River basin management using a stochastic model of the salmon life cycle.

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Abstract: Effective management of natural populations of Atlantic salmon (Salmo Salar L.) requires the ability to evaluate the impact on salmon survival of human activities such as agricultural practices (nitrogen pollution, suspended solids emission, deforestation, ...), river management (e.g. fishways, dams), industries practices and catches by fisheries and angling. The salmon life is also influenced by natural environmental constraints: characteristics of the river basin, local home-river quality, climate, flows. A stochastic model of the life cycle was built in order to have a better understanding of effect of these constraints on the abundance. The model considers the life of a salmon as a succession of different stages: embryo-larval, juvenile, adult and reproduction. The total population is split up into different sub-populations depending on life stage and age: salmon can live one or several years in river then in sea. From one stage to the following one, a survival rate is applied to the sub-population. This rate is age-dependent and depends on constraints: some are measurable as juvenile growth areas, competitors density or catch levels. Because of uncontrolled conditions (flows, erosion, ...), some rates are considered random and are specified in the model by a distribution. A software, written in Splus, is able to compute simulations after specifying interactively or not the parameters characteristics, the horizon and the number of simulations. Graphical analyses of river management strategies are available. We are able to compare influence of catch levels, juvenile growth areas increase (due to fishways), agricultural practices (which control the level of suspended solids) on the distribution of the abundance. Applied on River Adour and its Gaves characteristics, analysis of river managements highlights the main under-gravel survival sensitivity compared to catch levels or juvenile growth areas.

1 INTRODUCTION

In this paper, we are concerned in management of natural population of Atlantic salmon (Salmo Salar L.). This management has to be thought at a river basin level because of the conflict of interests between fisheries, anglers, ecologists, ... (Prouzet et al. [1996]). Advices need to be provided in term of conservation reference levels: what lower (or upper) boundaries point for stocks beyond which it is undesirable to permit stock levels to go. This has to be connected to management reference points such as setting catch options (Potter [1996]).

An effective management of natural salmon population requires the ability to evaluate the impact on salmon survival of human activities such as agricultural practices (nitrogen pollution, suspended solids emission, deforestation, ...), river management (e.g. fishways, dams), industries practices and catches by fisheries and angling. The salmon life is also influenced by natural environmental constraints: characteristics of the river basin, local home-river quality, climate, flows. Because some of these factors are not fixed, a stochastic model of the life cycle was built in order to have a better understanding of effects of these constraints on the abundance. The salmon life is separated into three main phases: hatching and juvenile life in river, downstream migration and maturation and growth in the ocean and upstream migration to home river for reproduction. During each phase, salmon survival is constrained to specific environmental conditions. Our model was designed to integrate interaction between salmon life and human and environmental factors. Instead of the stock-recruitment model usually used in the fisheries biology, our model is based on the salmon life cycle.
2 MODEL OF THE LIFE CYCLE

Salmon females bury their eggs at the end of Fall in stream gravel substrates immediately upstream from swift current zones (figure 1). In Southern Europe, undergravel development lasts for 3.5 months (egg incubation, hatching, and yolk sac absorption).

![Diagram of salmon life cycle](image)

**Fig. 1 - Biological Cycle of Salmon.**

During March, fry emerge from the substrate and they are called emerging fry. At this stage, they are very mobile and disperse in the neighboring riffles, rapids and to a lesser extent in the flats, where they settle and establish a territory (in April-May). They are then called parr. According to their rate of growth, they remain in fresh water for one or two years, seldom three, before undergoing the smolt transformation and migrating out to sea. Indeed, young of the year split into two subpopulations in early Fall. The largest group is made up of fast growing parr (called pre-smolt) which will reach the smolt stage in one year, the following April. The other group (called the sessile fraction) consists of slower growing parr, which will have to spend another year in freshwater before smolting. The marine growth phase lasts from one to three years in relation to growth rate, before they come back as adults in their home river. The returning salmon show up in the estuaries from February to September, the oldest fish first. They are named differently according to their sea-age: 1 sea-winter (grilse), 2 or 3 sea-winters (small and large salmon). Before reproduction, a further distinction can be made between the potential spawner which survived fishing (escapement) and the spawners. Only about 1% of spawners come back for a second reproduction. Therefore, their contribution to generation renewal is minimal.

The model (figure 2) takes into account key stages of development and the environmental constraints which affect stock dynamics. From egg to emerging fry, mortalities in the substrate are mostly due to smothering of the redds by fine sediments or to mechanical destruction during high floods. These causes often find their origin in (or may be aggravated by) agricultural practices and/or forest exploitation that reduce water retention and increase soil erosion.

**Fig. 2 - Simplified process chart of CBS. yoy = young-of-the-year, EF & A = Estuary Fishing and Angling, LEC = Local Environmental Conditions, JGA = Juvenile Growing Areas.**

During the rest of the juvenile period in freshwater (fry to smolt), number regulation depends mostly from two groups of factors:

- surfaces of juvenile rearing habitats; their use depends on their accessibility (adults can clear dams to access these areas) and their quality (these habitats may be subjected to multiple damages such as clogging up of substrate and various chemical pollutions);

- interspecific competition, already taken into account by Gros and Prouzet [1988]; Fall parr abundance depends on productive habitat surface and on individual surface of territories granted to young-of-the-year by older parr; some overlapping of territories of different age individuals may occur.
The equation of the model can be written as follows:

\[ P = \tau_f \cdot F \times \exp\left(-\frac{\tau_f + F}{P_{\text{max}}}\right) \]

where \( P \) is the first Parr population, \( F \) is emergency fry, \( \tau_f \) is a survival rate without any density-dependence competition, \( \gamma \) a parameter and \( P_{\text{max}} \) is the maximum Parr carrying capacity for young-of-the-year. It corresponds to the remaining juvenile growth area not occupied by older parrs.

During the smolt downstream migration, survival depends mostly on the efficiency of fish diversion devices for water intakes (hydropower plants, irrigation channels ...), water quality of the lower and estuarine segments of the stream, and predation. In the sea, and during the migration into freshwater, exploitation by the fisheries prevails on the others factors. However, during upstream migration, delays in getting over obstacles (inefficient fish ladders, low flows) associated with poor water quality can induce significant mortalities between the escapement stage and the actual spawner stage.

This model describes the changes in number of a given population over the year (Charron [1994]; Dumas et al. [1996]). Years and cohorts are linked among themselves during a chosen period of time. Numbers from one stage to the next are computed with a parameterized function which takes into account environmental conditions.

There are four types of functions:

- survival rate (periods of undergravel development, juvenile stages of each age during the warm season, then the winter season, marine period for each year spent in the sea, finally adult stage in freshwater);
- splitting rate (between future one-year-old smolt and sedentary parr, between adult and marine sub-adult);
- fishing exploitation rate (marine, coastal and estuarine waters, and by angling);
- reproduction (transformation of the number of spawners into a number of eggs deposited in the reds).

The parameters of these functions can be considered either as being constant (e.g., fishing exploitation rates), or variable and associated to a distribution law (e.g., fresh water survival).

For example, under gravel survival rate is modelled as \( F_{\text{ry}} = \alpha \times \text{Eggs} \) where \( \alpha \) follows a lognormal distribution with parameters \( \mu \) and \( \sigma^2 \) depending on the redd water quality. Estuary Fishing and Angling is modelled as \( \text{Escapement}_j = \beta_j \times \text{Return}_j \) where \( j \) denotes the sea-winter age and \( \beta_j \) are deterministic catch levels. We considered fixed survival rates between Escapement and Spawners, depending on sea-winter age. A complete description of all the functions and parameters can be found in Charron [1994].

### 3 SIMULATIONS

A software named CBS (French acronym for Biological Salmon Cycle) developed in S-Plus (SPLUS [1993]) was written to simulate the evolution of a salmon population. CBS is able to compute a large number of simulations after specifying interactively or not the parameters characteristics, the horizon and the number of simulations. Graphical analyses of trajectories are also available interactively. CBS is split up into 5 parts:

1. Specification of model parameters. All the parameters (survival rates, eggs production, ...) can be modified interactively: the values (when deterministic) or the characteristics (distribution with their parameters as mean and variance).

2. Specification of simulations. The horizon (in years) and the number of simulations are asked.

3. The initial population. We can apply the model to an existing real abundance or to assess stocking efficiency (with eggs or juveniles).

4. Executing the simulations. One simulated trajectory is based on the following. From an initial population, the different functions of survival, separation, competition, exploitation, renewal, ... are applied sequentially to the different sub-populations depending on chronology: from one development stage to the next. When parameters are not deterministic, we simulate them using their specific distributions.

5. Graphical analyses. Different plots are available: quantiles of distributions of sub-populations (2-D or 3-D), cohort based return data, ...

As an example, quantiles evolution of abundance of 1-sea-winter spawners (from 1 and 2-year old smolts pooled) over 50 years is presented (figure 3). This simulation is obtained with the following characteristics: a juvenile growing areas of 57 ha corresponding to the River Gave d’Oloron (South-West of France) stocked with 1 million eggs (~ 250 spawners) in 1985. We have proceeded to 1000 simulations of trajectories over 50 years. The river management parameters were: egg survival rate of under gravel with a log-normal distribution (mean and standard error value \( \mu = 10\% \), \( \sigma = 3\% \)), deterministic catch levels in estuary and angling equal to 30% for 1-sea-winter fish (or grilse), 20% for 2-sea-winter fish and 10% for 3-sea-winter fish. These parameter values and the others not presented here were determined according to data observed in the same region on the River Nivelle (Dumas [1985-1996]) and literature (Gros and Prouzet [1988]; Prouzet [1994]).

On this figure, comparing the upper and lower quantiles with the median, we can notice an asymmetry of the distributions (due to lower bound 0 and log-normal distributions) and the slow positive trend of the median.
recruit; when analysing just one trajectory (here a “good” one), we can notice that the number of spawners is quite year-by-year randomly distributed. Nevertheless, because this evolution is almost always in the upper quantiles, there exist a trend in the evolution: to start with a good renewal is important.

As a first conclusion, we can see that in mean we will need for a long time to have a “natural salmon population”. Catch levels had to be determine with respect to the knowledge of the yearly variations in abundance.

4 ANALYSING STRATEGIES

As presented in the introduction, river basin manager mainly acts on anthropic effect influencing the salmon survival rate. In our model design, we have disconnected natural biological survival (such as mortality in the sea not due to catches for example) from mortality due to fish (which can be regulated). Three of the main actions are:

1. opening (or closing) the juvenile growth areas in building fish ways (or dams),
2. regulating the catch efforts of estuarine fisheries and angling,
3. regulating agricultural practices (subsidies or taxes) to reduce erosion and suspended solids in streams and, as a consequence, decrease the amount of dissolved oxygen supplied to eggs and alevins.

These three factors are translated in our model into three parameters which are the juvenile growth areas, the catch effort and the survival rate of eggs under gravels. We wrote a specific software ACB (French acronym for Analysis of Biological Cycle) which manages CBS in batch and proposes comparison plots. We simulate various management strategies specified with the parameter values presented in table 1.

<table>
<thead>
<tr>
<th>UGS</th>
<th>μ = 10%, σ = 3%</th>
<th>μ = 20%, σ = 5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE</td>
<td>p1  p2  p3</td>
<td>p1  p2  p3</td>
</tr>
<tr>
<td>JGA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>57 ha</td>
<td>1  2  3</td>
<td>4  5  6</td>
</tr>
<tr>
<td>144 ha</td>
<td>7  8  9</td>
<td>10 11 12</td>
</tr>
<tr>
<td>209 ha</td>
<td>13 14 15</td>
<td>16 17 18</td>
</tr>
</tbody>
</table>

Tab. 1 - Identification numbers of the different strategies used in figure 4. UGS: under-gravel egg survival, CE: catch effort, JGA: juvenile growth area. p1, p2, p3 are salmon exploitation level, μ the mean and σ the standard deviation.

The three juvenile growth areas correspond to reach accessibility of salmon to different stretches and tributaries of River Gave d’Oloron. The two under-gravel egg survival rates correspond to changes in agricultural practices and the three levels p1, p2 and p3 to various catch efforts. These catch efforts are age-dependent: net size and position in the River. Level p1 corresponds to 30%, 20% and 10% of salmon exploitation respectively for 1-year-old, 2-year-old and 3-year-old, p2 respectively to 40%, 30% and 20% and p3 respectively to 50%, 40% and 30%.

Graphical analysis of these river management strategies is shown in figure 4. We are able to compare influence of catch levels, juvenile growth areas increase, water quality (for the survival of eggs and alevins) on the distribution of return abundance.

Fig. 4 - Analysis of management scheme using ACB relatively to the mean of upstream of 2-year-old smolts and 2-year-old salmon. The strategy numbers are presented in table 1.
Figure 4 presents the results concerning the means of the simulated evolutions. We do not present here those concerning quantiles but conclusions are the same. Curves 4-5-6, 10-11-12 and 16-17-18 correspond to the higher under-gravel egg survival rate ($\mu = 20\%$, $\sigma = 5\%$); abundance is much better than with the lower under-gravel survival rate. Curve 15 (UGS with $\mu = 10\%$, $\sigma = 3\%$; CE = p3; JGA = 209 ha) corresponds to the higher juvenile growth areas. To open upper reaches to salmon alone is not equal to have a good recuitment if fishing pressure is high and if the water quality is poor (not enough dissolved oxygen in redds).

The main survival rate sensitivity during the first stages of the salmon life compared to catch levels or juvenile growth areas increases is highlighted by this river management analysis.

5 DISCUSSION

Results presented in the former section are of particular interest for managers. Meanwhile, we need to be concerned with validation even if it is difficult to validate such model because of the the few number of data (one data for each sub-population per year).

Model parameters are estimated and calibrated on past and actual data (Badia et al. [1996]). We can also use the few number of data to validate year-by-year the model. Starting the simulation with the observed data, we can measure the level of probability for the population predicted by our model the next year and compare to observed values: this can be done only for the next years because we cannot use the same data to estimate and to validate the model. Meanwhile, this year-by-year evaluation is not a complete validation of our model if we assigned to it long-term prospective (many decades). In that case, we need for example to address potential climatic change because of its incidence on rainfall regime and stream distribution.

Our model is designed to study such cases especially as for interaction between natural and human environmental factors and salmon life cycle. This was the basis of our strategy analysis. We have seen on figure 3 the use of our stochastic model to predict quantiles of the return distribution. As shown in figure 4, analysis of the strategies give us a very interesting information concerning their mean responses. It was also possible to plot strategy comparison relatively to any quantiles of the evolution. For managers, this is useful because river basin development decision should be based on risk analysis.

Another interest of such a stochastic model is emphasized on figure 5 where we plotted different estimated Stock - Recruitment curves based on Ricker’s model (Ricker [1954]).

$$R = aS e^{-bs}$$

Only some simulated evolutions are drawn but some are

![Stock-Recruitment curves estimated on some simulated evolutions (recruit in egg equivalent). In bold and large, the mean estimated Ricker’s model. The 1:1 line corresponds to the Replacement line.](image)

very far from the mean estimated Stock - Recruitment curve (in bold).

Using the Replacement line, we see that catch strategies should be completely different according to these likely behaviors (Allen [1973]). The probability of the strategy leading to stock extinction can be obtained by examining various levels of return from a given escapement.

Analysing the strategy effect on salmon population dynamic, our preliminary results emphasized the sensitivity of abundance to the under-gravel egg survival rate. It points out a very interesting scientific question: how is the determinism of this survival rate.

In our application, we have translated deforestation, banks development or agricultural practices directly into survival rate. If this link is evident, the relative quantitative impact on the survival rate of banks development for example should be more studied because of some lack of knowledge about this process. A qualitative modeling of the process of redd filling could be used to analyse it (Guerin et al. [1997]).

When salmon travel upstream, they have no need for food. Because of the fact that the salmon are surviving off of stored nutrients, it is important that they reach their spawning ground as expeditiously as possible. It is important that the salmon’s path stay shaded with trees. Without trees lining their path, the water becomes warm and the salmon are not able to retain enough oxygen from the warm water and they end up suffocating. The trees also protect the banks from ero-
sion and keep fine silt and sediment from dumping into their water.

An effective management needs to mixed our model with a Geographical Information System (GIS) to better inform on the variability of hydro-morphological and environmental tributaries and redds characteristics. River basin managers often decide relatively to large buildings. They now need to think in term of controlling human practices or bank vegetation development as we have shown that the increasing of the juvenile growth areas has to be related to estuary fishing and angling pressure and water quality control.

6 ACKNOWLEDGMENTS

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7 REFERENCES


