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Back-calculation modelling from Atlantic salmon (*Salmo salar*) scales

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Introduction

Life history traits are directly related to fitness. They include the number of offspring, the age and size at maturity and the growth pattern (Wake 2003). When resources are limited, which is most often the case in the wild, the available resource allocated to one trait would be traded against its allocation to another competing trait. The allocation strategy that is the most adapted to the environment is then selected through natural selection. (Braendle *et al.* 2011, Brown & Choe 2019).

Since the 1970s, the sea surface temperatures have increased overall under the effect of global warming (Polyakov *et al.* 2010, Hausfather *et al.* 2017). This change in abiotic factors may be partly responsible for modifications of life history traits of Atlantic salmon *Salmo salar* (Jonsson *et al.* 2016, Bal *et al.* 2017). Available literature suggest an indirect effect due to a decrease in feeding resources available for *S. salar* during the marine phase (Capuzzo *et al.* 2017), what may induce a slower growth, a delayed maturation and a decrease of marine survival (Beaugrand & Reid 2012). The observed decrease in wild *S. salar* population growth rate would modify population viability and thus fisheries management (Bal *et al.* 2017).

S. salar is an anadromous migratory fish. Its reproduction takes place in upstream rivers, where the water is well oxygenated. Juveniles, called parr at this stage, stay in freshwater until they are big enough to become smolts and go into the sea. Smolt stage is characterized by modifications at morphological, physiological, biochemical, hormonal and behavioral levels that make the fish adapted to life at sea and capable of osmoregulating (Boeuf 1994). The residence time in the river depends on the growth rate of individuals. In France, parrs spend between one and two years in freshwater before becoming smolts (Heland & Dumas 1994). Those who leave after one year in the river are called one-freshwater-winter (1FW) fish, those who leave after two years are called two-freshwater-winter (2FW) and so on. Once in the sea, *S. salar* take transoceanic currents of North Atlantic and continue to grow. *S. salar* coming from French populations spend between one and three years at sea until they attain sexual maturity and come back to their natal river to reproduce. When spawning after one year in the ocean, they are called one-sea-winter (1SW) fish, and after two or more years they are called multi-sea-winter (MSW) fish. Growth affects the key transitions of *S. salar* life cycle (migration, survival, maturation). A change in growth conditions would lead to modifications in life history traits. Understanding the mechanisms underlying these modifications would help to predict the response of salmon populations to future changes in the environment and adapt fisheries management.

The present study is part of the SAMARCH project that aims at providing a better understanding of the life cycle of salmonids, especially in response to changes in the marine environment (<https://samarch.org/>). Because of the difficulty to sample salmon in the ocean, individual monitoring is almost impossible during the marine phase. Calcified structures are natural markers that bring indirect information concerning the growth history of each individual. Back-calculation virtually allows for estimating lengths at any ages, even when no direct observation is available. Bones, otoliths and scales can be used for growth analysis. However even though scale reading is the least precise method (Abecasis *et al.* 2008), scales are much easier to sample and their use does not require the sacrifice of individuals.

The aim of this study is to estimate the growth and length of salmon during their marine phase through back-calculation based on the analysis of adult scales. A set of back-calculation models were selected from literature (Francis 1990, Vigliola & Meekan 2009). Their relative performance was tested through quality of fit and cross-validation test, and recommendations were made on their use in order to get the best estimation of fish length at a given age.

Material and methods

Study site and fish sampling

The Scorff is a river long of 75 km, situated in south Brittany. Its estuary is located near Lorient. *Salmo salar* Scorff population is monitored thanks to fish traps since 1996.

The capture site is located on the head of the tide in Pont-Scorff at the Princes' mill and is operated by INRA and the local angling association (47°50'12.5"N 3°23'37.5"W). Fish are caught at smolt stage during their migration to the sea, as well as at adult stage during their anadromous migration to reproduce upstream. As those sites do not cover the entire width of the river, the individuals sampled represent a random part of the total population. Some smolts were marked using a PIT tag (Passive Integrated Transponder) containing a unique number which enabled to recognize every individual fish throughout its life. Most of the PIT tags were implanted at the parr stage during electro-fishing sessions, some survived to become smolts and went into the sea. Each captured fish got its length to the fork measured, and a sample of scales was taken in the standard zone. The standard zone is located above the lateral line, on the axis connecting the anal fin to the dorsal fin (Fig. 1). This zone was chosen because this is where the first scales are formed on the fry, so it contains the oldest history (Shearer 1992).

Finally, for this analysis, we used a subsample of thirty smolts and sixty adults per year (30 1SW and 30 2SW) over the period 1996 to 2018. The sample size is 1738 individuals: 441 1FW smolts, 225 2FW smolts, 614 1SW adults (in which 424 were 1FW and 188 2FW) and 458 2SW adults (in which 354 were 1FW and 104 2FW).

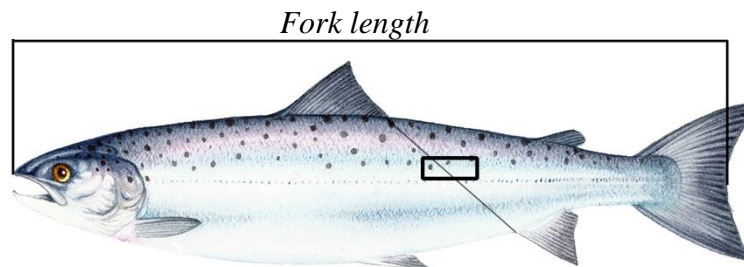


Figure 1. Standardized measurements and scale sampling area for *Salmo salar* (Baglinière & Porcher 1994). The rectangle indicates the standard zone for scale sampling. The drawing was made by Lizzie Harper.

Scale analysis

We used the protocol and nomenclature set out by the International Council for the Exploration of the Sea in 1984 (ICES 1984). A technician examined scales using a stereomicroscope and Image Pro Premier software. The distance between the center of the scale (focus) and each radius (circuli) was measured on the longest axis of each scale.

Based on the species biology, it was possible to associate key periods to the differences of growth shown on the scale (Fig. 2). The growth during winter is limited, due to the low temperatures (Pörtner & Farrell 2008), low amount of resources (Duston & Saunders 1999) and low photoperiod (Døskeland *et al.* 2016). As a result, winter phases are recognisable by tightened circuli forming a ring (Ombredane & Baglinière 1992). As growth in freshwater is lower than growth at sea (Davaine & Prouzet 1994), the transition from the river to the sea is clearly visible by the transition from small intercirculi distances to larger ones. The position of the end of winters and the transition from river to sea are references for our study. Based on the number of winters visible on a scale in freshwater (and in sea for adults), it is possible to approximate the age of the fish at the time of the capture. A dataset containing focus-circuli distances for one scale of each individual was already available.

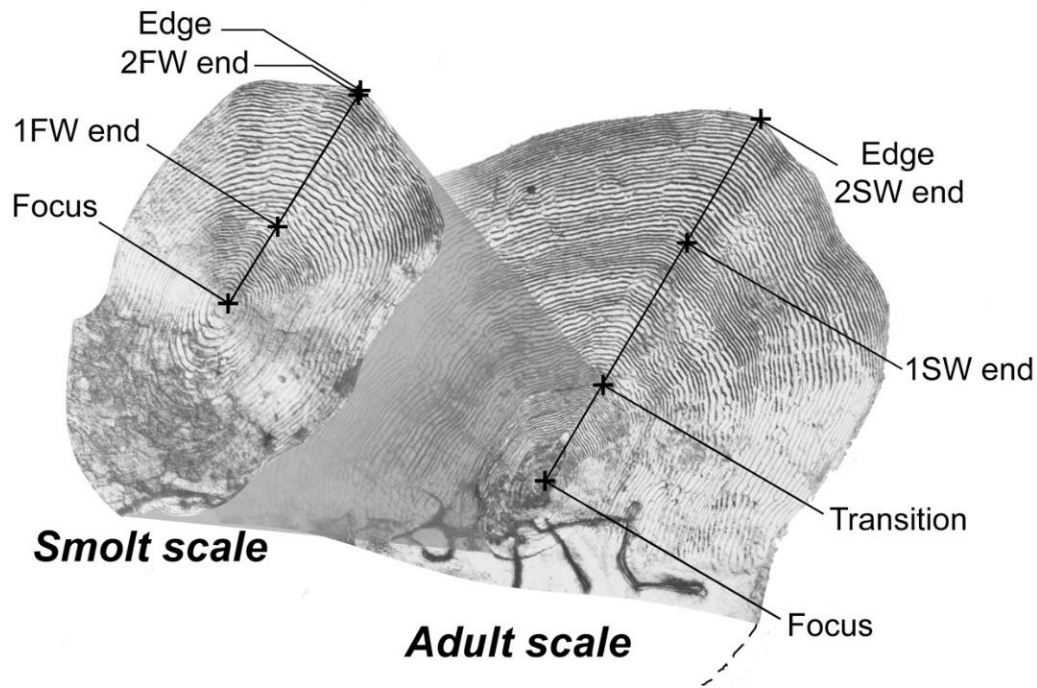


Figure 2. Pictures of two scales of a PIT tagged Atlantic salmon at the smolt stage (a) and taken 737 days later as an adult (b).

Back-calculation models

All statistical analyses were conducted with R version 3.4.4 (R Core Team 2018). Back-calculation models enable to estimate the size of an individual throughout its life based from patterns recorder in a calcified structure. For each circuli on the scale, the length of the individual at the time of its formation was estimated. A back-calculation formula defines a family of lines for a population. Back-calculation for a particular fish will involve just one of these lines, the one adjusted for individual body length and scale radius at the time of the capture (Francis 1990). The back-calculation of fish length has to be made in two steps. The first one consists in fitting a regression model (linear or nonlinear, depending on the modelling hypothesis) between body length and scale radius to the whole dataset containing both adults and smolts (Fig. 3). This describes the mean body-scale relationship in the population. In the second step, the parameters obtained in those regressions are used on each adult through a back-calculation formula derived from the average relationship fitted at step 1 but corrected for each individual to account for inter-individual variability. In fact, each individual has a specific body-scale relationship that differs more or less from the mean. Table 1 summarizes the different back-calculation formulas published in the literature (Francis 1990, Vigliola & Meekan 2009).

Table 1. Summary of back-calculation models. Regression models represent body-scale relationships used to calculate average parameters for the population before being applied through back-calculation formula to each individual. L is the fork length, S is the scale radius, L_c is the fork length at capture, S_c is the scale radius at capture, L_i is the fork length at the formation of the i^{th} circuli, S_i is the scale radius at the formation of the i^{th} circuli and a , b , c and d are parameters specific to each regression. In the modified Fry back-calculation formula: $\bar{a} = (a_1 + a_2)/2$.

Model	Hypothesis	Regression(s) used	Back-calculation formula	Reference
Dhal-Lea	The scale grows in exact proportion to the length of the individual. <i>Intercept at the origin.</i>	-	$L_i = L_c \frac{S_i}{S_c}$	Lea (1910)
Fraser-Lee	The growth increment of the scale is a constant proportion of the growth increment of the fish. <i>Mathematical intercept (0; a).</i>	$L = a + bS$	$L_i = a + (L_c - a) \frac{S_i}{S_c}$	Fraser (1915) Lee (1920)
BPH (Linear BPH)	There is constant proportional deviation from the mean body size. <i>Mathematical intercept (0; a).</i>	$L = a + bS$	$L_i = L_c \frac{(a + bS_i)}{(a + bS_c)}$	Francis (1990)
SPH (Linear SPH)	There is constant proportional deviation from the mean scale size. <i>Mathematical intercept. (a; 0).</i>	$S = a + bL$	$L_i = (-\frac{a}{b}) + (L_c + \frac{a}{b}) \frac{S_i}{S_c}$	Francis (1990)
Monastyrsky BPH (Non-linear BPH)	The relation between body size and scale length is described by an allometric function. Corresponds to a non-linear BPH. <i>Intercept at the origin.</i>	$L = bS^c$	$L_i = L_c (\frac{S_i}{S_c})^c$	Bagenal & Tesch (1978)
Monastyrsky SPH (Non-linear SPH)	The relation between body size and scale length is described by an allometric function. Corresponds to a non-linear SPH. <i>Intercept at the origin.</i>	$S = bL^c$	$L_i = L_c (\frac{S_i}{S_c})^{\frac{1}{c}}$	Bagenal & Tesch (1978)
Campana	Same hypothesis than Fraser-Lee but with a <i>biologically determined intercept</i> ($S_0; L_0$).	-	$L_i = L_c + (S_i - S_c) \frac{(L_c - L_0)}{(S_c - S_0)}$	Campana (1990)
Modified Fry	The relation between body size and scale length is described by an allometric function. <i>Biological intercept ($S_0; L_0$).</i>	$L = a_1 + bS^c$ $R = (\frac{L - a_2}{b})^{\frac{1}{c}}$	$L_i = \bar{a} + \exp(\ln(L_0 - \bar{a})) \frac{[\ln(L_c - \bar{a}) - \ln(L_0 - \bar{a})][\ln(S_i) - \ln(S_0)]}{[\ln(S_c) - \ln(S_0)]}$	Vigliola <i>et al.</i> (2000)

Two competing hypothesis for the individual corrected factor used in back-calculation were compared: the body proportional hypotheses (BPH) and the scale proportional hypothesis (SPH) (Francis 1990). The BPH states: “if a fish at capture was 10% smaller than the average fish with that size of scale, the fish would be 10% smaller than the expected length for the size of that scale throughout life”. The SPH states that: “if the scale was 10% larger when the fish was caught than the average scale for that size of fish, the scale would be 10% larger than normal throughout the life”. Some models are based on other hypotheses (*e.g.* Dhal-Lea, Fraser-Lee, Campana, modified Fry). However, Fraser Lee and BPH models are based on the same regression, thus they will produce very similar results (Francis 1990).

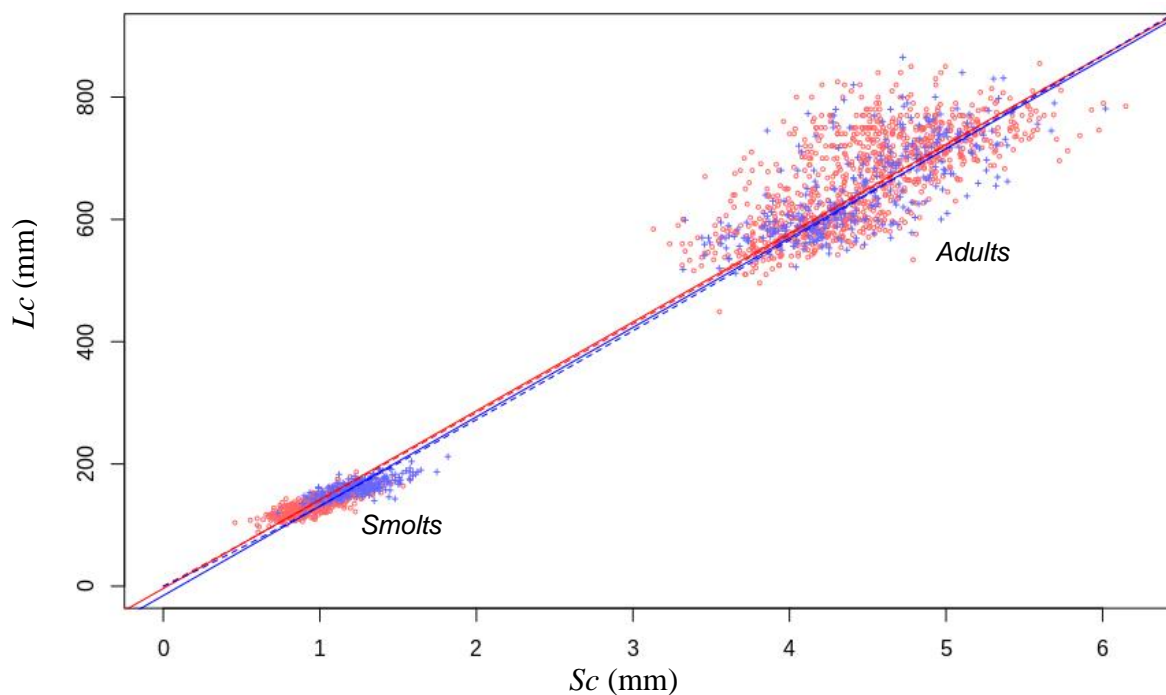


Figure 3. Example of fork length (L) on radius scale (S) regressions. L_c is fork length at capture and S_c is scale radius at capture. Red dots stand for 1FW individuals, blue dots for 2FW individuals. Solid lines are linear regressions ($L = a + bS$) and dotted lines are non-linear ($L = bS^c$).

The intercept represents the length of the fish when its scales are beginning to form (Ricker 1992). It can be approximated mathematically with linear regressions (so called “mathematical intercept”, *e.g.* Fraser-Lee, BPH, SPH), or fixed by the user based on biological criterias. In this last case, we are talking about “biological intercept” (*e.g.* Campana, modified Fry). However, it is known that the relationship between scale and body size for *S. salar* differs according to the development stage with an allometric growth in freshwater and an isometric growth at sea (Tremblay & Giguère 1992, Dietrich & Cunjak 2006). As this study focuses on

the marine phase, we use the mean body size and the mean scale length at the time of transition from freshwater to the sea as the starting point of our models.

Parameters estimation: effect of life history

Smolts that have spent two years in freshwater are significantly bigger than the ones that smoltify at one year (on the fork length level, the difference between 2FW and 1FW smolts was 28 ± 3 mm, $t=22.3$, $Df=664$, $P<0.001$, and on the scale radius level $\text{diff}_{(2FW-1FW)}=0.27 \pm 0.03$ mm, $t=19.6$, $Df=663$, $P<0.001$). Thus, all regressions (Tab. 1) were made for each age class (1FW and 2FW) separately (Fig. 3) which led to different parameters. Moreover, as it is biologically reasonable to consider a different intercept for 1FW and 2FW smolts, the biological intercept (S_0 ; L_0) was also different according to the time the individual spent in freshwater.

Model selection and model averaging

Validation at the individual level

The ability of the back-calculation method to accurately estimate the smolt length from an adult scale was tested using 14 pit-tagged individuals caught at both the smolt and adult stage. For those individuals, scale radius and fork length at two different ages were available. For each model, the least square method was used to quantify the distance between the observed length and the back-calculated estimated smolt length based on the adult scale from the curve having a slope of 1 and passing by the origin (for which the observed length is equal to the estimated one).

Validation at the population level

We also assess whether back-calculation models were successful in estimating the mean and variation range of the smolt length. The distribution of back-calculated smolt length (BSL) estimated by each model based on adult scales was compared to the distribution of observed smolt length (OSL). The scale radius at smolt stage was approximated by the radius from the focus to the transition on the adult scale. We made the hypothesis that the focus-transition distance on the adult scale is representative of the focus-edge distance on the smolt scale at the time of capture at the fish trap.

Model averaging

Instead of selecting the best model, a model averaging procedure was used to provide predictions that integrate over model uncertainty (Burnham & Anderson 2002). Based on the sum of squared residuals of the validation at the individual level and on the fit to the observed smolt length at the validation at the population level, one model seemed to give inaccurate estimations. Thus it was removed. Then back-calculated estimations of smolt length from all other models were averaged to provide an average prediction that accounts for model uncertainty and to quantify model uncertainty about this prediction. Each model was given the same weight in the averaging.

Results

Validation at the individual level

Based on the PIT tagged individuals, the two models working with a biological intercept (Campana and modified Fry) best fit to the observed smolt length from adult scales (Tab. 2). The Dhal-Lea overestimated almost all lengths.

Table 2. Sum of squared residuals to quantify the distance between the observed smolt length and the estimated smolt length for each model from the 1:1 curve on 14 individuals.

Models	Modified Fry	Campana	Monastyrsky SPH	Monastyrsky BPH	BPH	SPH	Fraser Lee	Dhal Lea
SSR	4739	4983	7212	7616	7879	7932	8190	9642

Validation at the population level

The overestimation of lengths by the Dhal-Lea model also occurs for the distribution of estimated smolt length, with the pink dotted curve isolated on the right (Fig. 4). The two models using biological intercept (Campana and modified Fry) have different shapes than models with mathematical intercept. They also seem to be the only ones to fit the right mean for 2FW smolts (Fig. 4b). Fraser-Lee and BPH models gave about the same result with their curves overlapping, for both 1FW smolts and 2FW smolts.

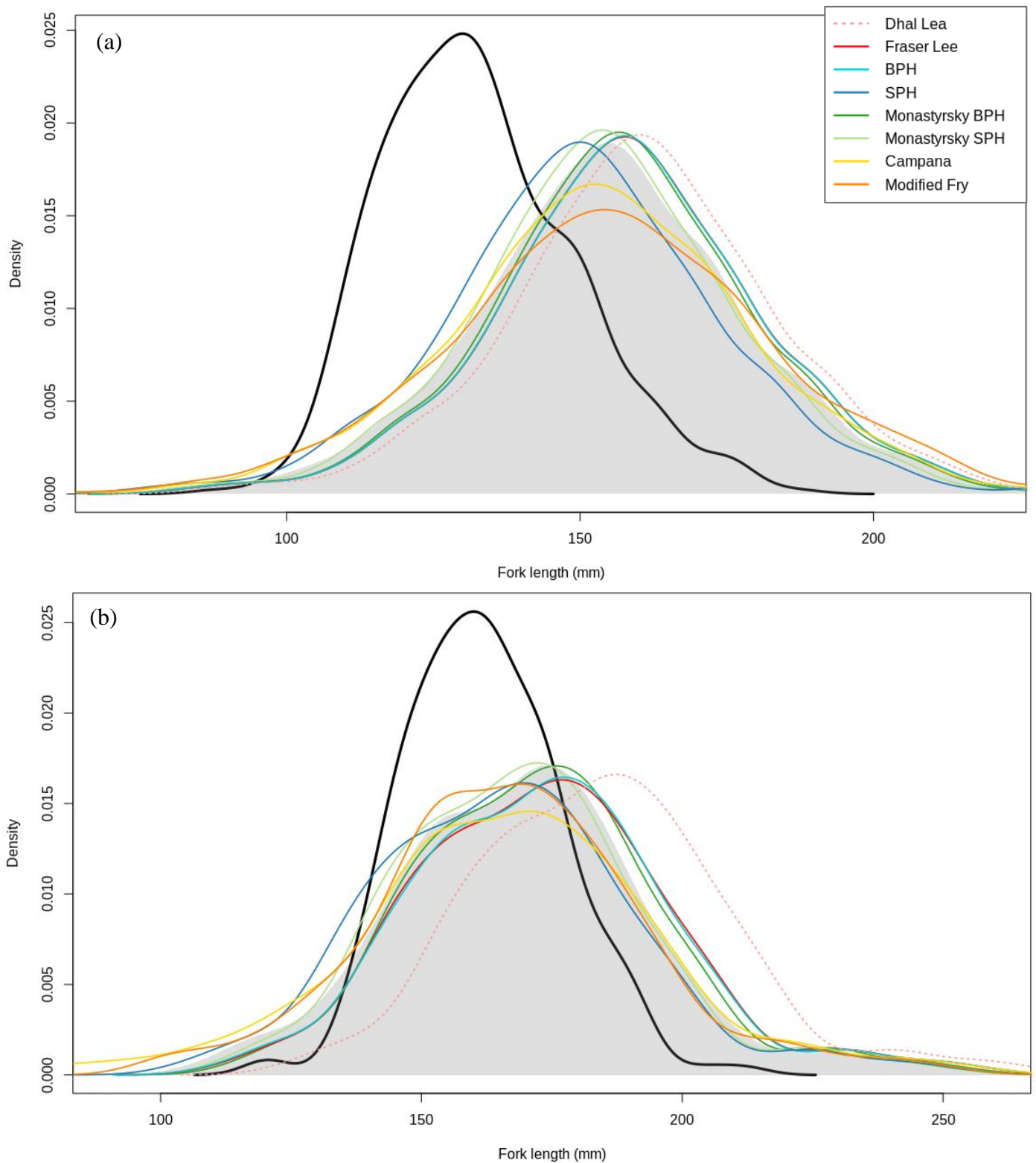


Figure 4. Observed smolts lengths distribution (thick black line) and estimated smolts lengths distributions for 1FW smolts (a) ($N_{\text{observed}} = 441$, $N_{\text{estimated}} = 778$) and 2FW smolts (b) ($N_{\text{observed}} = 214$, $N_{\text{estimated}} = 292$). The dotted line represents the model that was not selected for the model averaging. The model averaging is represented by the grey area. The curves of Fraser Lee and BPH models overlap, especially for 1FW smolts.

Model averaging

The Dhal-Lea model was removed from the model averaging procedure as it strongly overestimated lengths at the individual and population level.

Finally, the models kept for model averaging were Fraser Lee, BPH, SPH, Monastyrsky BPH, Monastyrsky SPH, Campana and modified Fry models (Fig. 5).

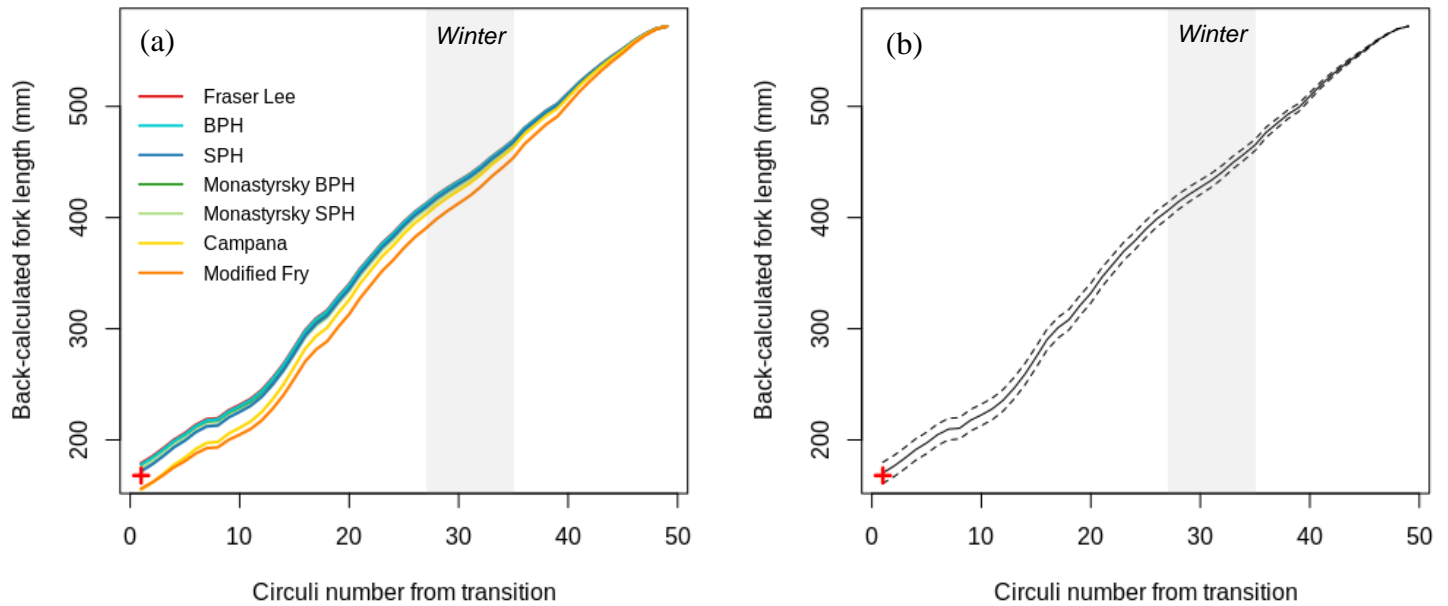


Figure 5. Back-calculated length for each circuli from transition of a PIT tagged 1FW 1SW fish. Red cross stands for real smolt length at capture. The results of different back-calculation models are given in (a) and the model averaging is shown on (b) with the confidence interval at 95% as dotted lines.

For the individual shown on Figure 5, the two models using a biological intercept underestimated the real smolt length of the individual whereas the models using mathematical intercept overestimated it. The model averaging enabled to find the right smolt length, and in addition produced a measure of uncertainties over fork length throughout the sea growth. The winter phase visible on the scale corresponds to a period of slow body growth. Concerning the pattern around the tenth circuli from transition, it corresponds to a period in which the growth was limited without explanation. Those patterns are called “checks” (Shearer 1992).

On the 14 PIT tagged individuals for which the smolt length was known, the average difference between the model averaging estimate and the observed smolt length is $16 \text{ mm} \pm 4 \text{ mm}$ (standard error of mean).

Discussion

Back-calculation models

Model selection

The validation at the individual level step was made on only fourteen individuals, hence limiting the robustness. Yet, results were confirmed by the validation at the population level. Because of its low accuracy the “traditional model” (Dhal-Lea) was the one left on the side in our study, even though it is widely used in back-calculation studies (Heidarsson *et al.* 2006, Kuparinen *et al.* 2009, Jensen *et al.* 2011) while its tendency to misestimate lengths is known (Heidarsson *et al.* 2006). Hanson *et al.* (2019) already showed that Dhal-Lea model underestimated small smolt length and overestimated large smolt length. Moreover, Dhal-Lea hypothesis considers a linear body-scale relationship beginning at the origin which does not correspond to the observations on *S. salar* as the body-scale relationship differ between freshwater growth and sea growth (Tremblay & Giguère 1992, Dietrich & Cunjak 2006).

In the present study, models including biological intercepts (Campana and modified Fry) revealed the most accurate. Working on gobies otoliths, an analysis made by Wilson *et al.* in 2009 also found that the modified Fry was the best back-calculation model. In his case, Campana model did not provide relevant length estimations because of the growth effect present in his dataset. The growth effect is the phenomenon when otoliths from slow-growing fish are larger than those of fast growing fish (Morita & Matsuichi 2001). As scales do not grow continuously along the time as otoliths do, the growth effect is not present in our dataset of *S. salar*.

Model improvement

The back-calculated smolt length (BSL) distribution has a larger variance than the observed smolt length (OSL). This can be explained by the fact that BSL are back-calculated from adults, which exhibit a larger diversity in length than their corresponding smolts (*i.e.* those which spent the same amount of time in freshwater). In fact, different parameters were considered according to the time spent in freshwater, but the adult dataset contains adults that stayed different time in sea (1SW and 2SW). The longer the time spent in ocean, the bigger the

salmon. For further studies, in order to reduce this variance and get more accurate smolt length estimations, it could be interesting to take into account the time spent in ocean. This would result in four different groups on which making the regressions: 1FW and 1SW, 1FW and 2SW, 2FW and 1SW, 2FW and 2SW.

The models only estimate one length for each circuli. Having an idea of the uncertainties generated on our back-calculated lengths would represent an added value to the present study. So in order to go further, the models could be built in a Bayesian framework to produce measure of uncertainties about back-calculated lengths.

Age approximation and growth analysis

Back-calculating length is useful to predict the size of a fish for which only the age is known. Some authors tried to estimate ages by calculating the timing and periodicity of ring formation using the number of circuli and the inter-circuli distance (Vaz-dos-Santos & Rossi-Wongtschowski 2007, Abecasis *et al.* 2008). The growth coefficient obtained can be used in Von Bertalanffy equation. Another method consists in using a simple quadratic method to date the formation of each circuli (Todd *et al.* 2013). However, those methods can be biased because circuli do not deposit at a constant rate (Thomas 2018). In fact, the circuli formation rate is driven by factors like the feeding regime or the temperature. Moreover, Thomas *et al.* (2019) showed that inter-circuli distance is highly variable and does not represent fish growth. Tightly packed circuli occurred during periods without food when growth was depressed, but also during periods of rapid growth at 15 C. Therefore, the next step of this study, which is aging circuli, still remains challenging.

Size-dependent selection happening during the marine phase

BSL are bigger than OSL for 1FW smolts. This difference has two possible explanations. First, the hypothesis we made about the focus-edge distance on smolt scale equal to the focus-transition distance on adult scale may not be verified. In fact, if the deposition of the transition circuli is not immediate, the focus-edge distance on smolt scale would be slightly smaller than the focus-transition distance on adult scale. As BSL are calculated from adult scales, this could explain why the back-calculated lengths obtained are larger. However, this explanation does not seem to be the right one. In fact, if there was such a bias it should have

the same impact on 1FW and 2FW smolts, which is not the case as the difference between BSL and OSL is bigger for 1SW smolts.

The second explanation would be that there is selection happening in sea, which would preferentially select the bigger smolts. Size-dependant selection in ocean is a known phenomenon (Armstrong *et al.* 2018, Gregory *et al.* 2018, 2019). The bigger the smolt, the higher its survival probability in the early post-smolt phase in sea. This size-dependent selection may be due to size selective mortality due to higher capacity of large smolts to escape predators (Riley *et al.* 2011, Berejikian *et al.* 2016, Friedland *et al.* 2017). When back-calculating smolt lengths from adult scales, the smolt lengths would be bigger, because coming from the larger individuals that survived selection. As 2FW smolts are bigger than 1FW smolts, they are less affected by selection, which is why the difference between BSL and OSL is smaller for 2FW smolts.

Therefore, our models and results are biased due to the use of only the individuals that were seen returning (the “winner” bias). In fact, the adults sampled do not correspond to the smolts sampled, but represent a biased sample towards the bigger ones. In order to limit this bias, parameters may be estimated only from PIT tagged individuals, for which the smolt and the adult lengths are known and that returned after surviving in sea conditions. Removing the selection bias could also be possible by studying hatchery populations, but still with the issue that growth would then not be representative of wild populations.

Conclusion

Models including a biological intercept seem to perform best to estimate smolt length based on adult scales. However for further studies, some recommendations are made in order to improve the models. Firstly, splitting the dataset according to the time spent in river but also to the time spent at sea could provide more accurate results. Second, a Bayesian analysis would allow for readily quantification of uncertainties about predictions. Third, the dataset used should be based on only the PIT tagged individuals to limit size dependent selection bias. Of course, ideally, sampling in ocean could provide a stronger validation in model selection, bringing new information concerning marine growth.

Back-calculation of fish lengths is of major interest for population dynamics studies as it allows for estimating the length of individuals at key ages that are not directly observed.

Those lengths could also allow the implementation of population dynamics models structured by size, which are a critical step towards a better understanding of the effect of environmental changes on populations dynamics. Thus, the population growth and viability can be estimated, which will enable to give recommendations concerning the species management especially through the regulation of fisheries.

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What a place to work in!

References

- ABECASIS, D., BENTES, L., COELHO, R., CORREIA, C., LINO, P.G., MONTEIRO, P., GONÇALVES, J.M.S., RIBEIRO, J., ERZINI, K., (2008). Ageing seabreams: A comparative study between scales and otoliths. *Fisheries Research*, 89(1), 37–48.
- ARMSTRONG, J. D., MCKELVEY, S., SMITH, G. W., RYCROFT, P., & FRYER, R. J. (2018). Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, 92(3), 569–578.
- BAGENAL, T. B., & TESCH, F. W. (1978). Age and growth. In *Methods for assessment of fish production in freshwater* (3rd ed. pp. 101–136). Oxford, UK: Bagenal T. B.
- BAGLINIERE, J. L., & PORCHER, J. P. (1994). Caractéristiques des stocks de reproducteurs et comportement lors de la migration génésique. In J. C. Gueguen & P. Prouzet (Eds.), *Le Saumon Atlantique, biologie et gestion de la ressource* (IFREMER, pp. 101–122). Plouzané.
- BAL, G., MONTORIO, L., RIVOT, E., PREVOST, E., BAGLINIERE, J.-L., & NEVOUX, M. (2017). Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 90(6), 2375–2393.
- BEAUGRAND, G., & REID, P. C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69(9), 1549–1562.
- BEREJIKIAN, B. A., MOORE, M. E., & JEFFRIES, S. J. (2016). Predator-prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. *Marine Ecology Progress Series*, 543, 21–35.
- BOEUF, G. (1994). La phase de préadaptation à la vie en mer : la smoltification. In J. C. Gueguen & P. Prouzet (Eds.), *Le Saumon Atlantique, biologie et gestion de la ressource* (IFREMER, pp. 47–63). Plouzané.
- BRAENDLE, C., HEYLAND, A., & FLATT, T. (2011). Integrating mechanistic and evolutionary analysis of life history variation. In A. Heyland & T. Flatt (Eds.), *Mechanisms of life history evolution : the genetics and physiology of life history traits and trade-offs* (Oxford University Press, pp. 3–10). Oxford, UK.
- BROWN, J. L., & CHOE, J. C. (2019). Behavioral ecology and sociobiology. In J. C. Choe (Ed.), *Encyclopedia of Animal Behavior* (2nd ed, pp. 103–108).
- BURNHAM, K. P., & ANDERSON, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed). New York: Springer.
- CAMPANA, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, 47(11), 2219–2227.

- CAPUZZO, E., LYNAM, C.P., BARRY, J., STEPHENS, D., FORSTER, R.M., GREENWOOD N., MCQUATTERS-GOLLOP, A., SILVA, T., LEEUWEN, S.M. VAN, ENGELHARD, G.H. (2017). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24(1), 352–364.
- DAVAINE, P., & PROUZET, P. (1994). La vie marine du saumon atlantique dans son aire géographique. In J. C. Gueguen & P. Prouzet (Eds.), *Le Saumon Atlantique, biologie et gestion de la ressource* (IFREMER, pp. 64–85). Plouzané.
- DIETRICH, J. P., & CUNJAK, R. A. (2006). Body and scale growth of wild Atlantic salmon smolts during seaward emigration. *Environmental Biology of Fishes*, 80(4), 495.
- DØSKELAND, I., IMSLAND, A.K.D., FJELLDAL, P.G., STEFANSSON, S.O., ROTH, B., ERIKSEN, K.E., MIKALSEN, B., HANDELAND, S. (2016). The effect of low temperatures and photoperiods on growth and vertebra morphometry in Atlantic salmon. *Aquaculture International*, 24(5), 1421–1434.
- DUSTON, J., & SAUNDERS, R. L. (1999). Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in seawater. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(2), 201–207.
- FRANCIS, R. I. C. C. (1990). Back-calculation of fish length: a critical review. *Journal of Fish Biology*, 36, 883–902.
- FRASER, C. M. (1915). Growth of the spring salmon. *Transactions of the American Fisheries Society*, 29–39.
- FRIEDLAND, K. D., DANNEWITZ, J., ROMAKKANIEMI, A., PALM, S., PULKKINEN, H., PAKARINEN, T., & OEBERST, R. (2017). Post-smolt survival of Baltic salmon in context to changing environmental conditions and predators. *ICES Journal of Marine Science*, 74(5), 1344–1355.
- GREGORY, S. D., ARMSTRONG, J. D., & BRITTON, J. R. (2018). Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival. *Journal of Fish Biology*, 92(3), 579–592.
- GREGORY, S.D., IBBOTSON, A.T., RILEY, W.D., NEVOUX, M., LAURIDSEN, R.B., RUSSELL, I.C., BRITTON, J.R., GILLINGHAM, P.K., SIMMONS, O.M., RIVOT, E. (2019). Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*.
- HANSON, N. N., SMITH, G. W., MIDDLEMAS, S. J., & TODD, C. D. (2019). Precision and accuracy of Dahl-Lea back-calculated smolt lengths from adult scales of Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 94(1), 183–186.

- HAUSFATHER, Z., COWTAN, K., CLARKE, D. C., JACOBS, P., RICHARDSON, M., & ROHDE, R. (2017). Assessing recent warming using instrumentally homogeneous sea surface temperature records. *Science Advances*, 3(1), 13.
- HEIDARSSON, T., ANTONSSON, T., & SNORRASON, S. S. (2006). The relationship between body and scale growth proportions and validation of two back-calculation methods using individually tagged and recaptured wild atlantic salmon. *Transactions of the American Fisheries Society*, 135(5), 1156-1164.
- HELAND, M., & DUMAS, J. (1994). Ecologie et comportement des juvéniles. In J. C. Gueguen & P. Prouzet (Eds.), *Le Saumon Atlantique, biologie et gestion de la ressource* (IFREMER, pp. 29–47). Plouzané.
- ICES. (1984). *Atlantic salmon scale reading: report of the Atlantic scale reading workshop*. Aberdeen, Scotland: International Council for the Exploration of the Sea.
- JENSEN, A. J., FISKE, P., HANSEN, L. P., JOHNSEN, B. O., MORK, K. A., & NAESJE, T. F. (2011). Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(3), 444–457.
- JONSSON, B., JONSSON, N., & ALBRETSSEN, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *Journal of Fish Biology*, 88(2), 618–637.
- KUPARINEN, A., GARCIA DE LEANIZ, C., CONSUEGRA, S., & MERILÄ, J. (2009). Growth-history perspective on the decreasing age and size at maturation of exploited Atlantic salmon. *Marine Ecology Progress Series*, 376, 245–252.
- LEA, E. (1910). On the methods used in the herring-investigations. *ICES Journal of Marine Science*, 1(53), 7–33.
- LEE, R. M. (1920). A review of the methods of age and growth determination in fishes by means of scales. *Fishery Investigations London Series*, 4(2), 32.
- MORITA, K., & MATSUISHI, T. (2001). A new model of growth back-calculation incorporating age effect based on otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(9), 1805–1811.
- OMBREDANE, D., & BAGLINIERE, J. L. (1992). Les écailles et leurs utilisations en écologie halieutique. In J. L. Balignière, J. Castanet, F. Conand, F. Meunier (Eds.) *Tissus durs et âge individuel des vertébrés* (pp. 151–192). Paris.

- POLYAKOV, I. V., ALEXEEV, V. A., BHATT, U. S., POLYAKOVA, E. I., & ZHANG, X. (2010). North Atlantic warming: patterns of long-term trend and multidecadal variability. *Climate Dynamics*, 34(2), 439–457.
- PÖRTNER, H.-O., & FARRELL, A. (2008). Physiology and climate change. *Science (New York, N.Y.)*, 322, 690–692.
- RICKER, W. E. (1992). Back-calculation of fish lengths based on proportionality between scale and length increments. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(5), 1018–1026.
- RILEY, W. D., IBBOTSON, A. T., BEAUMONT, W. R. C., PAWSON, M. G., COOK, A. C., & DAVISON, P. I. (2011). Predation of the juvenile stages of diadromous fish by sea bass (*Dicentrarchus labrax*) in the tidal reaches of an English chalk stream. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21(3), 307–312.
- R CORE TEAM (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- SHEARER, W. M. (1992). *Atlantic salmon scale reading guidelines*. Copenhagen: International Council for the Exploration of the Sea.
- THOMAS, K. (2018). *Scale Growth Analysis of Atlantic salmon (Salmo salar Linnaeus) Unlocking Environmental Histories* (Thesis, Galway Mayo Institute of Technology).
- THOMAS, K., HANSEN, T., BROPHY, D., MAOILEIDIGH, N. Ó., & FJELLDAL, P. G. (2019). Experimental investigation of the effects of temperature and feeding regime on scale growth in Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*.
- TODD, C. D., WHYTE, B. D. M., MACLEAN, J. C., REVIE, C. W., LONERGAN, M. E., & HANSON, N. N. (2013). A simple method of dating marine growth circuli on scales of wild one sea-winter and two sea-winter Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 71(5), 645–655.
- TREMBLAY, G., & GIGUERE, L. A. (1992). Relation longueur/écaille allométrique chez le saumon atlantique (*Salmo salar*) durant la phase marine. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(1), 46–51.
- VAZ-DOS-SANTOS, A. M., & ROSSI-WONGTSCHOWSKI, C. L. (2007). Age and growth of the Argentine hake *Merluccius hubbsi* Marini, 1933 in the Brazilian South-Southeast region during 1996-2001. *Neotropical Ichthyology*, 5(3), 375–386.
- VIGLIOLA, L., HARMELIN-VIVIEN, M., & MEEKAN, M. G. (2000). Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of Diplodus from the Mediterranean Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(6), 1291–1299.

- VIGLIOLA, L., & MEEKAN, M. (2009). The back-calculation of fish growth from otoliths. In *Tropical fish otoliths: Information for assessment, management and ecology* (Springer Science & Business Media, pp. 174–211).
- WAKE, M. (2003). Life history evolution. In B. K. Hall & W. M. Olson (Eds.), *Key concepts and approaches in evolutionary developmental biology* (Harvard University Press, pp. 234–242).
- WILSON, J. A., VIGLIOLA, L., & MEEKAN, M. G. (2009). The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. *Journal of Experimental Marine Biology and Ecology*, 368(1), 9–21.

MODÈLES DE RETRO-CALCUL À PARTIR D'ÉCAILLES DE SAUMONS ATLANTIQUE (*SALMO SALAR*)

Résumé

Les traits d'histoire de vie sont des propriétés des organismes directement liées à leur survie et leur reproduction. Le réchauffement climatique a modifié les traits d'histoire de vie du saumon atlantique *Salmo salar* en retardant la maturation, en réduisant la longueur des individus et en diminuant la survie en mer. *S. salar* est un poisson migrateur qui écloit en rivière, croît en mer avant de revenir dans sa rivière natale pour frayer. Ils sont rarement observés au cours de leur phase marine. Le but de cette étude est d'estimer la croissance et la longueur des saumons en milieu marin grâce à de la modélisation à partir d'écaillles d'individus adultes. Au total, 1738 individus (smolts et adultes) ont été collectés entre 1996 et 2018 dans le Scorff à l'aide d'un piège. Des modèles de rétro-calcul ont été trouvés dans la littérature et ont permis d'estimer la longueur d'individus pour chaque distance focus-circuli sur l'écaille. La validation des modèles a été effectuée au niveau individuel à l'aide d'individus marqués avec des PIT et au niveau de la population en comparant la distribution des longueurs smolts rétro-calculées à la distribution des longueurs observées. Ces étapes de validation ont recommandé l'utilisation de modèles utilisant une interception biologique pour le rétro-calcul des longueurs de smolts. Des recommandations ont été faites pour des études complémentaires, en particulier afin de prendre en compte la sélection taille-dépendante qui se produit en mer. Les modèles de rétro-calcul pourraient faciliter la mise en œuvre de modèles de dynamique de population structurés par la taille. La croissance et la viabilité de la population de *Salmo salar* pourraient être estimées, ce qui permettrait d'améliorer la gestion de l'espèce et de réglementer la pêche.

Mots-clés : phase marine, croissance, transpondeur passif intégré (PIT), survie en mer, Scorff

BACK-CALCULATION MODELLING FROM ATLANTIC SALMON (*SALMO SALAR*) SCALES

Abstract

Life history traits are properties of organisms directly related to their survival and reproduction rate. Global warming has been changing Atlantic salmon *Salmo salar* life history traits by delaying maturation, reducing individual length and decreasing marine survival. *S. salar* is a migratory fish, hatching in river and growing in sea before returning to its natal river to spawn. They are rarely observed during their marine phase. The aim of this study is to estimate growth and length of salmon in the marine environment through modelling based on adult scales of returning fish. Scales bring indirect information concerning growth. In overall, 1738 individuals (smolts and adults) were caught between 1996 and 2018 in Scorff river using fish trap. Back-calculation models were found in the literature and allowed the length estimation of individuals for each focus-circuli distance on scale. Model validation was made at an individual level using PIT tagged individuals and at the population level by comparing the distribution of back-calculated smolt lengths to the distribution of observed smolt lengths. These validation steps recommended the use of models using a biological intercept for smolt lengths back-calculation. Recommendations were made for model improvement in further studies, especially in order to take into account the size-dependent selection which happen at sea. Back-calculation models would be useful to improve population dynamics models, by accounting for a structuration by size. *Salmo salar* population growth rate and viability could be estimated, which would enable to improve species management and fisheries regulation.

Keywords : marine phase, growth, passive integrated transponder (PIT), sea survival, Scorff