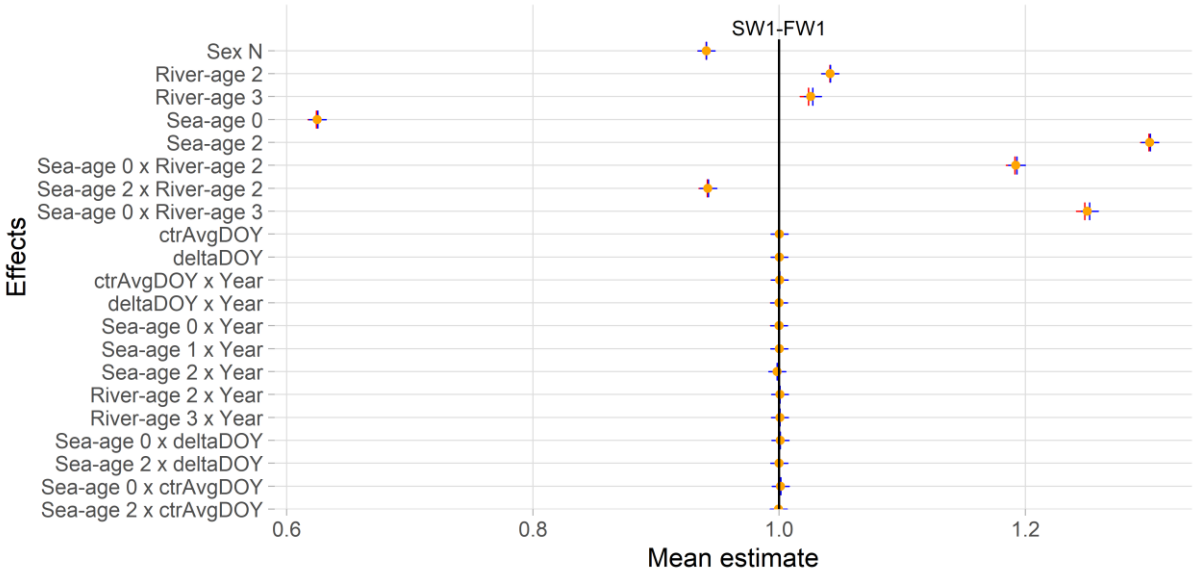

Figure 5 - Mean estimated effects of each predictor's modality, compared with a reference SW-1-FW-1 sea trout with a kype for ctrAvgDOY and deltaDOY = 0 (black vertical line). Orange dot, red and blue crosses indicates respectively mean estimate, lower and upper 95% Confidence Intervals (See Table 1 for the definition of variables.). Effects are presented in the 'response' scale, i.e. back-transformed from log-scale. For example, length of a reference fish without a kype ($L_{ref\text{-}N}$) would be: $L_{ref\text{-}N}$ = Sex N x L_{ref}.

Weak and contrasting evidence of changes in growth

Interactions between year and both river age and sea age were included in the best models, which supports the hypothesis of temporal changes in the length-at-first return as a function of life history strategy. The effect of the year on length-at-first return remained small and

relatively stable for 1FW, but increased slightly over time for 2FW and 3FW, both of which had similar variations (Figure 4). Furthermore, length-at-sea-age over time differed, being stable or slightly positive for 0SW and 1SW individuals, but decreasing for 2SW individuals. Overall, except for 2SW individuals, trends remained weak, with only slight changes in the length-at-age for 0SW and 1SW individuals.

Discussion

Results indicate that individuals returning to the Bresle River for the first time became progressively smaller over the 39 years of the study period. This trend mainly resulted from change in the age structure and contrasted variations in length-at-age. In the study population, an increasing percentage of sea trout returned for the first time at age 0SW and the return migration timing advanced. This decrease in duration of the marine sojourn can explain the decrease in body length, while length-at-age remained constant or slightly increased over time for 0SW and 1SW individuals. At the same time, the percentage and length-at-age of 2SW individuals decreased.

Strengths and limitations of long-term datasets

Sampling biases are inevitable during long-term monitoring of wild populations. It is often challenging to maintain sampling effort constant over long periods, whether due to changes in the sampling protocol, a lack of resources, modifications of the observation device or objectives, or varying environmental conditions. In this study, the need to control for sampling biases required rebalancing the dataset. The long duration of data collection on the Bresle River ensured that the dataset remained large and deep enough for exploratory analysis and modelling. Using the bootstrap procedure enabled multiple iterations of subsampling and

349 modelling, which increased the stability and robustness of the results. Ultimately, this ap-
350 proach is a useful example of how such a long-term dataset can be analysed, despite the lat-
351 ter's inherent flaws. One downside of long term datasets is that the amount of data is likely
352 to be important which can lead to the rejection of the assumption of normality in the residu-
353 als. In GLMs, this may be improved with the use of non-Gaussian distributions, such as the
354 Gamma distribution, which in the present case did not greatly enhanced the results of nor-
355 mality tests. However, McCullagh and Nelder (1989) reported that this assumption was not of
356 major importance in the case of "large datasets", where small deviations from normality will
357 most likely lead to rejection of the assumption. Everything kept equal, large deviations in the
358 residuals suggests either errors in the age determination, or significantly higher or lower per-
359 formances of some individuals. Considering the very high within strategy length variation that
360 can be observed in sea trout, it is likely to be a major factor here. Despite these difficulties,
361 long-term datasets are crucial for understanding highly complex ecological and evolutionary
362 processes (Eliott and Eliott, 2006; Hughes et al., 2017).
363

364 **An additional case study of decreasing average length of salmonids**

365 With a decrease of *c.* 8% in sea trout body length over the past four decades, the results add
366 to the growing corpus of literature that describes a decrease in the length of salmonid species
367 around the world (Bal et al., 2017; Jeffrey et al., 2017; Lewis et al., 2015; Morita and Fukuwaka,
368 2007; Ohlberger et al., 2018; Oke et al., 2020). The extent of the changes observed in the
369 Bresle sea trout population agrees with results of Oke et al. (2020) for four species of Pacific
370 salmon (Chinook, *Oncorhynchus tshawytscha*: -8.0%, coho, *Oncorhynchus kisutch*: -3.3%,
371 chum, *Oncorhynchus keta*: -2.4%, and sockeye, *Oncorhynchus nerka*: -2.1%), but in contrast,
372 we found little support for major changes in the length-at-age. Consistently with our results,

structural changes in the age at return have previously been reported by Milner et al., (2017) in sea trout. Change in the proportion of low-weight fish in rod catches of four Welsh rivers suggested of an increasing proportion of 0SW between 1977 and 2007.

The importance of considering the entire life history

We found that river age had a significant effect on length-at-first return, which indicates that the increase in length acquired in the river had long-term consequences until the first return to the river. This effect could have major implications for individuals' future life history, such as the timing of maturation and duration of the sea sojourn, as length can strongly influence when smolt reach key thresholds that drive life history transitions (Bohlin et al., 1996; Hutchings and Jones, 1998; Tréhin et al., 2021). Several studies have described mechanisms of compensatory growth in brown trout (Fahy, 1978; Johnsson and Bohlin, 2006; Marco-Rius et al., 2012) or other salmonid species (Al-Chokhachy et al., 2019; Mortensen and Damsgård, 1993; Nikki et al., 2004). In these studies, shorter smolts exhibited higher subsequent growth at sea than larger smolts and thus reached similar lengths at return. In a review of biological characteristics of 72 populations of sea trout in the British Isles, Fahy (1978) found no correlation between smolt length and adult length. However, it seems likely that slower growth rates there did not provide sufficient resolution to do so, as there were large overlaps in length among age classes. In contrast, faster growth rates in chalk streams such as the Bresle likely enabled us to more easily detect an influence of the river on the first return. A study from a nearby area and similar period (Pratten and Shearer, 1983) found that the mean length of the most common age classes (2FW and 3FW) in the North Esk River, Scotland, differed by a mean of 1.32 cm (SD = 0.36) from 1976-1980. In comparison, the mean length of smolts in the two

396 most common age classes in the Bresle (1FW and 2FW) differed by 3.94 cm (SD = 1.08) (un-
397 published data). In contrast, results of Marco-Rius et al. (2012) and Johnsson and Bohlin (2006)
398 do not seem to contradict ours. Marco-Rius et al. determined growth trajectories from scales,
399 but studied only a single age class (2FW) and excluded all individuals that had not spent an
400 entire year at sea (*i.e.* 0SW). Our results suggest that length differences are most visible in
401 0SW and tend to decrease as time at sea increases. Similarly, Johnsson & Bohlin (2006) con-
402 sidered only 1FW individuals, in which they induced length differences by depriving some of
403 them of food. While small differences within an age class can be compensated for within a
404 few months, this may not be the case for larger differences between age classes. The current
405 study also covers a longer period, more individuals, and focuses on fish that were not subject
406 to experimentally induced length differences.
407
408 **Effect of migration timing on length-at-first return**
409 Variations of the return date had little influence on length, despite major changes in sea-age
410 classes 0SW and 1SW, which arrived earlier by 53 and 47 days, respectively. This observation
411 is consistent with, but larger than, the advance of 2.6 days per decade observed by Legrand
412 et al. (2021), in the migration timing of sea trout at 40 monitoring stations in France. It is also
413 concordant with data from the River Dee, where length at return of 0SW individuals was found
414 to be independent from the day of return, with a complex non-linear pattern (Celtic Sea Trout
415 Project, 2016). Effects of a longer sea sojourn were positive and stronger for sea trout that
416 returned after 0SW, which is consistent with brown trout growth curves, which have steeper
417 slopes for younger age classes before reaching a plateau (Davaine et al., 1997). This dynamic
418 illustrates that younger fish benefit more from additional days at sea than older counterparts.
419

Contribution of growth opportunities and survival to age-dependent changes

It was surprising to detect a clear negative temporal trend in the length-at-age only for 2SW first returns, while those of 0SW and 1SW remained relatively stable. Marine trophic webs are under tremendous pressure in the context of climate change. The general consensus is that ocean productivity has decreased in the past few decades and that the composition of its eco-systems has changed greatly (Behrenfeld et al., 2006; Gohin et al., 2019; Hoegh-Guldberg and Bruno, 2010; Möllmann and Diekmann, 2012). One would thus expect to observe a decrease in growth also in younger age classes, as observed in Atlantic salmon (*Salmo salar*) (Tréhin et al., 2021). However, our results suggest that growth conditions for 0SW and 1SW may not have been greatly degraded. In fact, Davidson et al., (2006) even reported increased post-smolt growth for these two age-class on the River Dee. This differing response among sea-age classes could indicate local changes in the conditions that sea trout encountered at sea, rather than a broad decrease in growth opportunities. During migration at sea, salmonids gain access to different feeding grounds and sets of prey (Knutsen et al., 2004, 2001; Rikardsen et al., 2006, 2007; Thorstad et al., 2016). Consequently, changes in food availability and quality on the feeding grounds used by older and larger sea trout may explain their lower growth. Addi-tionally, local variations in sea temperatures could also influence sea trout return size, as re-ported before by Milner et al., (2017) in the Irish sea.

The age-specific decrease in length-at-first return may have been due to length-specific selec-tive pressure that targeted mainly larger individuals (Reznick et al., 1990), which could explain the progressive disappearance of 2SW individuals in the Bresle population. Overfishing has been widely demonstrated to influence many characteristics of fish populations, such as length at reproduction (Hard et al., 2008; Neuheimer and Taggart, 2010; Ojuok et al., 2007).

Intensive net fishing occurred at sea near the Bresle, especially during the first half of the study period, with up to 37% of the population being caught each year either by professional or leisure net fishing at sea or rod-and-line fishing in the river (Fagard and Beaulaton, 2018). More recently, the resurgence of marine apex predators with specific feeding behaviours has been associated with a decrease in the mean length of Chinook salmon (Ohlberger et al., 2019). However, although the Bresle River is located near the Bay of Somme, which hosts the largest breeding colony of harbour seals (*Phoca vitulina* L.) in the English Channel, analysis of 86 scat samples from this colony revealed no evidence of salmonids in the seals' diet (Spitz et al., 2015). Furthermore, most seal predation on salmonids seems to be opportunistic, with no indication of length-dependent selection for larger fish (Suuronen and Lehtonen, 2012; Thomas et al., 2017). Therefore, it seems unlikely that seal predation would have driven the population-wide changes in sea trout age structure observed in this study.

Parasitism by sea lice (*Lepeophtheirus salmonis*, Krøyer, 1837) has also been demonstrated to be a major factor of reduced survival in wild salmonids (Bjørn et al., 2001; Thorstad et al., 2015). Sea lice may have been responsible for the collapse of the sea trout population in the Burrishoole River (Gargan et al., 2006) and for profound changes in life history traits of that in the Eriff River, Ireland (Gargan et al., 2016). In the Bresle River, most returning sea trout show evidence of sea-lice parasitism, but the youngest and smallest individuals usually have the highest parasite loads. Premature returns, in which individuals with heavy sea-lice loads return to freshwater sooner than individuals that are not infested, have been well documented in the literature (Birkeland, 1996; Birkeland and Jakobsen, 1997; Serra-Llinares et al., 2020). Thus, parasitism could provide an explanation for the increase in the percentage of 0SW observed in this study.

468

469 **Future research and implications for management**

470 Although length-at-age changed little overall, a decrease in the age-at-first-return appears to
471 be the main reason of the decrease in the length-at-first return observed for sea trout in the
472 Bresle River. A change in the fitness-driven trade-off between survival and growth can change
473 the duration of the sea sojourn or the prevalence of migratory or resident ecotypes in trout
474 (Archer et al., 2019; Thorstad et al., 2016). Accordingly, future research should explore tem-
475 poral changes in growth at sea, which would entail analysing fine growth increments in scales.
476 For instance, increased growth opportunities could explain the shift toward shorter sea so-
477 journs, as fish could reach the suitable condition to mature earlier. On the other hand, reduced
478 growth at sea, potentially associated with reduced survival, could also lead to selective pres-
479 sure against long marine sojourn. Indeed, age at maturation has been demonstrated to be a
480 partially heritable life history trait in sea trout (Ferguson et al., 2019; Reed et al., 2019). Thus,
481 natural selection and change in allele frequency could potentially explain the progressive shift
482 toward shorter sea sojourn observed in this study.

483

484 The potential carry-over effect of a trout's freshwater life on its length-at-first return could be
485 relevant for salmonid management. Growth potential at sea is much higher than that in fresh-
486 water, accordingly the latter often seems to be viewed as a mere transitional habitat between
487 hatching and smoltification. Nevertheless, the hypothesis that a mechanistic length threshold
488 drives the probability of maturing (Hutchings and Jones, 1998) predicts that smolts that are
489 larger when entering the sea will reach the critical maturation length sooner and thus return
490 after fewer years at sea. Thus, the freshwater and marine phases of the sea trout life cycle
491 could both influence the life history changes observed during the return migration (Russell et

al., 2012). Consequently, management actions could be aimed at alleviating pressures on juveniles, by mitigating the effects of climate change and improving freshwater habitats. These actions should especially include managing and protecting water resources (Waco and Taylor, 2010), restoring habitat connectivity (Forget et al., 2018), and creating thermal refuges (Blann et al., 2002).

Changes such as the progressive loss of a sea-age class, as observed for 2SW individuals in this study, can strongly influence a population's resilience (Erkinaro et al., 2019; Stewart, 2011). Reduced diversity of life history strategies could weaken the "portfolio" effect (Markowitz, 1952), which could increase the risk of population collapse (Figge, 2004; Schindler et al., 2015, 2010). The loss of older age classes can also have an especially detrimental effect due to the loss of "big, old, fat, fecund, female fish" (BOFFFFs). These older female fish contribute greatly to reproduction as they produce more and often larger eggs than younger females do (Hixon et al., 2014; Ohlberger et al., 2020; Pope et al., 1961). Therefore, management actions such as specific fishing regulations to protect these older fish could be implemented in the Bresle River.

The lack of knowledge about the reproductive status of first-time returning individuals is a potential disadvantage for future studies of population dynamics, especially for the role of the 0SW life history strategy. The return status of the individuals included in this study was determined from the analysis of patterns on scale reading. However, it provides an imperfect record of previous reproduction history (Baglinière et al., 2020). Assessing whether 0SW returns are mature individuals which will spawn the following winter or immature individuals which will overwinter in the river Birkeland, 1996) would help understand consequences of their recent

relative increase on population dynamics. However, the percentage of the Bresle population that does so is unknown. In contrast, a study of 0SW trout in the nearby Calonne River showed that most summer 0SW and all autumn 0SW individuals were mature (Maisse et al., 1991), which bring support to the hypothesis that the immature-return strategy has been uncommon in rivers in Normandy.

We showed that change in the length-at-first return of the Bresle sea trout population was explained mainly by a change in the mean sea age of first returns, which decreased over time. Other factors also had an influence on the long-term change in the length of returns, such as a small decrease in length-at-age, an advanced mean date of return, as well as the carry-over effect of the river age. Further studies investigating sea trout life and growth at sea would be needed to better understand the response of this complex species to ongoing environmental changes.

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Data availability

Data analysed in this study are available on the GBIF repository at:

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Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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