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Energy budget modeling of the environmental and individual determinism of precocious maturation in male juvenile Atlantic salmon (*Salmo salar* L.)

Hélène Baillif

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Energy budget modeling of the environmental and individual determinism of precocious maturation in male juvenile Atlantic salmon (*Salmo salar* L.)

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Abbreviations

<i>Notation</i>	<i>Unit</i>	<i>Signification</i>
E	J	Energy reserve
E_H	J	Maturity
E_R	J	Reproduction buffer
V	cm ³	Structural volume
$V^{1/3}$	cm ²	Structural length
$V^{2/3}$	cm	Structural surface
f	-	Functional response
T	K	Environmental temperature
E_0	J	Initial reserve energy
$[E_G]$	J.cm ⁻³	Volume-specific costs of structure
E_H^b	J	Maturity at birth
E_H^p	J	Maturity at puberty
κ	-	Fraction of mobilized reserve allocated to soma
\dot{k}_J	d ⁻¹	Maturity maintenance costs
κ_R	-	Efficiency of reproduction
$\{\dot{p}_{Am}\}$	J.cm ⁻² .d ⁻¹	Surface-area-specific maximum assimilation rate
$[\dot{p}_M]$	J.cm ⁻³ .d ⁻¹	Specific volume-linked somatic maintenance rate
$\{\dot{p}_T\}$	J.cm ⁻² .d ⁻¹	Specific surface-linked somatic maintenance rate
T_A	K	Arrhenius temperature
T_1	K	Reference temperature
\dot{v}	cm.d ⁻¹	Energy conductance
x_{iWE}	kJ.g ⁻¹	Whole-body energy density of dry biomass
\dot{p}_A	J.d ⁻¹	Assimilation rate
\dot{p}_C	J.d ⁻¹	Mobilization rate of energy
\dot{p}_G	J.d ⁻¹	Power used in growth
\dot{p}_J	J.d ⁻¹	Power used to pay for maturity maintenance costs
\dot{p}_R	J.d ⁻¹	Power used for maturation
\dot{p}_S	J.d ⁻¹	Power used to pay somatic maintenance costs

Summary

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1. Introduction

Life history strategies permit to achieve the reproduction in a variable environment for the organisms (Thorpe et al. 1998). By adopting different strategies, organisms ensure some share of reproductive success under strong competition for reproductive resources, including mates (Shuster and Wade 2003; Oliveira et al. 2008). Different life history strategies can be expressed as alternative reproductive tactics, which are widespread throughout the animal kingdom. Alternative reproductive strategies are characterized by the existence of individuals with extreme values of a reproductive trait within members of the same sex, such that the overall variation appears discrete (Páez et al. 2010). Those reproductive traits can be phenotypic such as the horn or the wing length as in many species of insects (Roff 1996; Emlen et al. 2007) or the body size as in many fish species (Taborsky 1998; Oliveira et al. 2008). Alternative phenotypes can depend on switch mechanisms with thresholds of internal or environmental signals. These thresholds control the development of the organism throughout the phenotype (West-Eberhard 2003). Switch thresholds can depend on an individual's somatic state, usually quantified by measures of body size or energy storage, but it can also be affected by a combination of physical factors and social interactions (Gross 1996; Roff 1996; West-Eberhard 2003).

Anadromous fish spend their juvenile phase in freshwater, migrate to spend a part of their life in seawater, after what they come back in freshwater to reproduce. Anadromous species are interesting to study the consequences of environmental variations like the temperature since they spend a part of their life in freshwater, and the other part in the ocean, which permit to study those consequences in the two environments (Mooney 1991). The consequences of the environmental variations on fish are important, and salmonids could be key species to give information about the constraints which environmental variables imposes on life history traits (Lobon-Cervia 2000). Among salmonids, the Atlantic salmon (*Salmo salar* L.) present an interesting alternative reproduction tactics which is the precocious maturation of mature parr males. Atlantic salmon eggs are buried under the gravels in freshwater during winter. Upon hatching, larvae have not assimilated all of their sac yolk. When they achieve it, they emerge from the gravel and start to feed by themselves. Those individuals are called fry, they follow their development and adopt the patterns of parr individuals. Some of those male parr start to develop their gonads and will be able to reproduce the next spring, they are called mature parr. They look like other parr (non-maturing ones) and are two or three order of magnitude smaller than anadromous males (Lepais et al. 2017). During the reproduction period, those individuals will sneak into female nests and furtively gain paternity (Tentelier et al. 2016). Other parr salmon continue their development and some of them, both males and females, begin to metamorphose to become smolt and migrate to sea during one or several years to become anadromous salmon. Those anadromous salmon come back in freshwater for the reproduction. Salmon parrs that don't smolt the first year can become mature parr one or several years later. There is a lot of study of life history patterns among salmonids focused on aspects of life-history theory. For example through studies of age and size at maturity (Schaffer and Elson 1975; Healey and Heard 1984; Holtby and Healey 1986; Thorpe et al. 1998; Bohlin et al.), alternative reproductive strategies (Hutchings and Myers 1988; Hutchings and Myers 1994; Gross 1996), smolt metamorphosis (Mangel 1994) and other life history characteristics (Hutchings and

Morris 1985). The life history strategies that the Atlantic salmon choose to reproduce are responses to the opportunities the environment offers them (Thorpe et al. 1998) depending on their genotype and on their past development.

Consistently with the existence of an internal state threshold for precocious maturation, there are differences in the growth patterns of maturing parr, non-maturing parr and future smolt. Let's first describe the growth patterns common to all Atlantic salmon individuals, whatever their life history strategy. At the beginning of life, when the relative growth in length is higher than the relative growth in weight (Bacon et al. 2005). All individuals also show similar seasonal trends until spring (Kadri et al. 1996). In May, there is a peak of appetite, due to higher temperature and larger amounts of food (Bacon et al. 2005), where salmon increase their lipid reserves. Lipid levels decrease after June, where the growth rate declines (Kadri et al. 1996; Bacon et al. 2005). For parr less than one year old (called parr 0+), winter survival and/or sexual maturation require high level of stored energy (McCormick et al. 1998). There is a peak of weight growth in autumn because of high temperature (same as peak of May) (Bacon et al. 2005). Wet weight and energy content (fat and protein fraction) of parr decrease from October to December without change of fork length (Gardiner and Geddes 1980), because reserves are used to maintain body functions (Rowe et al. 1991). During the latter part of winter, wet weight stabilizes by an increase in water content despite a decrease of energy density (Gardiner and Geddes 1980) (Figure 1).

Differences between maturing and non-maturing parr are first observed in the later spring and early summer, when maturing parrs increase in weight at a greater rate than non-maturing ones, while their length increase similarly (Kadri et al. 1996; Bacon et al. 2005). Non-maturing parr invest more in their skeleton (length) than in muscle (weight) growth during this period. Mesenteric fat decreases during summer and autumn, because it is mobilized for reproduction, for maturing parr while it increases for non-maturing ones to prepare for overwintering (Rowe et al. 1991). Body lipid levels increase in early winter for maturing fish (Kadri et al. 1996). In the spring, maturing parr need to replenish lipid reserves, depleted during the period of low temperature, reproduction and loss of appetite in winter, if they want to smoltify (Rowe et al. 1991; Smith et al. 1993; Taranger and Hansen 1993) (Figure 1).

To summarize these patterns, growth is similar between the different future strategies until the peak of growth in May which is followed by a slowing growth during the rest of the spring. Maturing and non-maturing parr begin to differentiate in spring with higher growth in weight for maturing ones. Despite their low growth in weight, non-maturing salmon in late spring have a weight/length ratio that increase, because they invest more energy in fattening than in length growth. In autumn, the loss of mesenteric fat for maturing parr (mobilized for gonad formation) contrasts with its increase in non-maturing ones (to prepare for winter). Finally, in winter, mature parr lipids content increase whereas weight generally decreases for all individuals (Figure 1).

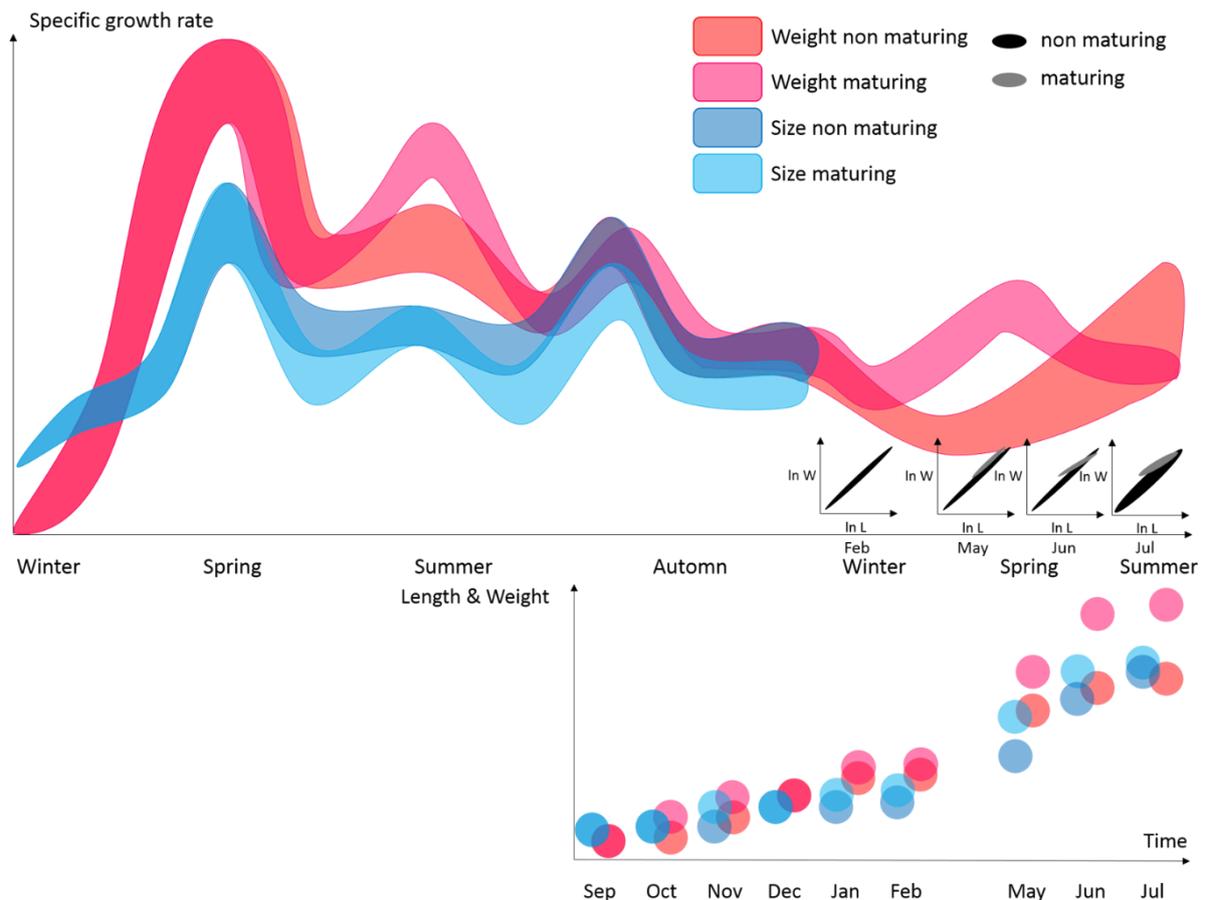


Figure 1 Growth patterns of length and weight from literature for precocious mature parr and non-maturing parr of Atlantic males salmon.

To predict the life history strategies that will adopt an individual depending on environmental and individual factors, a model can be created. This particular life cycle could be integrated through physiological growth models, since they are fruitful examples of blending experimental and observational studies in ecology (Bacon et al. 2005). Water temperature is a crucial constraint on fish growth rates (Tucker and Rasmussen 1999) and temperature driven growth models have been developed for Atlantic salmon parr (Elliott and Hurley 1997; Forseth et al. 2001). Furthermore, links between the precocious maturation with the fork length or the lipidic reserve have been shown. The acquisition and the assimilation of the energy seem essential to study in those species to understand their reproductive strategies. Which is why bioenergetic models could be a good solution. Bioenergetic models represent the flow and transformation of energy within and between living organisms and between living organisms and their environment. It exists several bioenergetic models: some are based on a theoretical basis such as the Metabolic theory of ecology (MTE) (Brown et al. 2004) or the Dynamic Energy Budget (DEB) theory (Kooijman and Metz 1984) whereas other models are rather based on empirical observations like the DEBlipid model (Martin et al. 2017). In this study, we choose to build a model based on the DEB theory, because it allows studying the acquisition and the assimilation of energy from food with variability in temperature. The aim of this study is to model the life history traits variability depending on environmental and individual variability in populations of Atlantic salmon (*Salmo salar* L.) focusing on juveniles males. To achieve this, we built a standard DEB model applied to the Atlantic salmon and estimated its parameters based on

previously published data. We then compared the simulations of the models under different environmental conditions to the patterns of growth known from the literature. A sensitivity analysis was done to see the consequences of the variability of the estimated parameters of the Atlantic salmon DEB model. Those parameters were then used in a new model at population scale with maturation and smoltification decisions and environmental and individual variations at different scales. We compared the proportions of the different life history strategies simulated by this model for three different years with observations in the Scorff River (Brittany, France) for these three years.

2. Material and methods

The DEB theory

The present study will present a bioenergetic model based on the Dynamic Energy Budget theory. The DEB theory have been introduced by S.A.L.M. Kooijman in the 1980s (Kooijman and Metz 1984). The aim of this theory is to describe the use of mass and energy of an organism to stay alive and mature in a changing environment during its whole life.

In the standard DEB model, the individual doesn't change of shape during growth (isomorph) and is modelled as composed by three components, (1) a reserve of energy (in J), (2) a structural volume (in cm^3) and (3) the maturity/reproduction buffer (in J). The component named maturity is actually the quantity of energy invested in developing new structures. At the beginning of his life, the individual is only a pool of energy reserve with a quasi-null structural volume and a maturity and a reproduction buffer equal to zero. During the embryo phase, there is no feeding of the individual, the energy from the reserve is allocated to the structure and the maturity. A fraction named κ is allocated to the development of the structure and to its maintenance, with a priority to the maintenance. The rest of the energy allocated go to the increase of the maturity and to its maintenance, with, again, a priority to the maintenance. If maintenance costs are not payed, the individual die. When maturity reach the threshold of birth E_H^b (in J), the individual became a juvenile. When the individual is juvenile, it begins to feed by himself. So the individual assimilate energy from food and reject it as faeces. And when the maturity is at its maximum value, named E_H^p (in J), the individual achieves puberty and became an adult. In its adult phase, the individual is at its maximum of maturity, so the energy usually allocated to it is now allocated to the reproduction buffer. In the standard DEB model, in condition of food abundance, the modeled growth of the organism is the same as the Von Bertalanffy growth that is the most widely growth curve used (Bertalanffy 1938). With the Von Bertalanffy growth, the growth in length decrease linearly with the increase of the length of the organism if food and other conditions such as the temperature are constant. As the organism gets bigger, it grow less and less because the increase in maintenance (which is roughly proportional to structural volume) is higher than the increase in mobilization which means that less energy is available for growth. It stops growing when it achieves the ultimate length.

More precisely, the fluxes of energy in the organism are the following: initially the reserve of energy E contain an amount of E_0 J of energy, a structural volume V quasi equal to 0 cm^3 and an empty maturity E_H and reproduction buffer E_R (in J). During the embryo phase: the reserve

of energy E is drain by the mobilization rate of energy \dot{p}_C (in J.d^{-1}). In the equation of \dot{p}_C (Figure 2), E is always the energy reserve of the organism. $[E_G]$ (in J.cm^3) is the volume-specific cost of structure, that is the energy needed to build one unit of structural volume. \dot{v} (in cm.d^{-1}) is the energy conductance, $V^{1/3}$ (in cm) is the structural length, κ is the fraction of mobilized reserve allocated to soma and $[E]$ (in J.cm^{-3}) is the reserve density (E/V). And $[\dot{p}_S]$ (in $\text{J.d}^{-1}.\text{cm}^{-3}$) is the power used to pay somatic maintenance costs divided by the structural volume. In the equation of \dot{p}_S (Figure 2), $V^{2/3}$ (in cm^2) is the structural surface, $[\dot{p}_M]$ (in $\text{J.cm}^{-3}.\text{d}^{-1}$) is the specific volume-linked somatic maintenance rate and $\{\dot{p}_T\}$ (in $\text{J.cm}^{-2}.\text{d}^{-1}$) is the specific surface area-linked somatic maintenance rate. The maturity E_H increase by the power used for maturation \dot{p}_R (in J.d^{-1}). In the equation of \dot{p}_R (Figure 2), \dot{p}_J (in J.d^{-1}) is the power used to pay for maturity maintenance costs that equals the maturity maintenance costs \dot{k}_J (in d^{-1}) times the maturity E_H . And the reproduction buffer E_R remain equal to 0.

When the maturity reach the threshold of birth E_H^b , the organism become a juvenile and start to feed, as a consequence the dynamic of the energy reserve that was equal to minus the mobilization rate of energy \dot{p}_C , now become equal to the assimilation rate \dot{p}_A (in J.d^{-1}) minus the mobilization rate of energy \dot{p}_C . In the equation of \dot{p}_A (Figure 2), $\{\dot{p}_{Am}\}$ (in $\text{J.cm}^{-2}.\text{d}^{-1}$) is the surface-area-specific maximum assimilation rate, that indicates the maximum ingestion rate possible for the organism times the efficiency of assimilation food. $f(X)$ is the functional response, it describe the ingested food and introduce the connection with the available food in the environment. It's the available food divided by the available food plus the half saturation coefficient (the value of food density when ingestion is half its maximum). In consequence, the functional response is between 0 and 1. $V^{2/3}$ is the structural surface that is responsible for the ingestion or assimilation, for example the gut or the searching area. The other dynamics remains the same.

When the maturity reach its maximum that is the threshold of puberty E_H^p , the organism become an adult and start to allocate energy to the reproduction buffer. The dynamics of energy reserve E and of structural volume V remain the same, but maturity E_H becomes constant and instead the increase in the reproduction buffer E_R become equal to the efficiency of reproduction κ_R times the power used for maturation \dot{p}_R (Figure 2).

All parameters that are written with a dot on top indicate that they are rates, so of the dimension 'per time'. Because the speed of biochemical reactions increases with temperature, these parameters have different values depending of the temperature of the environment. Based on the empirical observation that this effect of temperature is similar for the different biological processes such as feeding, growth or reproduction, the same correction, referred to as Arrhenius correction and is applied on each of those parameters. The Arrhenius correction is a multiplication of the rate parameter by $e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)}$ with T_A the Arrhenius temperature, T_1 the reference temperature at which the rate parameter has been estimated and T the environmental temperature. We assumed all rates were affected in the same way (Kooijman 2000).

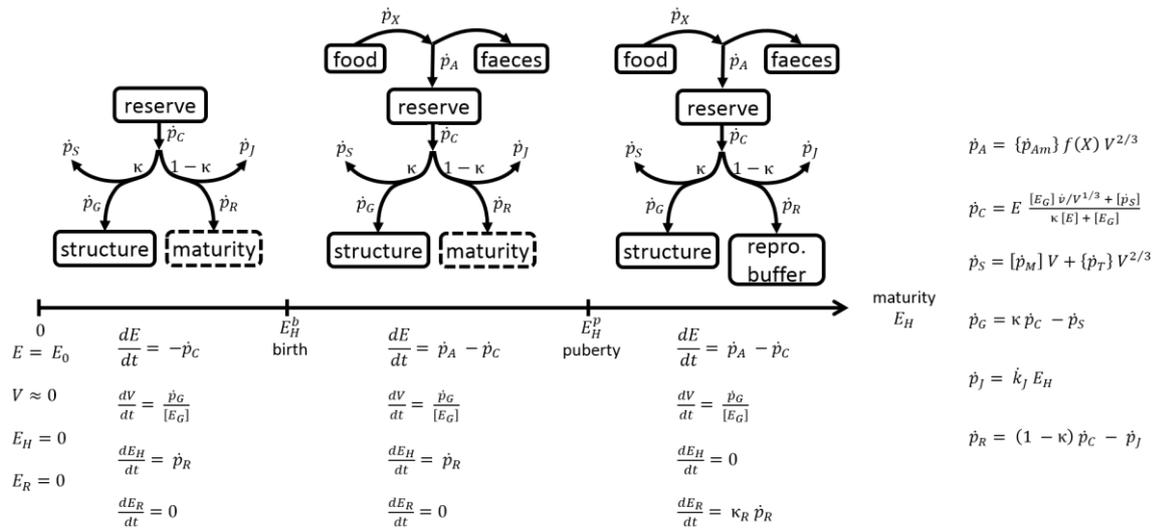


Figure 2 The standard DEB model

Parameters estimation

To use a standard DEB model for the Atlantic salmon, the values of the parameters have to be known. The estimated parameters of the DEB models for almost 2000 species are listed in the Add my pet database (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/species_list.html). But the Atlantic salmon (*Salmo salar*) wasn't one of them. That's the reason why in this study the parameters estimation was made for the Atlantic salmon and has been submitted. The parameter estimation is done with the software MatLab. The parameter estimation routine is the one exposed in Marques et al. 2018 and coded as a script available in the add-my-pet project on GitHub (https://github.com/add-my-pet/DEBtool_M/blob/master/lib/pet/estim_pars.m). The used algorithm of estimation is the Nelder-Mead method from (Nelder and Mead 1965). The algorithm permit to find the parameters values which minimized a loss function. This loss function reflects the difference between the model predictions and the observed data. The Nelder-Mead algorithm is based on the comparison of n+1 points in a n dimensions space (e.g. for two parameters, the space called simplex, is a triangle). At each iteration, one of the n+1 points is replaced by a new point value having a lower loss function calculate such as enlarge (or shrink) the simplex in the probable decreasing direction of the loss function. The algorithm ends when the maximum deviation of the loss function between the points of the simplex is inferior or equal to 10^{-4} and when the diameter (the maximum distance between the parameters of the simplex points) is also inferior or equal to 10^{-4} . This method have a major advantage since it can minimize continuous functions numerically, even without an analytical solution. The data used for the estimation are presented in Table 1 and Figure 3. These data have been taken from the literature and came from very different populations. The age at puberty found in literature are those of anadromous adults and mainly those from females. For the age at maturity and the lifespan, which are medians from Scottish populations, we assumed a temperature of 10°C for the estimation, but they probably experienced highly variable temperature throughout life. Data on length at hatching, age at hatching depending on the temperature and age at yolk exhaustion depending on temperature came from individuals that have parents from Dennis Stream (New Brunswick - Canada). Those of length at first feeding and weight at first feeding came from individuals with parents from River Blackwater (Scotland) with a mother that spent

only one year in seawater. For those of egg volume, egg weight, fork length depending on the wet weight of female spawners and reserve energy in egg, the data came from individuals that have parents from river Stjørdalselva (Norway). The length at spawning in the maximum of Scottish populations, for females only. The weight at hatching have been measured at a temperature of 4°C, and those individuals have parents from River Kent (Cumbria, northern England). The weight at spawning is the maximal value of females from Norwegian populations. The maximum reproductive rate is done for a temperature of 10°C for the estimation, but there was highly variable temperature throughout life, and this data is the maximum one at River Almond (Scotland). The fork length depending on the time since emergence is done for a temperature of 12°C for the estimation, but in the reality, the temperature increased from 10.4°C to 14.1°C throughout the experiment, and those data came from individuals from the Imsa River (Norway). Finally, the fork length of parr individuals depending on their wet weight came from Northeast Brook populations (Newfoundland, Canada).

The model used is the standard DEB model presented above (Table 1).

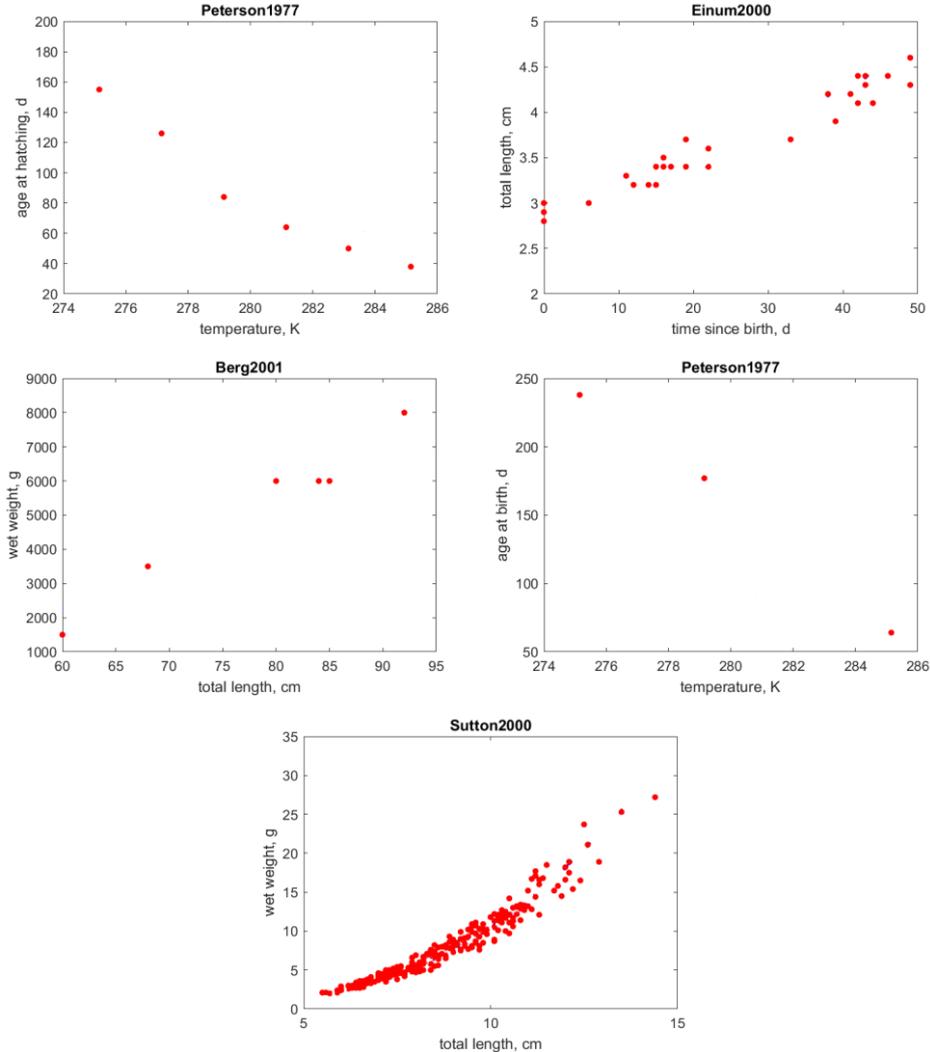


Figure 3 Observed univariate data used in the parameter estimation of Atlantic salmon

Table 1 Observed data used in the parameter estimation of Atlantic salmon

<i>Data</i>	<i>Symbol</i>	<i>Units</i>	<i>Description</i>	<i>Source</i>
1335	A_p	d	age at puberty	Thorpe et al. 1998
1700	A_m	d	life span	Thorpe et al. 1998
2.09	L_h	cm	total length at hatching	Peterson et al. 1977
2.825	L_b	cm	total length at birth	Van Leeuwen et al. 2016
95	L_i	cm	ultimate total length	Fleming 1996
0.09	V_0	cm ³	egg volume	Berg et al. 2001
0.035	W_{d0}	g	dry egg weight	Berg et al. 2001
0.1488	W_w^h	g	wet weight at hatching	Carrick 1979
0.16	W_w^b	g	wet weight at birth	Van Leeuwen et al. 2016
13130	W_{wi}^F	g	ultimate wet weight	Solberg et al. 2014
757	E_0	J	egg reserve energy	Berg et al. 2001
39.7	R_i	d ⁻¹	maximum reproduction rate	Thorpe et al. 1984

Models simulations

The aim of this study is to build a bioenergetic model for males Atlantic salmon until migration at sea. But the standard DEB model exposed above can't be applied to this species in this state. Furthermore, the standard DEB model is for all individuals during their whole life, whereas in this study the search model is applied to juvenile males in freshwater. And, this model don't take in account the precocious maturation nor the smoltification. For that, the model need to be modified in taking in account the maturation and the smoltification decisions. In this aim, a model using the standard DEB model has been created. This model is coded with the software R 3.5.2 (R Core Team 2014) and use the package deSolve. The model start from a single egg, like in the standard model, the individual hatch, and later emerge. And when it finished to consume its vitellus sac, it's the birth in the standard DEB model. After that, during a window of time that spans the entire month of May (Adams and Thorpe 1989; Berglund 1992a; Lepais et al. 2017), if the maturity of the individual reach the threshold of E_H^m , the organism become a maturing parr. In this case, the organism become an adult and start allocating energy for the reproduction buffer and will reproduce between November and December (Mangel 1994; Thorpe et al. 1998). If the individual don't reproduce, as model in the following, the organism re use a part (κ_{rest}) of the reproduction buffer to replenish its energy reserve and being able to re allocate it to pay maintenance costs for example. But this re use has its efficiency, noted α . If the organism does not reach this threshold, it remains in juvenile phase. During the August month (Metcalf et al. 1986; Metcalf et al. 1988; Thorpe et al. 1998), if this non-maturing parr reach the threshold size V_j , it will smoltify the next spring (Skilbrei and Holmström 2011). In other case the non-maturing parr non future smolt will stay in juvenile phase and will feed less during winter than future smolts (Simpson et al. 1996; Thorpe et al. 1998; Morgan and Metcalfe 2001). After the reproduction period, if the mature parr reach the size of V_j between the 31st December and 31st January (Metcalf and Thorpe 1992), it will smoltify the next spring. With the smoltification, the organism leaves the freshwater to go to the ocean. In this case, the individual is not modelled anymore. If the mature parr don't reach the threshold size, it will

follow its life in freshwater with individuals that haven't matured and that will not smoltify. The non futur smolt, which include mature and non-mature parrs that haven't reach the threshold size at time, recover their usual rate of feeding the 1st March (Simpson et al. 1996; Thorpe and Metcalfe 1998; Morgan and Metcalfe 2001). If those individuals reach the threshold of maturity E_H^m in May (Adams and Thorpe 1989; Berglund 1992a; Lepais et al. 2017), they will start (or continue) to allocate energy to the reproduction buffer. The simulation of the model end at 600 days.

The value of E_H^m is 1750 J and the value of V_j is equal to $(L_{wj} * \delta_M)^3$ with L_{wj} equal to 120 mm. These values have been taken according to literature. Indeed, it is established that parrs have to reach the size of 12 cm during their first spring to be able to smoltify the next spring (Kristinsson et al. 1985; Nieceza et al. 1991; Berglund 1995). The value of maturity threshold has been chosen by taking the value of maturity reached when an individual have a fork length equal to 72 mm and a wet weight equal to 6 g according to Berglund (1992).

The resulting model is a system of ordinary differential equations. It was solved numerically with the function `radau` of the package `deSolve`. When the maturity (resp. physical length) reach the birth or precocious maturation (resp. smoltification) threshold within the corresponding seasonal time window, the ODEs reach a root and a corresponding event is triggered. Indeed, the decisions of first maturation, smoltification and second maturation have been modelled as state variables. Their initial values are defined as all equal to 0. Then during the simulation in time, if a root is reached, the value of the decision in question changes to 1.

For the simulations of the DEB model of the Atlantic salmon, real environmental data was used to compare the simulations with real life-history data. For that, the temperature used in the simulations are taken from Jeannot (2019). They are Scorff river water temperature from the Environmental Research Observatory (ERO) on Diadromous Fish in Coastal Rivers (DiaPFC). Temperatures are sampled at 5 sites since 1995 for one and since 2005 and later for others. The Scorff river is a small coastal river in southern Brittany (France). In the simulations, the temperatures of the year 2005 to 2007 have been used from the Moulin des Princes site. The mean temperature per day has been fitted on a function with `splinefun` from the package `stats`. For the functional response, there is not a lot of information on the food availability for the Atlantic salmon in the Scorff River. Because of that, in this study there are several approximations of the functional response dynamics in time. Several models were used (Table 2), to see which one will be the more representative of the patterns known in the literature and to compare the simulations of these different models with real data. The first one called M1 use the same constant temperature and constant functional response for all individuals of the population. The second one named M2, use a same constant value of functional response and a same temporally-variable temperature corresponding to the Scorff river temperature data for all individuals. The third model M3 use the same temperature as in M2 but the functional response change in time with a peak in April-May and a low f in winter (Simpson et al. 1996; Thorpe et al. 1998; Morgan and Metcalfe 2001) (Figure 5). As with the temperature, a spline function is used for the functional response to implement it later in the ODEs system. The M4 and M5 models were made to compare two behavior hypothesis. The M4 model follow a behavior of dominant individuals versus dominated individuals in the acquisition of food (Metcalfe 1998).

And in the M5 model there is no group of individuals, so they have a random functional response.

Table 2 The different population models used for simulations

Model	Temperature (°C)	Functional response		
		Population scale	Individual scale	Time step scale
M1	12	0.5		
M2	Figure 4 (a) red curve	0.5		
M3	Figure 4 (a) red curve	Figure 4 (b)		
M4	Figure 4 (a) red curve		2 groups low/high : - $f_{prop} \sim \text{Unif}(0.3, 0.7)$ - $f_{prop} \sim \text{Unif}(0.7, 1)$	
M5.2005	Figure 4 (a) red curve			$f_{prop} \sim \text{Unif}(0.3, 1)$
M5.2006	Figure 4 (a) green curve			$f_{prop} \sim \text{Unif}(0.3, 1)$
M5.2007	Figure 4 (a) blue curve			$f_{prop} \sim \text{Unif}(0.3, 1)$

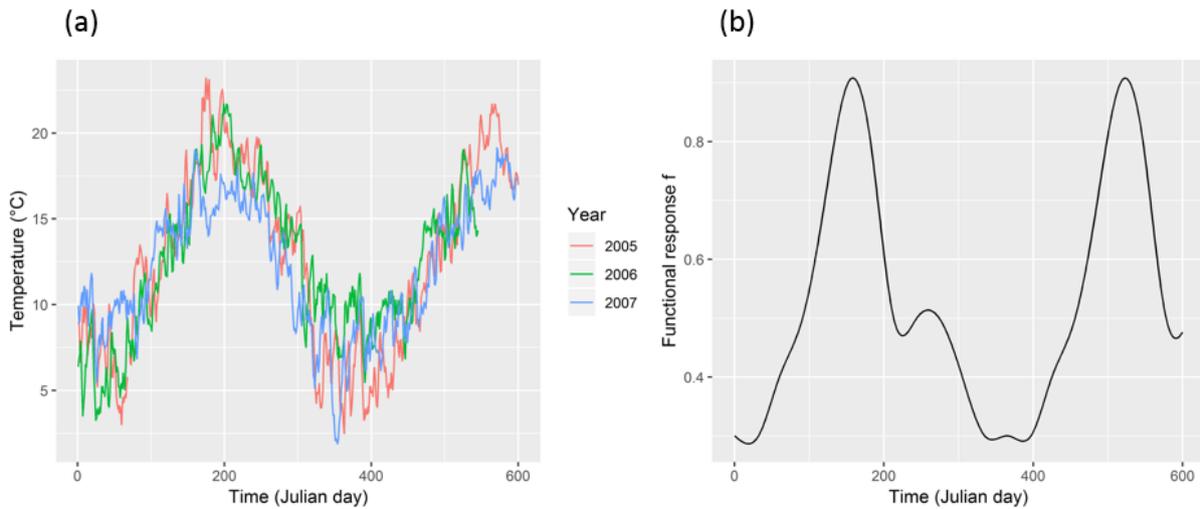


Figure 4 Environmental parameter values of (a) water temperature and (b) functional response.

The fourth model M4 use the same temperature as in M2 and M3 but for the functional response, half of the individuals are in a low group and the others in a high group. This means that the low group, have a lower functional response than the individuals of the high group. To apply that, the functional response curve of M3 is multiplied by a proportion (f_{prop}) randomly chosen between 30% and 70% for the low group and between 70% and 100% the high group according to a uniform law. Thanks to that, there is two groups of individuals that have inter and intra group differences of functional response. The fifth model M5 use always the same temperature as in models M2, M3 and M4 but the functional response is different for each individual at each time step. Indeed, out of the iteration by individuals and by time step, a data frame is created

with 21 time steps (one by month) (columns) for each individual (rows) and each of those values are multiplied by a random proportion between 30% and 100% according to a uniform law. After what there is a fitting of a function on each rows (for each individual) with splinefun (package stats) that are put in a list of functions, used lately in the function radau.

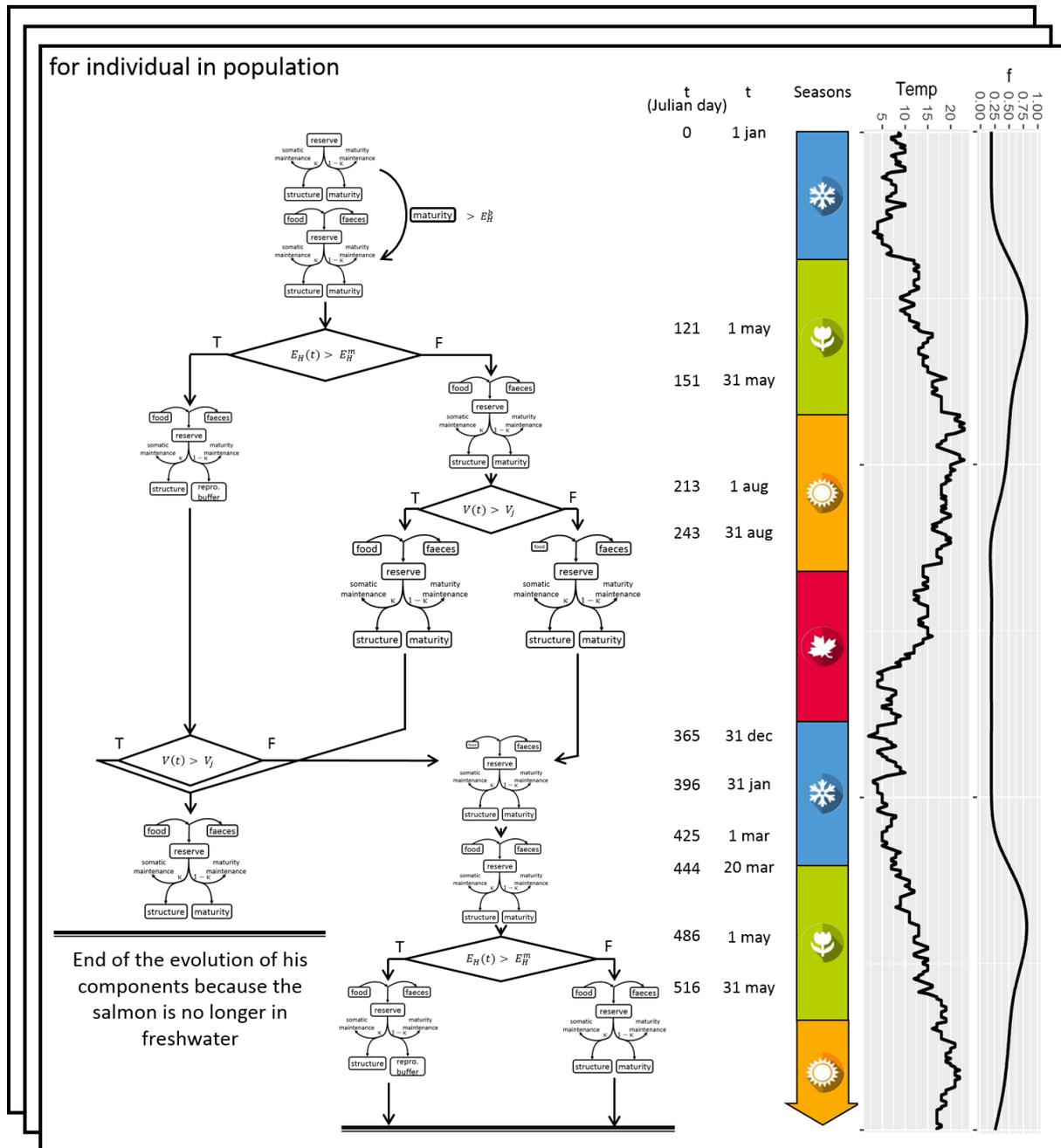


Figure 5 Schematic representation of the M3 population model

To represent the results of the simulations and compare them with available data such as the weight and the fork length of Atlantic salmon, the weight and the length have been calculated from the components of the DEB model. Wet weight W_W (in g) has contributions from the

structure (V), the reserve (E) and the reproduction buffer (E_R). Wet weight in this study is defined as follows with xi_{WE} the whole-body energy density of dry biomass:

$$W_w = \frac{0.2 V + \frac{E + E_R}{xi_{WE} * 1000}}{0.2}$$

And the physical length L_w (in mm) is defined as follows:

$$L_w = \frac{V^{1/3}}{\delta_M}$$

The proportions of adopted strategies in the simulated population are compared with the ones observed by the Environmental Research Observatory (ERO) on Diadromous Fish in Coastal Rivers (DiaPFC) between 2005 and 2007 in the Scorff River. These data are based on a mark-recapture program that starts in 2005. This program is based on individual following of a part of the local population in which the individual recognition is done with specific mark that attribute a unique code at each marked individual. Marked individuals are followed during their whole life during several recapture occasions where they are registered, sized and weighted and identify as parr, mature parr or smolt. In this study, only the information on the proportion of life histories (mature parr and later smolt during the first year for example) in the cohort is used.

Sensitivity analysis

To estimate the consequences of variation in the estimated parameters on the models predictions, two sensitivity analyses have been done on the M0 model on one individual. The aim of a sensitivity analysis is to study the uncertainty of a model depending on the uncertainty of his entries. The methods used for the two analysis are the One-At-a-Time (OAT) and the Morris method. 17 parameters have been tested, their nominal values were those specified below (Table 3 plus E_H^m and V_j). The bounds of the intervals of variability of the parameter values (terminals) used in this sensitivity analysis are equal to 75% of the nominal value for the lower one and equal to 125% of the nominal value for the upper one. The Morris method have regular grids between two variables as experimental design. This permit to show interactions of two parameter variability in the analysis in contrary to the OAT method.

3. Results

Parameters estimation

Ten parameters were estimated by the estimation procedure (Table 3). Comparison with *Salmo trutta* parameters (Thrane and Kooijman 2015), Chinook salmon (Pecquerie and Kooijman 2016) and the Chum salmon (Kooijman 2019) is made. The energy conductance \dot{v} (0.02707 cm.d⁻¹) is almost 10 times lower than the trout parameter value (0.1648 cm.d⁻¹) but is closer to the Chinook (0.07753 cm.d⁻¹) and the Chum (0.045117 cm.d⁻¹) salmons parameter values and close from the generalized animal value (0.02 cm.d⁻¹). But the value of Atlantic salmon is the double of the \dot{v} parameter values of chinook and chum. The κ value is very low compare to the generalized animal; indeed the value estimated for the Atlantic salmon is equal to 0.4146 whereas the generalized animal κ value is equal to 0.8. But the Chinook salmon also have a low κ ($\kappa = 0.4612$). The value of the $[\dot{p}_M]$ estimated (101.9 J.cm⁻³.d⁻¹) is close to the values of brown trout (115.3 J.cm⁻³.d⁻¹) and chum salmon (117.362 J.cm⁻³.d⁻¹) but not of the chinook one (20.56 J.cm⁻³.d⁻¹) and the generalized animal (18 J.cm⁻³.d⁻¹). The values of $[E_G]$ of all the 4 species are closed (Atlantic salmon: 5221 J.cm⁻³, trout: 5229 J.cm⁻³, Chinook salmon: 5242 J.cm⁻³ and

chum salmon: 5234.16 J.cm⁻³). The values of E_H^b are very different (Atlantic salmon: 69.33 J, chum salmon: 28.37 J) with the trout that have the lowest one (5.601 J) and the chinook which have the bigger one (1389 J). The Arrhenius temperature T_A (9800 K) is between the values of the three other salmonid species (chum salmon 8000 K, Chinook salmon 10000 K and brown trout 15690 K). The shape coefficient δ_M (0.08254) that is species specific is quite low compare to the three other ones (trout: 0.1571, chum salmon: 0.18483, Chinook salmon: 0.1958). The energy density of dry biomass (22.9328 kJ.g⁻¹) is very close to the other three ones (trout 22.2492 kJ.g⁻¹, Chinook salmon 22.0405 kJ.g⁻¹ and chum salmon: 22.5405 kJ.g⁻¹)

Table 3 Parameters values used in the population simulations

Symbol	Unit	Value	CI	Estimated	Description
T_1	K	293.1			Reference temperature
\dot{v}	cm.d ⁻¹	0.02707		yes	Energy conductance
κ	-	0.4146		yes	Allocation fraction to soma
κ_R	-	0.95			Reproduction efficiency
$[\dot{p}_M]$	J.cm ⁻³ .d ⁻¹	101.9		yes	Volume specific somatic maintenance
$\{\dot{p}_T\}$	J.cm ⁻² .d ⁻¹	0			Surface-specific somatic maintenance
\dot{k}_J	d ⁻¹	0.002			Maturity maintenance rate coefficient
$[E_G]$	J.cm ⁻³	5221		yes	Volume-specific cost for structure
E_H^b	J	69.33		yes	Maturity at birth
T_A	K	9800		yes	Arrhenius temperature
δ_M	-	0.08254		yes	Shape coefficient
xi_{WE}	kJ.g ⁻¹	22.9328		yes	Whole-body energy density of dry biomass
L_m	cm	12.7896		yes	Maximum structural length
$\{\dot{p}_{Am}\}$	J.cm ⁻² .d ⁻¹	3143.42			Surface-area-specific maximum assimilation rate $\{\dot{p}_{Am}\} = \frac{L_m [\dot{p}_M]}{\kappa}$
E_H^m	J	1750			Precocious maturity threshold (Berglund 1992b)
V_j	cm ³	0.971711			Smolt structural volume threshold $V_j = (12 \delta_M)^3$ (Kristinsson et al. 1985; Nicieza et al. 1991; Berglund 1995)
V_0	cm ³	0.000410			Initial structural volume of the egg $V_0 = (0.9 \delta_M)^3$ (Berg et al. 2001 see Table 1)
E_{init}	J	[500; 1100]			Initial reserve energy of the egg
xi_{WE}		22.9328		yes	Whole-body energy density of dry biomass
α	-	0.08			Efficiency of the re use energy in the reserve
β	-	0.5			Proportion of functional response (Simpson et al. 1996; Thorpe et al. 1998; Morgan and Metcalfe 2001)
κ_{rest}	-	0.7			Proportion of restitute energy

Standard DEB model simulation

A simulation of the model M0 was computed with those 10 estimated parameters and 13 other parameters from literature. The Figure 6 present the results of this simulation with the evolution of the 4 components of the organism in time from the initial egg to 600 days after. This individual didn't mature at his first occasion and didn't prepare for the smoltification but finally became a mature parr at the second opportunity.

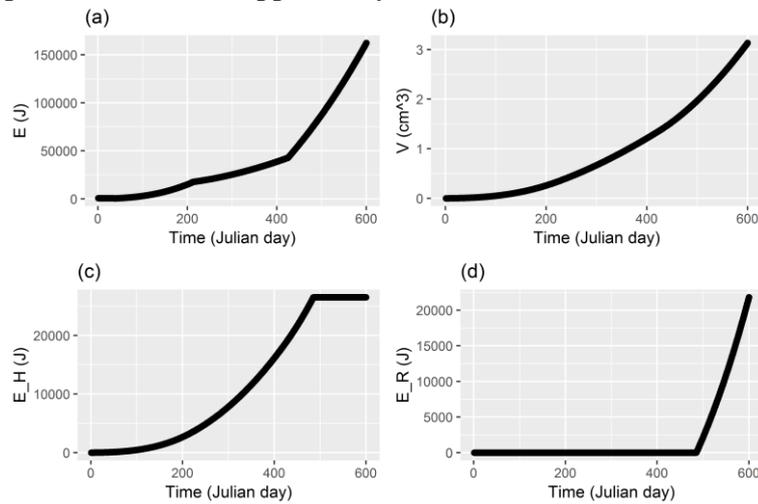


Figure 6 Evolution of the four components of an organism following the M0 individual model with (a) the energy reserve E , (b) the structure V , (c) the maturity E_H and (d) the reproduction buffer E_R

The Figure 7 shows the evolution of its length and its weight for the 600 first days of its life, reaching 18 cm for 44g. The evolution of the length is almost linear with a peak of growth during the two first months, the growth is almost linear until almost 280 days after what the growth decrease a little until 440 days of life and finally increase for the last days of the simulation. On the other hand, the evolution of the weight looks more like an exponential growth. During the first month, the weight decreases a little, after what it increase almost exponentially from 30 days to 220 days of life, a phase between 220 days and 430 with an almost linear growth at the lowest rate of the simulation, then a short time of also an almost linear growth but at a higher rate until 490 days to finally finish the simulation of its life with the higher increasing growth rate of the simulation.

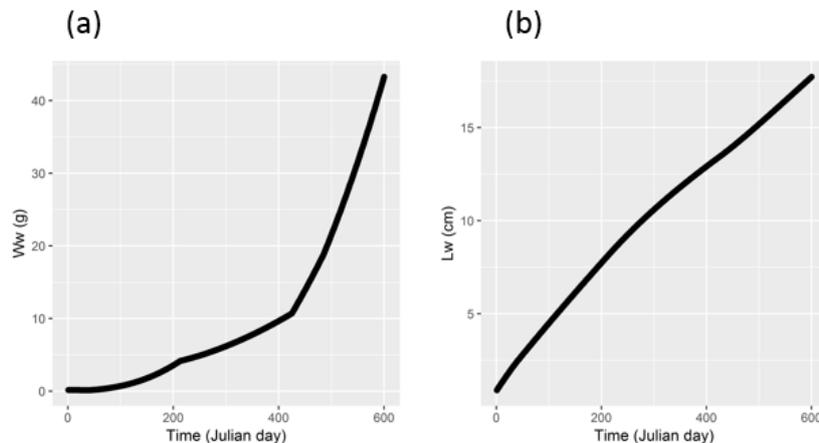


Figure 7 Evolution of the (a) weight and of (b) the length of the model individual with a M0 model

The weight/length ratio is always increasing, meaning that the growth rate of weight is always higher than the length one. The used values in this simulations was a missing reproduction, a temperature of 12°C, a functional response of 0.7 and an initial amount of energy in the egg of 700 J. But other simulations were made in exploring the parameters values of temperature equal to {5,10,15,20}°C, functional response equal to {0.4,0.6,0.8,1} and a E_{init} equal to {500,700,900,1100}J (results not shown). And this data exploration shows results of 1+ mature parr for all individuals with an environmental temperature lower than 15°C independently of other values and for other values the life history strategy was the precocious maturation during its first opportunity and to smoltify the same year.

Sensitivity analysis

OAT

The Figure 8 represents the sensitivity of the parameters, it's the absolute effect of an augmentation and a diminution of the parameters on the outputs, whereas the Figure 9 shows the elasticity, which is the relative effect of those modifications on the outputs. Elasticities of the parameters for the decision to mature or to smoltify in the first year were not computed because their calculation implied a division by zero because the first three outputs are qualitative outputs interpreted as quantitative ones. Parameters that shows the most important sensitivity and elasticity values for all outputs are the energy conductance (\dot{v}) and the fraction of energy allocated to soma (κ), after that the Arrhenius temperature (T_A) and the precocious maturation threshold (E_H^m) also have effects on all the outputs. For the length achieved at 600 days, the parameter that has the bigger effect is the shape coefficient (δ_M). Some parameters have an impact on both the length and the weight achieved at the end of the simulation. They are the shape coefficient (δ_M) (already cited), the proportion of functional response (β), the surface-area-specific maximum assimilation rate ($\{\dot{p}_{Am}\}$), the volume specific somatic maintenance ($[\dot{p}_M]$), the volume-specific cost for structure ($[E_G]$) and the maturity at birth (E_H^b). Other parameters variations only have influence on the weight output. They are the whole-body energy density of dry biomass (ξ_{WE}), the maturity maintenance rate coefficient (\dot{k}_j) and the reproduction efficiency (κ_R).

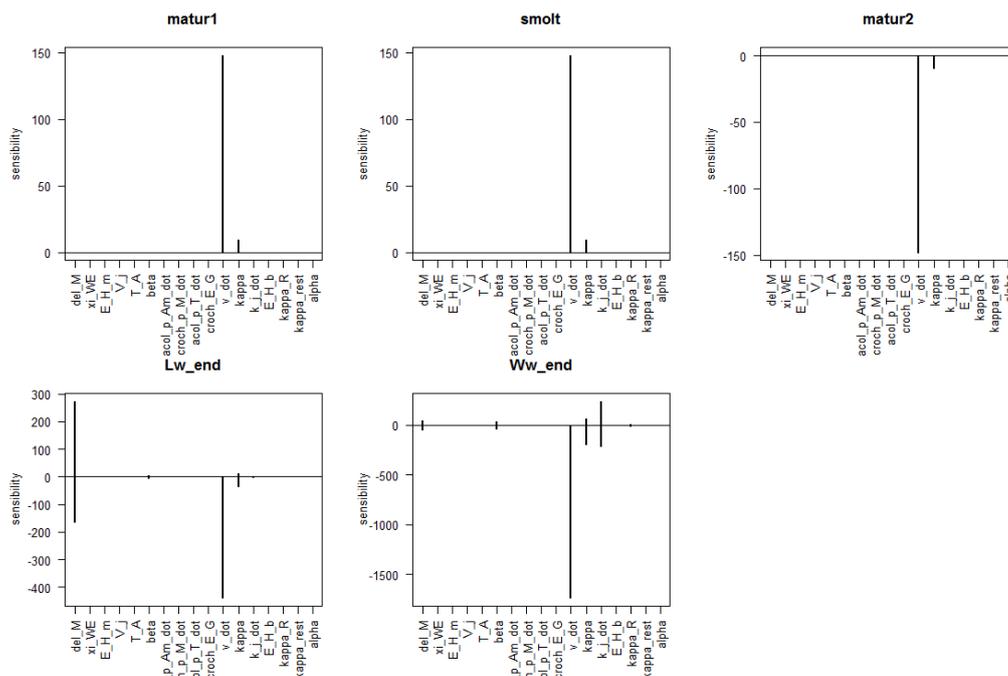


Figure 8 Sensitivity values of the OAT sensitivity analysis for the 5 studied outputs

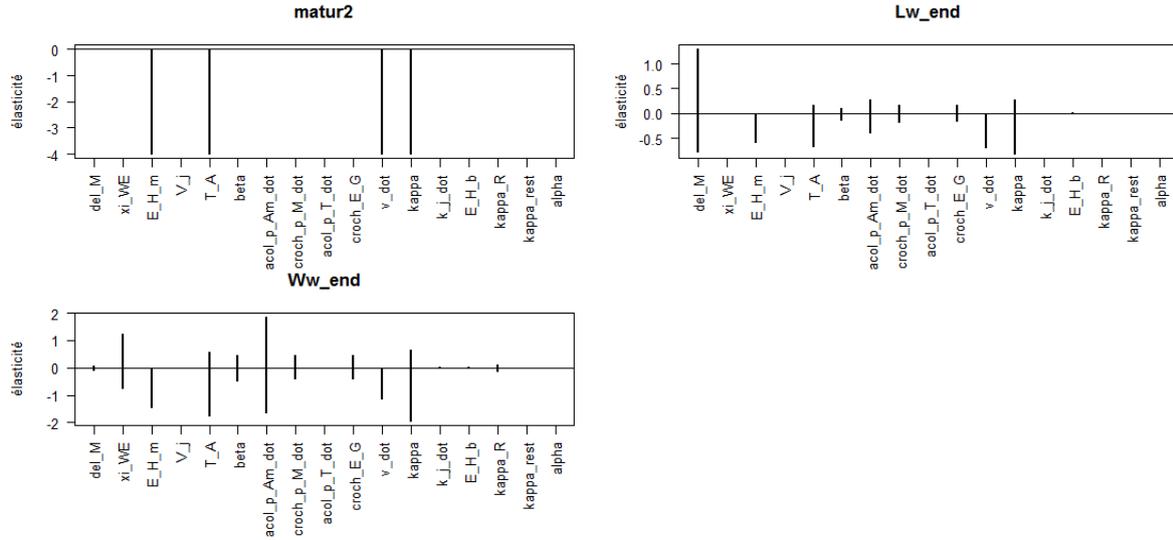


Figure 9 Elasticity values of the OAT sensitivity analysis for the second maturation decision, the length and the weight at the end of the 600 days of simulation.

Morris

The Figure 10 represent the main results of the Morris sensitivity analysis, called the Morris scatter plot, with for each outputs the standard deviation of the elementary effects on the output (σ) in terms of the mean absolute effect of the parameters on the output (μ^*). The mean absolute effect of the parameters on the output measures the global effect of each parameter on the study output and the standard deviation of the elementary effects on the output reports the interactions and/or the nonlinear effects of each parameter on the looked output. The points in the lower left corner of the plot are parameters that have a negligible influence on the output. The ones in the top left corner are parameters that have a negligible influence but which have a nonlinear influence and/or have an interaction effect coupled with another parameter. The points in the lower right corner have a big influence on the output and its effect is linear and/or the parameter have an interaction influence with the change of another parameter. Finally, the other points are in the area where they have an important influence on the output and their effect are nonlinear and/or have an interaction influence with the change of another parameter. For the precocious maturation decision, the parameters that have main effects and that have nonlinear effect or that have an interaction effect are T_A , \dot{v} , κ , E_H^m and $[E_G]$; the parameters that have a negligible influence but which have a nonlinear influence and/or have an interaction effect coupled with another parameter are $\{\dot{p}_{Am}\}$ and δ_M ; other parameters have a negligible effect on the output. For the smoltification decision, the parameters that have main effects and that have nonlinear effect or that have an interaction effect are T_A , κ , \dot{v} , δ_M , $[E_G]$ and $\{\dot{p}_{Am}\}$; the parameter that have a negligible influence but which have a nonlinear influence and/or have an interaction effect coupled with another parameter is E_H^b ; other parameters have a negligible effect on the output. The results of the second precocious maturation decision are the same as those of the smoltification decision. For the length at 600 days, the parameters that have main effects and that have nonlinear effect or that have an interaction effect are δ_M , T_A , \dot{v} , κ , $\{\dot{p}_{Am}\}$, $[E_G]$, $[\dot{p}_M]$, V_j , E_H^b , E_H^m and β ; other parameters have a negligible effect on the output. Finally, for the weight at 600 days, the parameters that have main effects and that have nonlinear effect or that have an interaction effect are $\{\dot{p}_{Am}\}$, T_A , \dot{v} , κ , $[\dot{p}_M]$, $[E_G]$, V_j , δ_M , ξ_{WE} , E_H^b , β , E_H^m , κ_R and κ_{rest} ; other parameters have a negligible effect on the output.

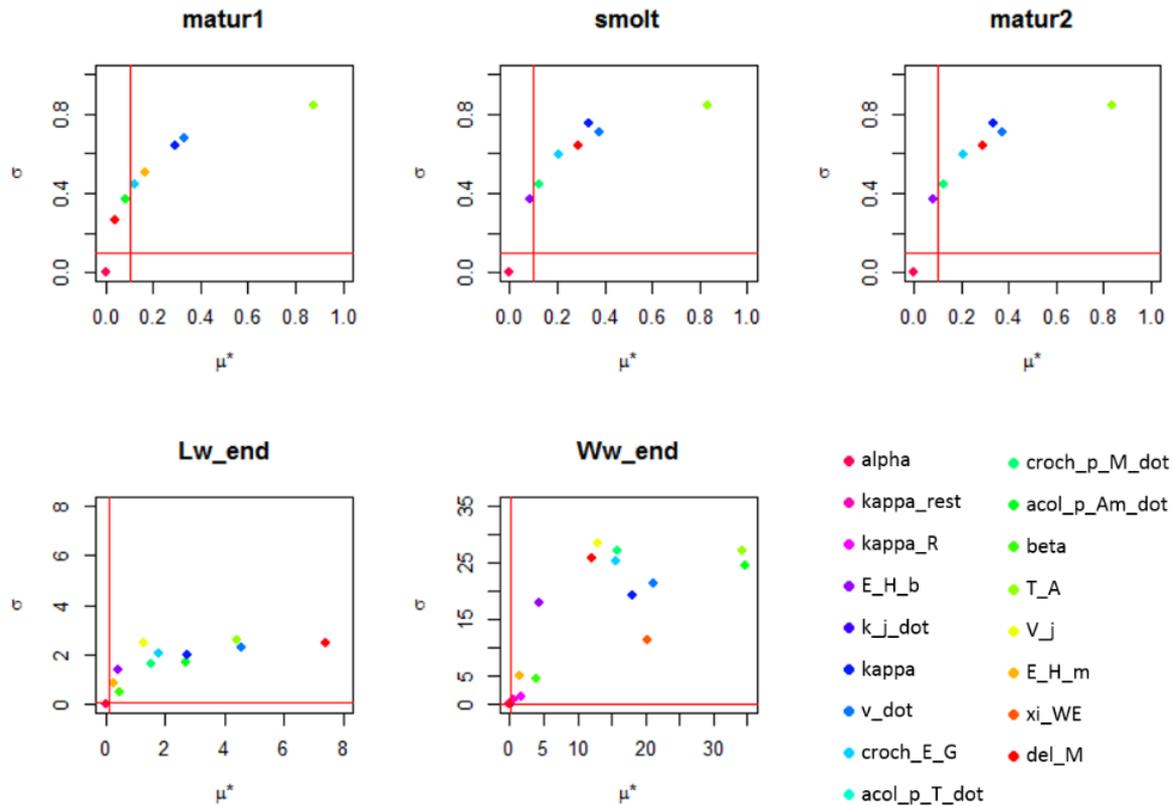


Figure 10 Morris scatter plot of the Morris sensitivity analysis for the 5 studied outputs

Models simulations

From the simulations of the different population models (M1, M2, M3, M4, M5.2005, M5.2006 and M5.2007), the proportions of the different life history strategies were examined. In the model M1, all the 100 individuals are 1+ mature parr and there are few variations in length between them. 1+ mature parr means that they are between 1 and 2 years old individuals that became mature parr (at their second opportunity to precociously mature). In the simulations of the M2 model, 99 percent of the individuals became 1+ smolt and only 1 percent became a 1+ mature parr. A 1+ smolt is an individual of between 1 and 2 years old that achieve the smoltification. In the simulations of the M3 model, all the individuals became 1+ smolt. In the M4 model, all the individuals of the lower group of feeding became 1+ mature parr, 62 percent of the upper group also became 1+ mature parr, and 38 percent off the upper group became 1+ smolt. In summary, 81 percent became 1+ mature parr and 19 percent became 1+ smolt. In the M5.2005 model, 61 percent of the population became 1+ mature parr and the 39 other percent became 1+ smolt. For the M5 model in 2006 (M5.2006 model), all the population became 1+ mature parr as for 2007 (M5.2007) but there is more variability of the lengths in 2006 compared to 2007.

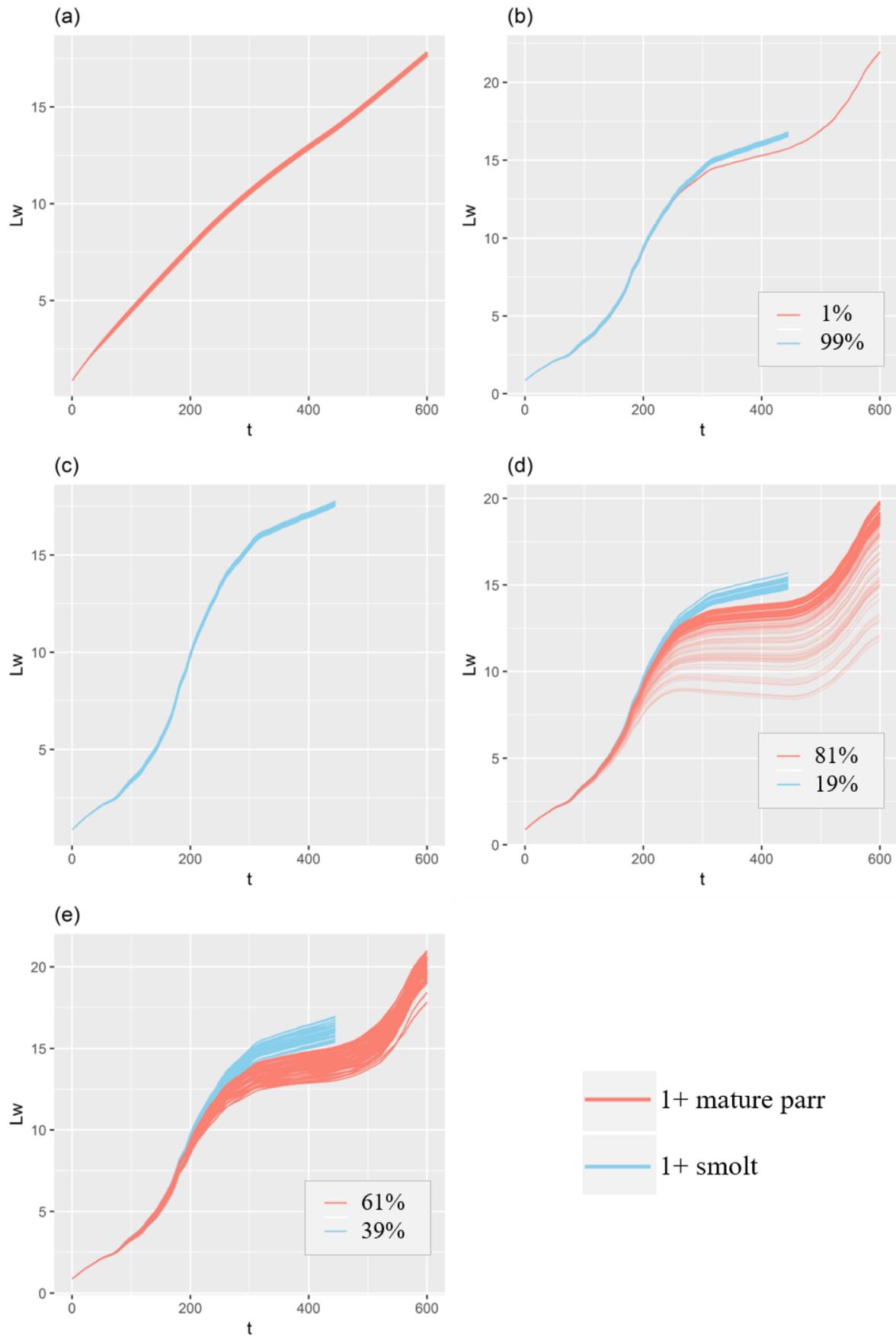


Figure 11 Evolution of the length of the 100 individuals of the populations following (a) the M1 model, (b) the M2 model, (c) the M3 model, (d) the M4 model and (e) the M5 model. The colors represent the life history strategy adopted and for (d) the transparent color represent the lower feed individuals whereas the opaque one represent the higher feed individuals.

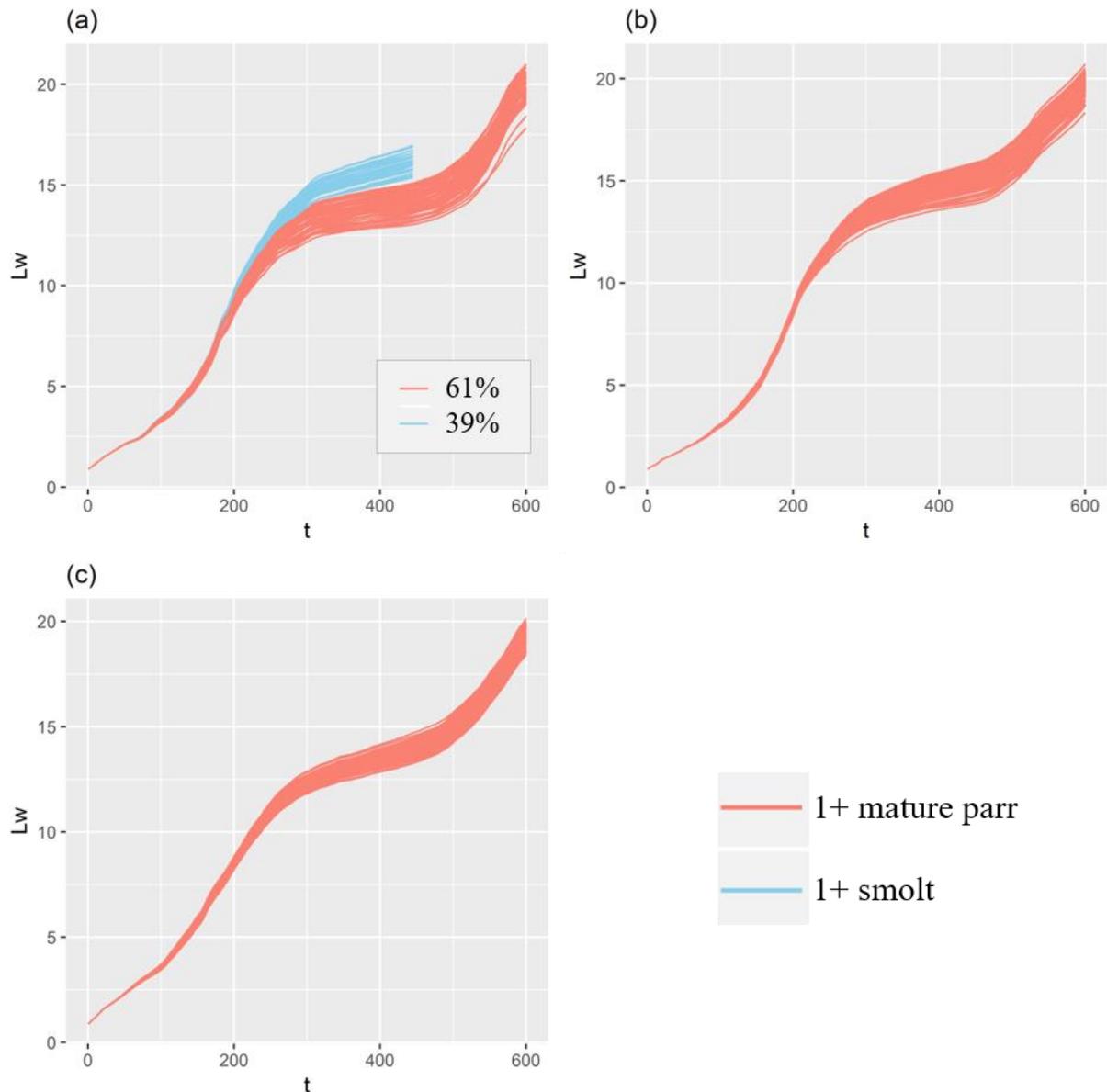


Figure 12 Evolution of the length of the 100 individuals of the populations following the M5 model for the (a) 2005-2006 temperatures, (b) the 2006-2007 temperatures and (c) 2007-2008 temperatures.. The colors represent the life history strategy adopted.

4. Discussion

Parameters estimation

The parameters estimation for the Atlantic salmon standard DEB model seems coherent with the parameters values of the other salmonids from whom DEB parameters have already been estimated and with the generalized animal. Some of them are not very close but for the majority of them it is denoting the species specificities. For example, the $[\dot{p}_M]$, the E_H^b and the δ_M are species specific. Indeed, the volume specific somatic maintenance $[\dot{p}_M]$ is the use of reserve which is dissipated into minerals to fuel the turnover of structure (like for the repair of proteins); to maintaining concentration gradients across membranes, where energy is needed for actively pumping the sodium ion out of the cell and the potassium ion into cell against their gradients; for osmotic work in fresh-water organisms and for movement costs.

The E_H^b is the maturity at birth, but the definition of birth in the DEB theory is the moment where the individual starts to feed by itself, and not the biological definition, such as hatching or emergence in salmonids. So, interspecific differences were predicable because there is a big dependence of this parameter on the initial energy reserve in the egg, on the mobilization rate of energy and on the maintenance cost of maturity. And δ_M is literally the shape coefficient of the species.

There is a big difference between the values of \dot{v} with different levels. The three values of the salmonids are closest but there is a difference of times 2 between the values of the two Pacific salmonids and the values of the Atlantic salmon. Nevertheless, this value for the Atlantic salmon is close from the generalized animal. It is simply the fact that Atlantic salmon and generalized animal are std model whereas the other ones are abj.

In the abj model the individual is not isomorphic during the acceleration phase, it change of shape (Kooijman 2000). For an isomorph, the surface area is proportional to volume power $2/3$ at all times, but for a non-isomorph, this relation is altered. Therefore, it have an influence on the parameters that have a length or area depending on the time unit dimension in their units. Here the surface-area specific assimilation rate have a unit of $J.d^{-1}.cm^{-2}$. During the acceleration phase, this parameter need to be multiplied by a shape correction function, in increasing it with the increase of the length. And this parameter have an influence on the energy conductance \dot{v} that equal $\frac{\{\dot{v}_m\}}{[E_m]}$ with $[E_m]$ the maximum reserve density (in $cm^3.d^{-1}$). This is why this difference in the parameter values is observed.

The kappa value is also quite different of the values of the other species, but in the estimation, if there is an incoherence between a parameter and his observed data associate, it is the kappa value that compensate this incoherence. Because as the sensitivity analysis demonstrates, the kappa parameter is one of the parameters that have the most influence on all the outputs studied (see Sensibility analysis below).

The other parameters are close to or in the intervals of the parameters of the 4 other species what demotes that the estimation seems quite good despite some big differences of parameters.

For the other parameters that are not estimated, there could be some bias on their choice. For example, the E_H^m parameter is not directly measured. It was needed to make a first simulation without specifying it to look at the maturity value reached at the observed size and weight found in the literature. Moreover, with length and weight values come from a different population than the one studied (Berglund 1992). All of that make the exactitude of this parameter value very difficult to obtain. Nevertheless, with a more measurable parameter value, the task is not easier. Indeed, for the V_j parameter, the observed values are very different between area and populations (Berglund 1995; Nicieza 1990; Kristinsson 1985).

Some other parameters are only based on suppositions, which make them very disputable. It would be better to estimate those values from an appropriate data set, expecting that there is no variability between cohorts, in which case it should be taken into account.

Standard DEB model simulation

The dynamics for the four individual components in the simulation of the M0 model and the dynamics of its length and weight seem consistent with the dynamics needed during the creation of the model. The same simulation was been computed with values of temperature, functional response, initial reserve energy and participation to reproduction such that the individual mature in its first year and participate to the reproduction (data not shown). The energy reuse from the reproduction buffer is however so weak that the increase in reserve energy is not perceptible. Moreover modulating the values of temperature, functional response, initial reserve energy and participation to reproduction (data not shown) showed no change of life history strategies,

which comforts the weak importance of the participation to reproduction by mature parr in their later decision to re-mature or to smoltify.

A decrease in energy reserve until the start of autonomous feeding is observed as expected, followed by an slowing weight growth during the low-feeding of the non-future smolt after the end of this phase. The growth in length doesn't vary as much as the growth in weight, which follow the expectations of the model. Indeed, there is a peak of length growth during the embryo phase, the surface/volume ratio being low during this phase permit to have lower maintenance cost of structure, leading to more energy allocated to the increasing of the structure (whose size is correlated). During the juvenile phase, there is an almost linear increase of the length whereas we expected a decrease during the late spring with another increase until autumn. Until this moment, the length growth rate decreases a little as expected. Finally, the length increase at a higher rate after the low feeding of overwintering. However, these patterns are not as pronounced as in the literature due to the environmental variation not already taken in account in this first model.

Sensibility analysis

Two sensibility analysis are presented in this study, but three were done. Indeed, a FAST analysis was made with an old version of the M0 model, and shows the same results as the Morris one. Which is it wasn't done with the M0 model neither presented.

OAT

This method is quite simple but permit to present the absolute and relatives effects, compare to other methods. Nevertheless, the calculation of the sensibility and of the elasticity of the decisions outputs does not have real mathematic sense. Contrary to the analysis of the outputs of length and weight, which highlight the great importance of the estimation of the parameters of energy conductance (\dot{v}), κ , T_A and E_H^m . That is consistent with the comparison of the estimated parameter value with other species, where some of those parameters shows specific importance. There is a lot of parameters that have a similar effect on both the length and the weight. Like the E_H^m , T_A , β , $[\dot{p}_M]$, $[E_G]$, \dot{v} and κ , which demonstrate of the importance to well estimate them proportional to them value of elasticity. But there is some parameters truly important for the looked output. For the length it's the parameters of shape coefficient as expected since it is the parameter that relate the structural volume to the length. And for the weight it's the whole-body energy density of dry biomass and the surface-area-specific maximum assimilation rate. For $x_{i_{WE}}$ its easily understandable since it is in the equation of the weight calculation. And for $\{\dot{p}_{Am}\}$ the reason is the more complicate, because it is due to the importance of this parameter in the assimilation of the energy which will conditioned the allocation and increasing the three values of weight that compose the total weight of the individual, where other parameters have consequences on less number of components. Above all, this parameter have a direct influence on the value on the energy reserve which is the component which participate the most to the weight.

Morris

The results of the Morris analysis are consistent with those of the OAT method. Indeed, as before the parameters that have the mains effects on all outputs are T_A , κ , \dot{v} and $[E_G]$. With the parameters that are found on both the weight and the length graphs with a significative effect that are the same as before. Which are T_A , \dot{v} , κ , $[E_G]$, $[\dot{p}_M]$, E_H^m and β . For the length, the main parameter is the shape coefficient as in the OAT analysis, such as the whole-body energy density of dry biomass for the weight. Finally the surface-area-specific maximum assimilation rate common to weight and length with a higher effect on the weight as before.

Models simulations

The model M1 have constant temperature and functional response for all individuals at each footstep. In this model the only parameter that change is the initial quantity of reserve in the egg E_{init} . This variability don't change a lot the length neither the life history strategy of the 100 individuals of the simulated population. In the models M2 and M3, respectively with a model where the temperature vary among days and the functional response is constant with the same values for all individuals for both the parameters and the same model but with a different value of functional response among days, the life history strategies are not the same as in the precedent model. Indeed, for those two models the population is composed of almost only 1+ smolt. The presence of two different strategies of life history if the M2 model show that it's possible to observe different strategies with a few variability, if the switch point is close enough from the mean individual. When there is more variability as in the M4 and M5 model, there is good representations of both strategies. The variability on the present strategies in the different populations model with M1, M2 and M3 attest of the importance of the environmental factors (the temperature and the functional response which indirectly shows the effects of the food availability) on those strategies. This comfort the choice of using a dynamic model for this study. In the model M4 where there is a dominant and a dominate group to the access of food, the variability of the reached length is very high (between 12 cm and 20 cm) and none of the lower group individuals reached the target size to become smolt salmons which will not prevent them from smoltify later. In both the model M4 and the M5 model, the dominant strategy is to became a 1+ smolt. But in the M5 model, the variability in length is less important than before (here length between 15 cm and 21.5cm). This is because in the M5 model the functional response change randomly between the lower proportion of the precedent lower group and the higher proportion of the precedent higher group, so the variability is compensate. On contrary, it is now surprising than there is as much variability. This is due to the fact that what happens if the embryo and the early juvenile phase is the more determinant phase to determine what will happen for adults. As observed and said in Metcalfe and Thorpe 1992 the salmons that present a higher feeding rate during the fry phase were dominant over the later ones. However, these early fish soon established and then maintained a size advantage. Which led to an increased probability of early-feeding fish to smolt as 1+ rather than 2+ or even more. Thus, a difference of less than 1 week in the relative timing of first feeding can translate into a year's difference in the timing of migration. Which is exactly what is observed here.

Table 4 Observed proportion values compare the estimated ones

Data	Life history	Cohort		
		2005	2006	2007
Predicted	1+ smolt	39 %	0 %	0 %
	1+ mature parr	61 %	100 %	100 %
Observed	1+ smolt	55 %	43 %	0 %
	1+ mature parr	40 %	52 %	100 %

In the comparison of proportion of strategies observed and predicted for the 2005, 2006 and 2007 cohort of the Scorff River (Table 4), the predictions are not as well as wanted. Indeed, for the 2005 cohort, the two main strategies are present but with the wrong dominance of strategy. For the 2006 cohort, the dominance is the good one but there is only one strategy predicted whereas two were expected. Nevertheless, for the 2007 cohort the prediction is perfect. The model cannot be validate with so few comparisons and with so few consistencies. However, the results are quite good regarding to the few data used and to the fact that the data for estimation

came from all ages and both sex individuals from very different populations, in sea and freshwater environment for being applied only on one specific population in only three cohorts. More years need to be compared with better measure of the environmental factors, mostly the food abundance that is hugely missing in this study. Moreover, a comparison with the evolution of the length and the weight would be great to be done.

5. Conclusion

To conclude, the model is not perfect and have to be improved. There is a lot of factors that haven't been taking in account in this study, for example the mortality of the individuals, the acceleration growth during a first part of the juvenile phase, which can be implement with an abj (metabolic acceleration) DEB model instead of a standard one, the link between the abundance food and the temperature, and more. With more adapted data, the estimation of all the parameters could be done in the aim of having better predictions. After that this type of model could be use taking in account both males and females during their whole life, with mortality, that can be extended to several generations to study the evolution of the life history strategies.

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Master de modélisation en écologie de l'Université de Rennes 1

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Résumé

Modélisation énergétique du déterminisme environnemental et individuel de la maturation précoce chez le saumon atlantique mâle juvénile (*Salmo salar* L.)

Cette étude présente l'utilisation d'un modèle basé sur la théorie de budget dynamique (DEB theory) afin de tracer l'évolution des variables d'états au cours du temps ainsi que des tailles et poids des individus en identifiant les stratégies d'histoire de vie adoptées par les individus en prenant en compte de la variabilité environnementale et individuelle. Un premier modèle qui sert de base à la suite de l'étude est créé, il s'agit d'un modèle DEB standard du saumon Atlantique (*Salmo salar* L.). Ses paramètres sont estimés à partir de données récoltés dans la littérature provenant de populations du monde entier. Un modèle est ensuite créé, se basant sur le précédent avec la prise en compte de la maturation précoce et de la smoltification. Ce nouveau modèle, contrairement au premier, représente uniquement les juvéniles mâles de saumon Atlantique (*Salmo salar* L.). Les simulations des modèles sont faites sur 600 jours depuis l'état œuf des individus. Différents modèles ensuite sont testés en prenant en compte la variabilité de la taille des œufs initial, la variabilité saisonnière de la température et de la quantité de nourriture présente dans l'environnement et enfin la variabilité individuel de l'acquisition de nourriture. Le dernier modèle permet grossièrement de prédire les stratégies adoptées par une population en prenant l'exemple d'une population du Scorff (Bretagne, France). Ce modèle est à améliorer afin de permettre la prédiction des stratégies d'histoire de vie des saumons en se basant sur leurs conditions au stade juvénile en commençant par estimé tous les paramètres de ce dernier modèle à partir d'observations.

Mots clés : Saumon Atlantique, DEB model, maturation précoce, traits d'histoire de vie

Abstract

Energy budget modeling of the environmental and individual determinism of precocious maturation in male juvenile Atlantic salmon (*Salmo salar* L.)

This study presents the use of a model based on the theory of dynamic energy budget (DEB theory) in order to trace the evolution of state variables over time as well as the sizes and weights of individuals by identifying the strategies of life history adopted by individuals taking into account environmental and individual variability. A first model that serves as a basis for further study is created, it is a standard DEB model of Atlantic salmon (*Salmo salar* L.). Its parameters are estimated from data collected in the literature coming from very different populations. A model is then created, based on the previous one with the consideration of precocious maturation and smoltification decisions. This new model, unlike the first one, represents only the juveniles of Atlantic salmon (*Salmo salar* L.). The simulations of the models are made over 600 days since the egg state of the individuals. Different models are then tested taking into account the variability of the initial egg size, the seasonal variability of the temperature and the quantity of food present in the environment and finally the individual variability of the food acquisition. The last model allows a rough prediction of the strategies adopted by a population by taking the example of a Scorff river population (Brittany, France). This model has to be improved to allow the prediction of salmon life history strategies based on their juvenile stage conditions, starting by estimating all parameters of the latter model from observations.

Key-words: Atlantic salmon, DEB model, precocious maturation, life history strategies