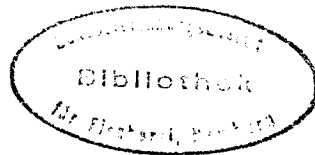


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GLOBAL MODEL OF THE DYNAMICS AND ECOLOGY OF THE POPULATION OF ALLIS SHAD (*Alosa alosa*) IN THE GIRONDE-GARONNE-DORDOGNE WATERSHED

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ABSTRACT

This article presents the form of modelization used to determine the main factors involved in the dynamics of the population of allis shad (*Alosa alosa*) in the Gironde-Garonne-Dordogne watershed. Using a model, it is possible to analyse the effects of the modification of factors that can be controlled by man.

The construction of the model is presented first ; it has deterministic compartments and is spatialized and structured by age group and sex; the timescale unit is the year. The first stage consists of structuring the data, selecting the models and fitting the parameters based on the analysis of observed data. The data used are commercial fishery CPUE indices for the period 1983-92, the biometric characteristics of the adults sampled in the estuary and the river from 1986 to 1988 and in 1994 and 1995, the numbers of adults estimated for the period 1989-93, abundance data for juveniles for the period 1989-93 and estuary temperature data for 1983-92. A method of sensibility analysis is then presented, highlighting the low influence of annual variations and the robustness of the population dynamics with regard to variations in the different parameters.

Keywords : *Alosa alosa*, deterministic model, population dynamics, sensibility analysis

I. INTRODUCTION

The allis shad, *Alosa alosa*, is an anadromous amphihaline migratory species which is of economic and heritage importance in France (Castelnaud and Babin, 1992). In the Gironde-Garonne-Dordogne watershed, where we work, the adult population is subjected to heavy commercial and amateur fishing and the juveniles to by-catches (Taverny, 1990). The population's reproduction area has been considerably reduced as a result of weirs that were insurmountable until 1985 (Cassou-Leins, 1982; Taverny, 1991). Since 1990, however, the allis shad has been gradually regaining its original spawning grounds, as a result of the creation of passages to allow the fish to climb the weirs (Belaud and Labat, 1992). Several studies have already been conducted with the aim of describing the ecology of the species in the Loire and the Gironde-Garonne-Dordogne watershed (Figure 1) and quantifying some of the human impact on the species (Cassou-Leins, 1982; Mennesson-Boisneau, 1990; Taverny, 1991).

In order to be able to implement the right management measures for maintaining the population, it is important to have a good knowledge of its dynamics and limiting factors, the impact of which can sometimes be modulated if it is of anthropic origin.

Modelization is a useful tool for identifying all the factors involved in the dynamics and analysing the effect of any change in their intensity.

We have therefore established a model of the dynamics of the population of the Gironde-Garonne-Dordogne watershed. This aid to management serves primarily to explain and describe the ecology of the allis shad and, in certain circumstance, can play a predictive role.

It is not a strict halieutic model; besides the fishing parameters, it also contains a large number of parameters associated with the age structure, spatialization and ecology of the species.

This article presents the two initial stages of modelization. We shall begin with the definition and construction of the model, moving on to an initial sensitivity analysis that will provide a qualitative description of the model.

The first stage of the work enables us to structure our knowledge and thus highlight any gaps. It also requires us to carry out a biostatistical and biomathematical analysis of the data with a view to finding a relevant representation of the ecological stages.

In the second stage, inspired by the method used by McCarthy (1996), we shall be able to qualify the extent of the interannual variables resulting from the determination of the number of anadromous migrants and qualify the robustness of the population dynamics with regard to the variations of the environmental parameters in the model.

II. METHODS

A. *The main stages of the ecological cycle*

The model (Figure 2) represents the ecological cycle (Figure 1) and the mode of operation of the Gironde-Garonne-Dordogne watershed population (Figure 3). This section will describe the main points of the ecology of this anadromous species. The individuals develop in the sea between the ages of 1 to 7 years; they grow in size and put on weight. The natural mortality rate varies with the age of the fish. Longevity is 6 years for males and 7 years for females. Sexual maturity is reached from the age of 3 years for males and 4 years for females. The allis shad exhibits homing behaviour towards the watershed (Douchement, 1981). The allis shad in this watershed are therefore considered to constitute a single population. In the estuary, the numbers of migrants are reduced by commercial fishing; once they arrive at the Garonne-Dordogne bifurcation, the choice of route is considered random. In the river, numbers are

further reduced by fishing. At the spawning grounds, a male may fertilize several females. The number of descendants will be a function of the biomass of female spawners (i.e. the total weight of fertilized females) and the environmental constraints.

B. Model structure and calibration

The model is structured by age group and sex; it is discrete, with deterministic compartments, and operates on an annual timescale. It therefore has the same type of architecture as the models produced by Charron (1994) for salmon and by Abbadi (1995) for trout. The model was implemented using MATLAB software.

For each part of the model, the parameters were calibrated by trying to obtain simulation results close to observed data; for the moment, the difference between the observed data and the simulation results has been estimated on a strictly qualitative basis. Calibration is an important stage in the construction of a model. Firstly, it is at this stage that the acceptable value intervals for each parameter are found; secondly, it makes it possible to carry out simulations using the estimated parameter values for the current state of the population. Thirdly, it makes it possible to simulate scenarios in which the value of one or more parameters is modified, representing a change in a factor that may have an impact on the dynamics of the population.

For the weight and size distribution and the age structure of the adults, we used Taverny's (1991) data for 1986-88 and our sampling data on the adults caught by professional fisheries in 1994 and 1995.

The data used to calibrate the number of anadromous migrants are estimates based on the sum of total commercial fishery landings, counts made at the spawning grounds and the numbers passing through the weirs furthest downstream in the period 1989-93, calculated using video recordings. The fishery parameters are fitted according to CPUE data and catch data for 1989-93. Estuary water temperatures 1983-92 were used to calibrate the environmental determinism parameters for entry into the estuary.

The stock-recruitment ratio is calibrated on the basis of estimates of the numbers of juveniles heading downstream, calculated for the period 1989-92, and the characteristics of the biomass of female spawners determined with the data on adults mentioned above.

1. Weight of individuals

The weight is required in order to determine the biomass of female spawners.

The weight distribution for each age group of individuals from 4 to 6 years old is assimilated to a normal distribution of average and standard deviation calculated from sampling data (table 1).

For the ages not observed, 3 and 7 years, we extrapolated the weight using Von Bertalanffy's ratio (1938) adjusted to catches of 4 to 6-year-olds:

$$\begin{aligned} \text{for males} \quad W &= 1.165 * 10^{-5} * L_t^{2.976} \\ \text{for females} \quad W &= 1.066 * 10^{-5} * L_t^{3.005} \end{aligned}$$

while for size we used a seasonal growth model by Gaschütz (1980) the parameters of which were determined by Taverny (1991) (Table 2):

$$\begin{aligned} L_t &= L_\infty(1 - \exp(-[KD(t - t_0) + (CDK / 2\Pi) * \sin(2\Pi(t - t_s))]))^{1/D} \\ D &= 3(1 - (0.6742 + 0.03574 \log(W_{\max}))) \end{aligned}$$

where L_t is the length at time t , L_∞ is the theoretical maximum length at which the fish has zero growth, W_{max} is the theoretical maximum attainable size, t_0 is the theoretical time at which $L_t = 0$, t_s is the constant of the time elapsed between birth t_0 and the start of the first growth oscillation, C is the empirical constant representing the size of the growth oscillation, and K is the constant of growth.

Table 1. Parameters of the normal distribution of total length and weight estimated from data on 4-to-6-year-old adults sampled in the estuary and in the river in 1994 and 1995 and calculated using ratios (1), (2) and (3) for individuals 3 and 7 years old

		3 yrs	4 yrs	5 yrs	6 yrs	7 yrs
female	numbers observed	(0)	17	243	92	(0)
	average L_t (cm)	(44.2)	55.2	56.5	57.9	(64.8)
	std L_t (cm)	(2.6)	2.5	2.7	2.6	(2.6)
	average weight (kg)	(0.9)	1.8	2	2.2	(3)
	std weight (kg)	(0.3)	0.4	0.3	0.3	(0.3)
male	numbers observed	(0)	66	277	33	(0)
	average L_t (cm)	(33)	50.8	51.9	53.1	(59.4)
	std L_t (cm)	(2.6)	2.3	2.7	2.7	(2.6)
	average weight (kg)	(0.4)	1.3	1.5	1.6	(2.2)
	std weight (kg)	(0.2)	0.2	0.3	0.3	(0.2)

Table 2. Parameters of the Gaschütz model (1980) determined by Taverny (1991)

parameters	male	female
W_{max}	3000	4000
D	0.6046	0.5912
t_0	-0.4512	-0.3375
t_s	0.3126	0.6527
c	1	1
k	0.4655	0.6996

2. Maturity parameters - Survival parameters - Age structure of adults in the estuary

In this paragraph, $c(k)$ (Table 3) represents for a given cohort the proportion of mature individuals that will return to the estuary at age k , compared to the number of individuals in the same cohort staying at sea. $s(k)$ (Table 4) represents the proportion of individuals surviving from age k to age $k+1$.

The number entering the estuary at a given age is expressed in the following equation:

$$e(k+1) = (1-c(k)) * s(k) * c(k+1) * N$$

where $e(k+1)$ is the number entering the estuary to spawn at age $(k+1)$, $e(k)$ is the number of individuals of the cohort entering at age k , $s(k)$ is the probability of survival from age (k) to age $(k+1)$, $c(k+1)$ is the proportion of entries at age $(k+1)$, and N is the number of 3-year-old individuals in the cohort.

We define the proportions entering, $y(k)$, at the different ages of the individuals of a cohort by :

$$y(k) = \frac{e(k)}{\sum_{i=1}^7 e(i)} \quad (1)$$

According to the field data, no individuals enter the estuary before the age of 3 years for males, therefore, $c(1) = c(2) = 0$ and 4 years for females, therefore, $c(1) = c(2) = c(3) = 0$.

We have no observed data for any of the other parameters (Table 3).

Numbers surviving from 1 to 2 years and from 2 to 3 years were determined according to the indications given by Taverny (1991), $s(1) = 0.3$ and $s(2) = 0.5$.

Since maximum longevity for females is 7 years, the survival figure for 7 to 8 years is nil.

Male longevity is 6 years, therefore survival figures $s(6)$ and $s(7)$ are nil. Furthermore, we determine survival values $s(3)$ and $s(4)$ as 0.8.

For females, we determine the numbers entering at three years as lower than those at 4 years and so that optimization gives a survival value $s(5)$ as close as possible to those of $s(3)$ and $s(4)$ (table 4).

In order to determine the other parameters, we considered the following postulate (often used in halieutics): the age structure of the adults, observed in an estuary in a given year (the $p(k)$ in table 5) is identical to the proportions $y(k)$ (equation (1)) of those mature adults of the same cohort entering the estuary at different ages (3 to 7 years).

This postulate is acceptable if the strength of the cohorts making up the flow of migrants and mortality is not too variable.

The last parameters are estimated using an optimization technique implemented under MATLAB, with the least squares of the distance between the proportions observed, $p(k)$, and the proportions calculated, $y(k)$.

Table 3 . Value of the parameters of proportions entering at different ages, $c(k)$, determined or calculated (in bold) by the optimization method under MATLAB

	male	female
$c(3)$ prop. entering at 3 yrs	0.0013	0.0000
$c(4)$ prop. entering at 4 yrs	0.0760	0.0550
$c(5)$ prop. entering at 5 yrs	0.7160	0.5700
$c(6)$ prop. entering at 6 yrs	0.6000	0.7290
$c(7)$ prop. entering at 7 yrs	0.0000	0.4980
$c(8)$ prop. entering at 8 yrs	0.0000	0.0000

Table 4 . Value of the parameters of proportions of individuals surviving at different ages, $s(k)$, determined or calculated (in bold) by the optimization method under MATLAB

	male	female
$s(3)$ prop. surviving from age 3 to age 4	0.80	0.80
$s(4)$ prop. surviving from age 4 to age 5	0.80	0.80
$s(5)$ prop. surviving from age 5 to age 6	0.60	0.84
$s(6)$ prop. surviving from age 6 to age 7	0.00	0.50
$s(7)$ prop. surviving from age 7 to age 8	0.00	0.00

Table 5 . Average proportions, $p(k)$, of ages k observed in the migrating adults sampled in the estuary and in the river for the years 1986-88 and 1994-95

age	female		male	
	average	standard deviation	average	standard deviation
3	0,00	0,00	0,00	0,01
4	0,03	0,02	0,11	0,06
5	0,65	0,18	0,77	0,08
6	0,30	0,14	0,11	0,06
7	0,04	0,05	0,00	0,00

3. Size of the annual stock of adults entering the estuary

The number of migrant adults will be determined by the number of potential adults in the sea and by the size of the physiological window that will allow them to enter the estuary (Kocik and Friedland, 1995).

Most of the studies conducted on the determinism of shad migration (genus *Alosa*) have underlined the influence of flow, temperature and tides (Richkus, 1974; Mennesson-Boisneau, 1990; Rochard, 1992; Sabatié, 1993; Prouzet *et al.*, 1994). The most evident relationship is with the temperature (Leggett et Whitney, 1972, Boisneau *et al.*, 1985). There would seem to be a temperature threshold of 10-12°C, below which migratory movements are frozen.

We tested for the existence of a relationship between annual CPUE indices (abundance in the year) and the number of days in the period February-June on which the temperature is higher than a particular threshold temperature.

Variance analyses were carried out for threshold values of between 5 and 16°C. There is a significant effect for values in the range 9-12°C. The most significant model is for a threshold of 10°C, the relationship being:

$$CPUE = 0.48 * Ts10 - 20.77 + \epsilon \quad \text{where } P = 0.002 \text{ and } R^2 = 0.72$$

with $Ts10$ as the number of days in the migration period on which the temperature was higher than 10°C.

The distribution observed in our $Ts10$ temperature series was assimilated to a normal distribution with an average of 104.5 days and a standard deviation of 34 days.

In the model, the annual value of $Ts10$ is set at random according to the normal distribution. The proportion of adults entering the estuary, between 0.4 and 1 inclusively, is calculated using the distribution function of the normal variable $\mathcal{N}(104.5, 34)$ (Fig 4).

4. Fishing catches

In our model, catches C are calculated using the fishing rate F and the abundance A of the individuals present in the fishing zone (estuary, Garonne, Dordogne):

$$C = F * A$$

The calibration value of F is determined by the product of the fishing effort, f_j , over a period of one year by an average fisherman (expressed in the number of days fishing with a net), with

the number of fishermen in the fishing zone n_j and a parameter e_j , a function of the ratio between the length of the net and the width of the fishing zone. The fishing rate for a fishing zone is expressed as follows:

$$F_j = e_j * n_j * f_j$$

Using this method, F is determined at 0.16 in the estuary, 0.7 in the Garonne and 0.5 in the Dordogne.

For the time being, we have not linked the fishing rate with the fishing effort (Laurec and Le Guen, 1981); it is difficult to establish a clear relationship between these two terms.

5. Reproduction

Reproduction is represented by a relationship giving the number of recruits (young individuals, usable or not) in the stock of usable individuals which can be limited to "mature individuals" (Laurec and Le Guen, 1981). In our case, recruitment is the number of one-year-old juveniles and the stock is expressed in terms of the biomass of female spawners, B_f , i.e., the number of kilograms of females.

We chose the Ricker relationship, a non-linear model, which expresses a density-dependent regulation of the number of descendants, y ; it is a model that is used often, along with the Beverton-Holt model (Laurec and Le Guen, 1981). The parameters were calibrated using estimates made on the basis of observed data, i.e. on average 200 000 adults per river giving 2 million juveniles passing downstream into the estuary (or a total of 4 million for the two rivers). We consider that the stock-recruitment ratio of the watershed population is currently at the maximum of the Ricker curve (Fig. 4):

$$y = 77 * B_f * \exp(1.4 * 10^{-5} * B_f)$$

The biomass of female spawners B_f is determined according to the number of females fertilized. For the time being, we have determined arbitrarily that one male would fertilize up to three females.

C. Sensitivity analysis

Using this method, we can study the sensitivity of the model for each of its 33 variable parameters. The variation interval for the calibrated parameters was determined directly from the confidence interval. For the other parameters, we selected an interval within the realm of the possible and which would be acceptable for the population and the site under study (Table 6).

Table 6 : variation interval for the variable parameters

Parameters	Estimated value	Variation interval in sensitivity analysis
cm(3) males prop. entering at 3 yrs	0.0013	0.0000-0.0800
cm(4) males prop. entering at 4 yrs	0.0760	0.0000-0.1200
cm(5) males prop. entering at 5 yrs	0.7160	0.6800-0.9800
cm(6) males prop. entering at 6 yrs	0.6	0.6-0.9800
cm(4) females prop. entering at 4 yrs	0.0550	0.0300-0.0800
cm(5) females prop. entering at 5 yrs	0.5700	0.4000-0.8000
cm(6) females prop. entering at 6 yrs	0.7290	0.5000-0.9000
cm(7) females prop. entering at 7 yrs	0.4980	0.3000-0.7000
s(1) males prop. surviving from age 1 to age 2	0.3	0.2-0.4

s(2) males prop. surviving from age 2 to age 3	0.5	0.3-0.7
s(3) males prop. surviving from age 3 to age 4	0.8	0.7-0.9
s(4) males prop. surviving from age 4 to age 5	0.8	0.7-0.9
s(5) males prop. surviving from age 5 to age 6	0.6	0.7-0.9
s(1) females prop. surviving from age 1 to age 2	0.3	0.2-0.4
s(2) females prop. surviving from age 2 to age 3	0.5	0.3-0.6
s(3) females prop. surviving from age 3 to age 4	0.8	0.7-0.9
s(4) females prop. surviving from age 4 to age 5	0.8	0.7-0.9
s(5) females prop. surviving from age 5 to age 6	0.84	0.60-0.90
s(6) females prop. surviving from age 6 to age 7	0.5	0.3-0.5
ampli. parameter for entering stock determination	0.31	0.28-0.34
mu, Ts10 normale distribution mean	104.5	94-114
sigma, Ts10 normale distribution std	34	30-38
mortality fishing in Gironde estuary	0.16	0.1-0.6
mortality fishing in Garonne river	0.7	0.1-0.8
mortality fishing in Dordogne river	0.5	0.1-0.8
females number that a male is able to fertilize	3	3-9
femal weight mean at 4 years	1.8	1.02-2.54
femal weight mean at 5 years	2	1.3-2.66
femal weight mean at 6 years	2.2	1.55-2.87
femal weight mean at 7 years	3	2.28-3.68
a, density-independance parameter of Ricker relation	77	63-81
b, density-dependance parameter of Ricker relation	$1.4 \cdot 10^{-5}$	10^{-5} - $1.8 \cdot 10^{-5}$
males proportion in offspring	0.5	0.2-0.8

We drew 4000 series of parameter values at random within the selected interval according to the normal distribution.

100 simulations were conducted, to take account of the deterministic character of the temperature, each simulation representing a possible future for the population over a period of twenty years. The criterion followed was the number of times that, over the last 10 generations (so as to be free of the initial conditions), the average catch over 3 or more years was less than 10 fish per day per fisherman.

III. Results and discussion of the sensitivity analysis

The histogram given at Figure 5 indicates three types of results for each value set: either the criterion is satisfied for each of the 100 simulations, or it is never satisfied, or it is satisfied in variable proportions. Out of the 4000 sets of parameters tested, the first type was encountered 500 times, the second 2500 times and the third 1000 times.

Our model simulates dynamics for the allis shad population that show very little sensitivity to environmental determinism (number of favourable days, i.e. where the temperature is higher than 10°C) and are very robust when faced with multiple factor changes.

IV. Discussion

At the moment, we are at the model behaviour analysis stage (Fournier and Warburton, 1989; Brown and Kulasiri, 1996). We need to establish whether, with its current architecture, it enables us to simulate the current dynamics of the population and understand the main factors controlling its mode of operation.

Our model seems heavily constrained by the stock-recruitment ratio; this may pose a problem for studying the sensitivity of the model with regard to its other parameters by masking their effects.

Furthermore, it remains to be seen whether the application conditions for the Ricker relationship will be verified; this relationship only applies if the spawning area remains

constant. For the allis shad, this condition is perhaps not satisfied, as the species is currently reclaiming its former spawning grounds in areas upstream of the weirs that can now be passed. However, rather than an extension, this phenomenon could result purely and simply in the spawning grounds moving further upstream.

Finer calibration is required for certain parameters; the lack of quantitative data or knowledge have forced us to make numerical hypotheses. Thus, in order to calculate the values for the proportion of mature individuals entering the estuary and survival rates, we have used the hypothesis of constant cohort strength. This hypothesis was supported by the supposed minimal fluctuation in the number of juveniles from one year to the next, estimated at around 4 million individuals. This observation has still to be confirmed by a finer analysis of the cohort strength using the method proposed by Guénette *et al.* (1994).

The construction of each part of the model is neither unique nor definitive. For instance, the "Dordogne-Garonne bifurcation" module is not strictly necessary if the stock-recruitment ratio between the two rivers is identical, but for the time being it allows us to describe the spatial distribution of the migration, its determinism and its impact on fishing catches.

The "determinism of the number of adults entering the estuary according to temperature" module has enabled us to express the interannual variability of the estimated number of adults using field data; it also describes the existence of preponderant limiting factors for the movement of migrants (Rochard, 1992, Prouzet *et al.*, 1994); it enables us to avoid having variable proportions of mature individuals from one cohort to another in our model, an aspect for which we have no data.

Furthermore, we will very quickly introduce into our "fishing catches" module a net selectivity parameter to take account of modifications of the population structure due to this particular mortality rate. Then we will also use a daily timescale for a finer analysis of the fish-fisherman relationship.

Finally, we used a "parsimony" hypothesis (equivalent distribution between the two rivers) for the choice of migration between the Dordogne and the Garonne. Since the CPUE indices observed in the Garonne are generally higher than those in the Dordogne, we propose testing the hypothesis of determinism linked to temperature or flow.

V. Conclusions

This model is the first ever constructed for the allis shad. It has enabled us to highlight gaps in our knowledge about survival rates, maturity rates by age group, the determinism of migration at the bifurcation, the fish-fisherman relationship and the stock-recruitment ratio. We have been able to increase our knowledge about the determinism of entry into the estuary, the structure and characteristics of adult spawners and losses through fishing. Furthermore, the model has provided a basis for discussion about the fishing process. Allis shad fishing in the Gironde-Garonne-dordogne watershed presents an interesting opportunity for the application of halieutic models to a migratory species.

The model could be used in a "prediction of stock from recruitment" version, which would free us of the stock-recruitment ratio which has not so far been validated. This type of model would then, on the basis of a number of juveniles estimated by sampling over 5 years from $n-7$ to $n-3$, make it possible to predict the number of individuals (3 to 7 years old) returning to the estuary as mature adults in year n .

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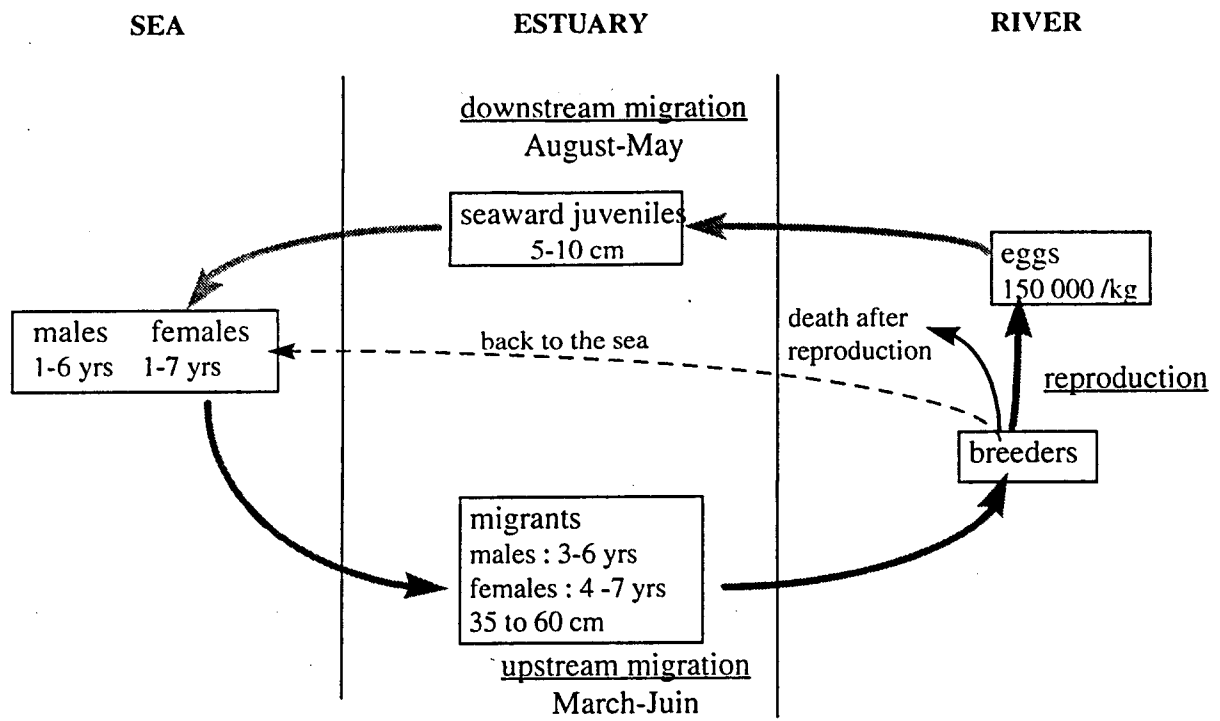


Figure 1 . The ecological cycle of the allis shad

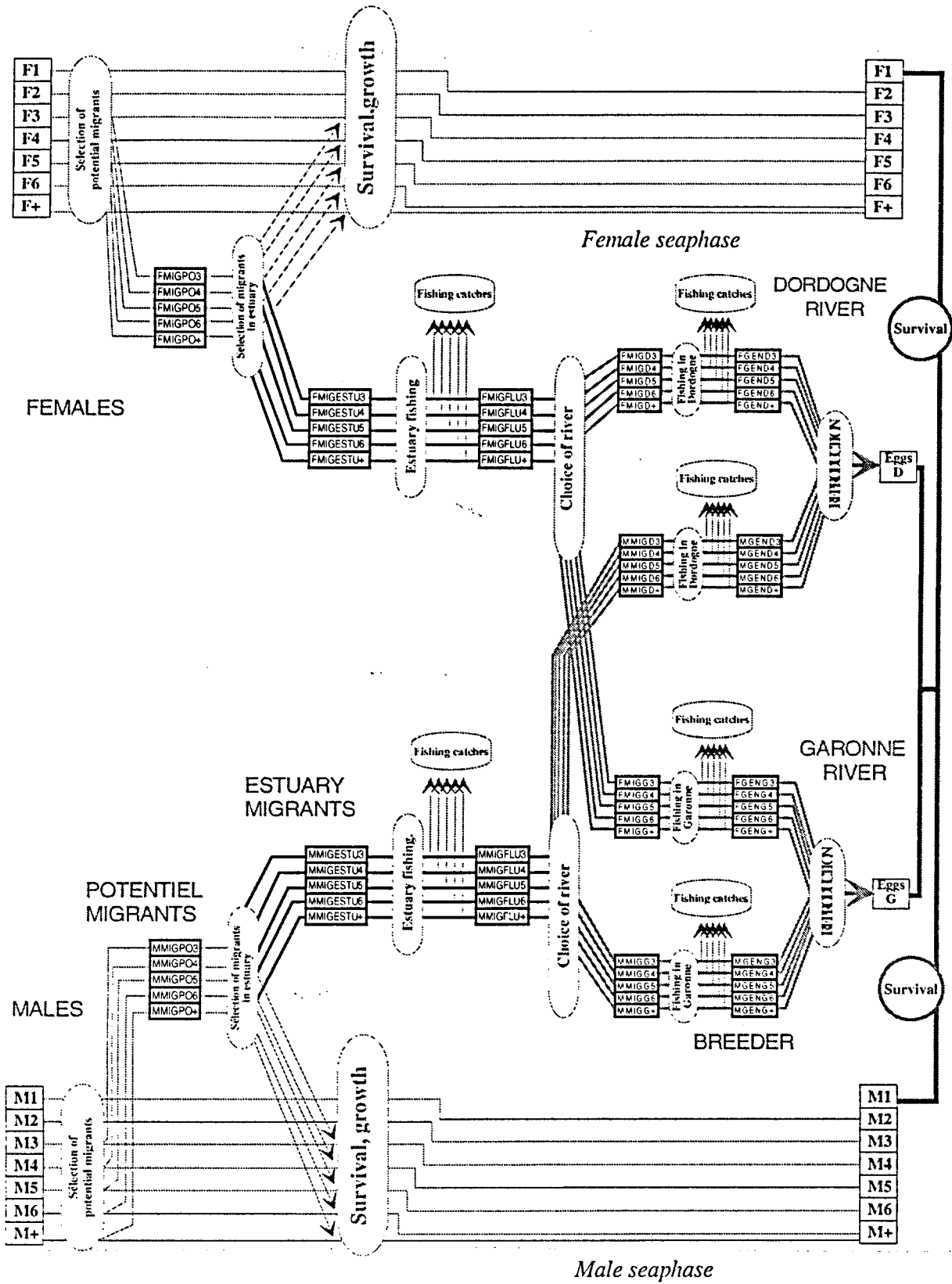


Figure 2 : Diagram of the model of the dynamics of the population of allis shad in the Gironde-Garonne-Dordogne watershed.

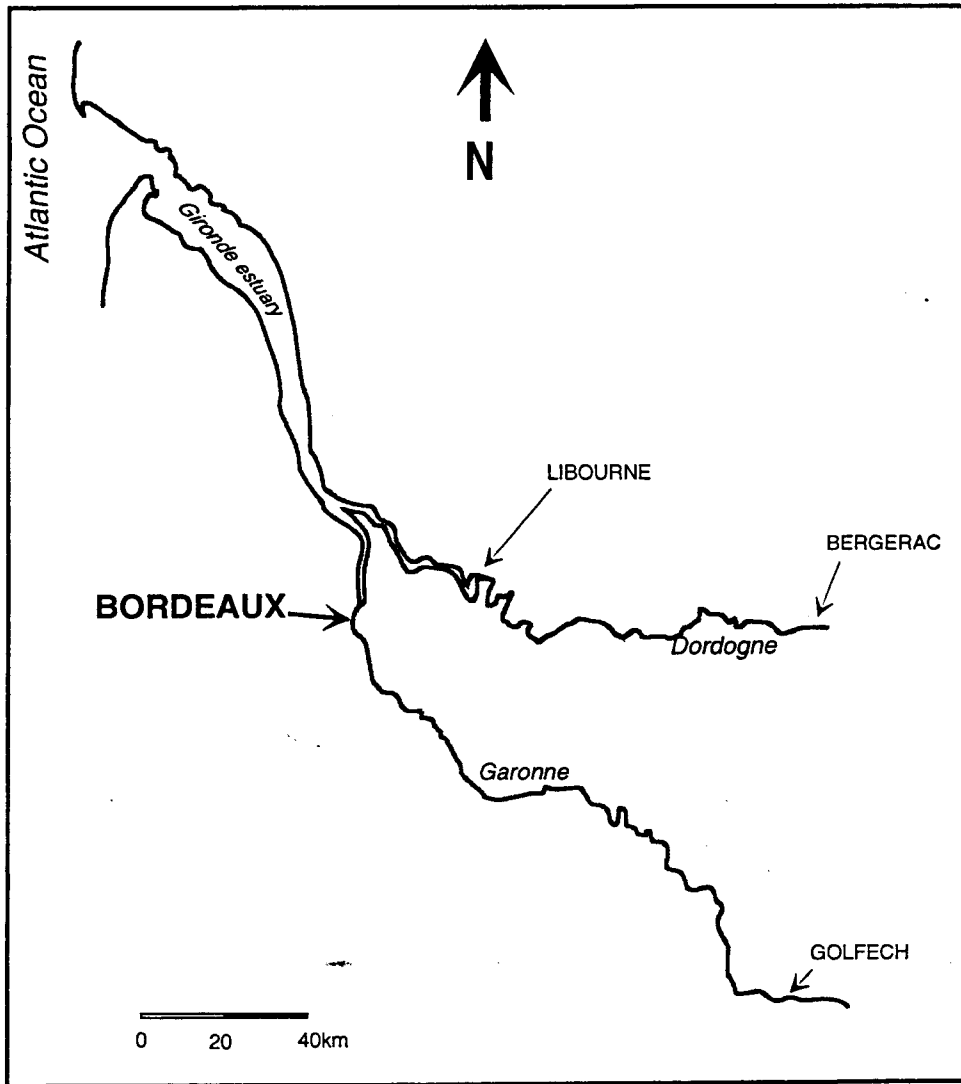


Figure 3 : Map of the Gironde-Garonne-Dordogne watershed

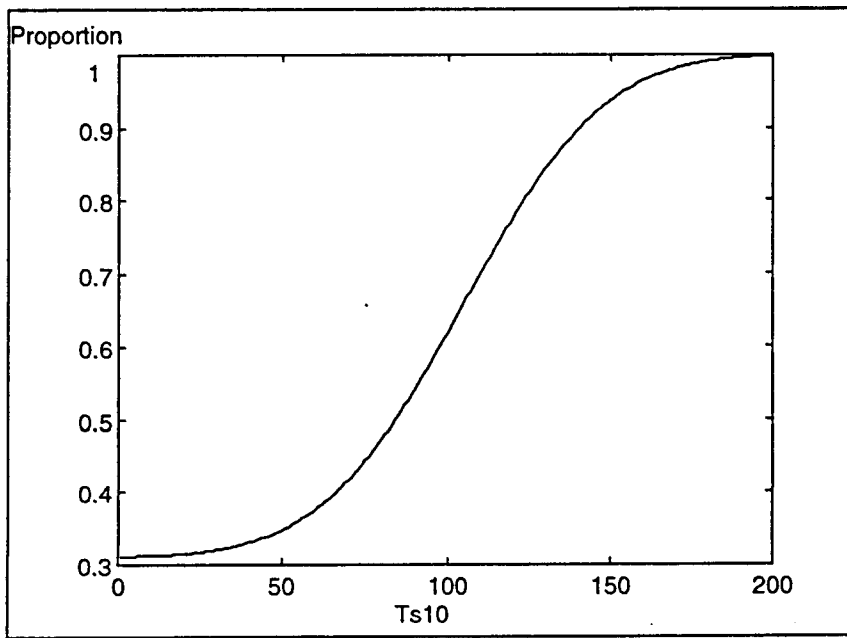


Figure 4 : Proportion of individuals entering the estuary to spawn according to Ts10

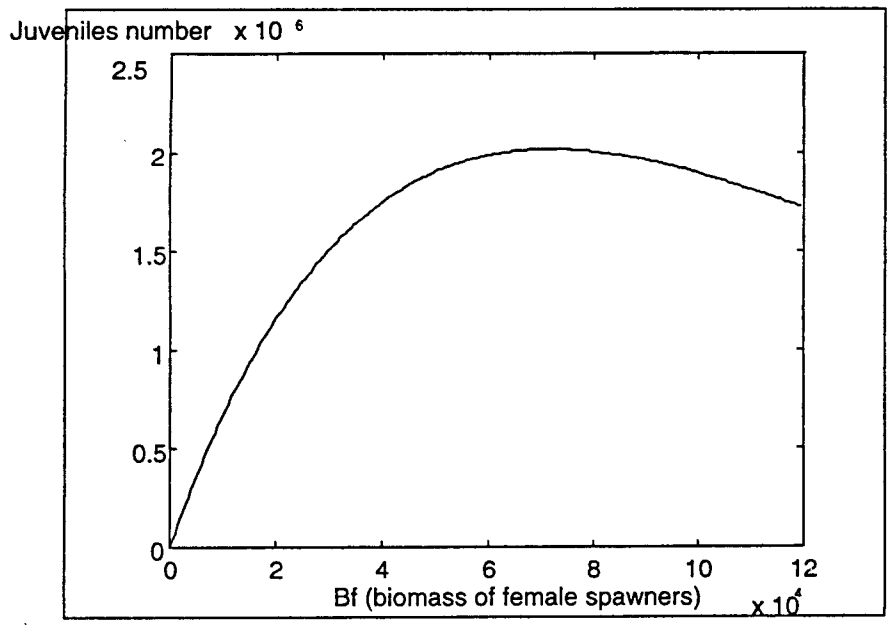


Figure 5 : Ricker curve

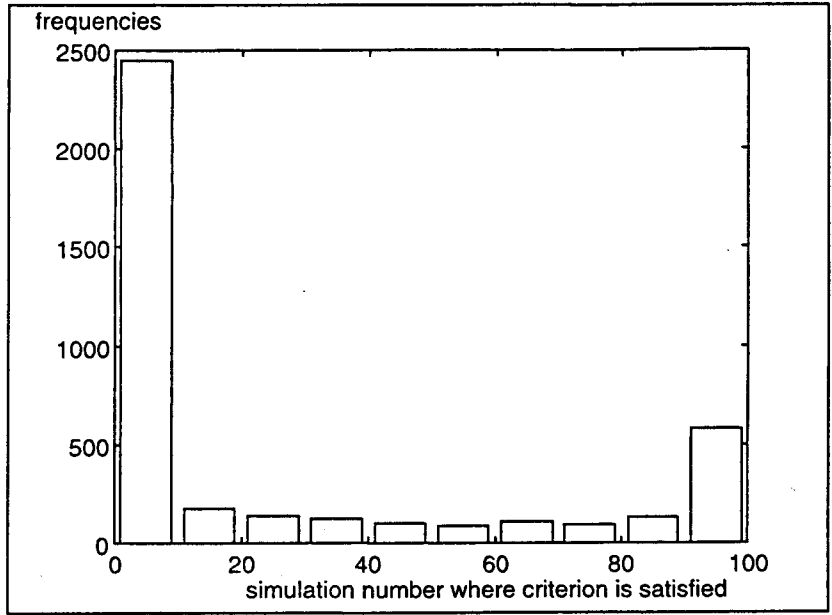


Figure 6 : Histogram showing the results of simulations for the sensitivity analysis method