Age Dependent Fecundity and the Dynamics of a Density-Dependent Population Model

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Abstract—The Ricker Stock-Recruitment (SR) relationship is one of the most common mathematical models used in fishery science. Without age-structure, this model is a first-order difference equation that shares with other and similar nonlinear models complicated behaviors, including chaotic ones. As many animal populations have demographic characteristics that differ with age, the importance of considering age-structure within population dynamics models may be critical. Introducing age-structure in the Ricker model considerably complicates the behavior of the population dynamics due to a great sensitivity to life-history parameters. The goal of this study is to explore some of those behaviors. A discrete self-regenerating and age-structured model, based on the Ricker SR relationship, is applied to small pelagic fish's species. As any synthetic reproductive function is not defined, the classical Leslie matrix notation is not used. Consequently, the exploration of the dynamic behaviors of the model is performed by numerical simulations with associated graphical tools (attractors and bifurcation diagrams). The main result of this study deals with the distribution among age classes of the "reproductive potential per recruit." This notion includes three basic life-history parameters: the natural mortality rate, the vector of mean weight and the vector of relative degree of fecundity. We focus on the effects of increasing the degrees of fecundity with age, in particular when it results in the uniformity of the reproductive potential's distribution among spawner's age classes. Thus, each adult age class brings the same contribution—in term of eggs laid—to the reproductive process. Such variation in age-dispersion of the reproductive potential of fish seems to have a dramatic power of stabilization on the population in the sense that chaotic behavior disappears. More numerical simulations are needed to explore the demographic consequences of age-dispersion of the reproductive potential, as recent trends in ecology suggest that ecological stability may not be a necessary condition to characterize evolutionary stability.

1. INTRODUCTION

One dominant theme in ecology is density-dependence, as it introduces stability and resilience in population dynamics. The fish Stock-Recruitment (SR) models attempt to describe the quantity

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of recruitment that is produced by the parental stock. The SR relationship proposed by Ricker [1] in 1954 has the following mathematical formulation:

$$R = \alpha.S.e^{-\beta.S},\qquad(1)$$

where

R is the number of recruits for a given year.

S is the parental egg production.

α is the density-independent probability of survival from egg to age 1.

β is the coefficient of density-dependent mortality.

This formulation produces a sharp decline of the right-hand limb of the curve (Figure 1). This feature expresses that the reproductive efficiency (the number of recruits produced per spawning fish) is decreasing at a higher rate for high values, because of the existence of density-dependent "compensatory" mechanisms. For population biologists, the curvilinear nature of the Ricker SR curve is one of the major properties of the population dynamics process in the sense that it is assumed to ensure resilience in stocks. Yet a striking relation between the magnitude of recruitment and spawning stock is rarely reflected in the body of fisherie's data [2]. All the same, some good fitting examples may be found in clupeoids [3,4]. Rothschild [2] stressed the point that there can be so little evidence for a relation of recruitment to parent stock when the very existence of such a relationship is so critical to population stability. Koslow [5] suggested that this paradox may come from the fact that the concept of a simple deterministic SR relationship does not appear applicable to organisms with high fecundities, such as teleosts. Despite some skepticism about the relevance of integrating SR relationships in the context of fish population dynamics, it is important to fully understand the properties of the Ricker's model, as it remains widely considered as a potential management tool [6].
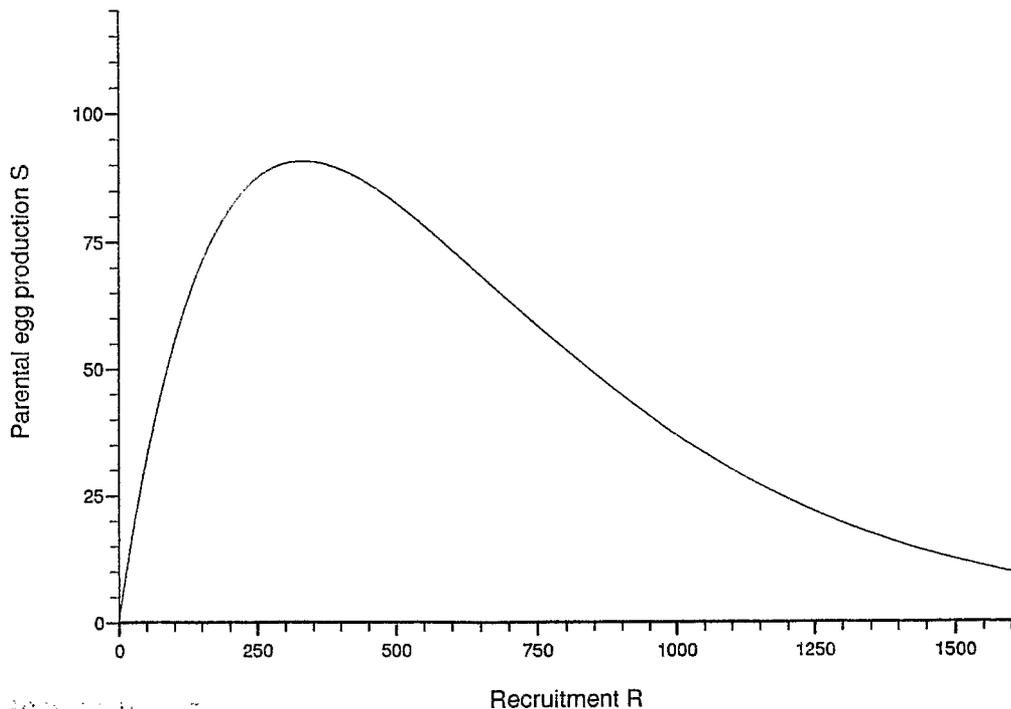

Figure 1. The Ricker [1] stock-recruitment curve, plotted here with $\alpha = 0.74$ and $\beta = 0.003$.

The simplest form of the model, assuming nonoverlapping generations, exhibits chaotic behaviors. This particularity, mentioned by Ricker in 1954, is now quite well understood and its mathematical properties have been widely discussed [7–12]. The effects of introducing age-structure into models of first order difference equations are most often measured by using the classical matrix-representation introduced by Leslie [13,14]. The matrix-notation is useful to study the stability of the equilibrium that is governed by the eigenvalues of the matrix (for a synthesis, see [15]). Many studies consider models that allow for the interaction of density-dependence and age-structure, some of them concerning fishery science [16–20]. Levin and Goodyear [20] discussed the stability of the Ricker model regarding the age-dispersion of reproduction. In their study, the life-history of the population is encapsulated in a "reproductive function." They noted that the frequency distribution of this reproductive function among mature age classes influences the extent of the stability region. They also underlined that it would be desirable to find some qualitative characterization of the most stable reproductive potential's distribution. The "maximization" of this distribution—in terms of stability effects on the dynamics—poses unsolved questions with potential biological interpretation, but so far, it remains difficult to explicitly analyze them. The present approach is based on this consideration, and aims to contribute to a better understanding of this puzzling question. First, a self-regenerating analytical model (described in the next section) based on the Ricker SR relationship is built for populations with overlapping generations. This model is somewhat different from previous works as the reproductive function that encapsulates the life-history strategy of a species (which is essential for the matrix notation) is split into basic parameters. Without matrix notation, analytical study of the model is not conceivable. Computer simulations and associated graphical tools may constitute a solution for going out of this deadlock [21]. They allow us to characterize some qualitative features of the model's dynamic behaviors that are presented in Section 3. In particular, we focus on different ways of sharing out the same reproductive potential among the mature age classes according to variations in relative degree of fecundity. It produces features that are analyzed and that sustain a general discussion about their biological interpretation that is presented in Section 4.

2. MODEL AND EXPLORATORY APPROACH

A classical structural self-regenerating model, distinguishing a recruited phase—simply described by an exponential model—and the Ricker SR relationship will be used.

Recruited Phase

The exponential model takes the year as a step in time. All the life-history parameters are supposed to be constant in time. It is assumed that there is no sexual dimorphism in demographic traits, so the model is reduced to females, and that the eggs are laid at the beginning of the year. The number of age classes (that is the life span) is denoted nc, and the age of a fish will be pointed by the index i. The abundance of age class i at the beginning of a year t is denoted $N_{i(t)}$. The individual weight is grouped in the vector $\mathbf{W}$, and W_i is the mean weight of an animal of age i. In the same way, the relative degree of fecundity of an i year-old fish is denoted a_i, a being called vector of relative fecundity.

For biologists, fecundity is mainly viewed as a measurement of the reproductive ability. It is possible to refer to more or less direct estimations, from the number of eggs able to be laid, to the spawning biomass, that is the biomass of adult fish. However, evidence suggests that egg production is not directly proportional to spawning stock biomass. The use of the spawning stock biomass as a proxy for egg production may thus introduce a bias in studies of SR biology [22]. But here, if it is acknowledged that there is no depensatory mechanism before the eggs are laid (increasing the effect of a decreasing spawning biomass on the recruitment), it is possible to reduce $N_{i(t)}.W_i.a_i$ to the number of eggs laid by class i at the beginning of year t [23,24]. The

parental egg production, denoted S, will therefore be given for a year t by:

$$S_{(t)} = \sum_{i=1}^{nc} N_{i(t)}.W_i.a_i. \tag{2}$$

From one year t to the next $t+1$, a fraction of the individuals of age class i dies, the other part joins the age class $i+1$. Using an exponential model, and if M is the natural mortality rate, the number of individuals that survives at time $t+1$ will be:

$$N_{i+1(t+1)} = N_{i(t)}.e^{-M}. \tag{3}$$

Stock-Recruitment Relationship

It is assumed that young fish are recruited when they are one year old. The Ricker relationship is then:

$$R_{(t+1)} = \alpha.S_{(t)}.e^{-\beta.S_{(t)}} = N_{1(t+1)}, \tag{4}$$

where the recruitment at a year $t+1$ is the number of the 1-year-old fish joining the population. Each age class number can be deduced from a single recruitment: it is the total number of survivors of a cohort. Combining relations (3) and (4), it comes:

$$N_{i(t)} = R_{(t-i+1)}.e^{-(i-1).M}. \tag{5}$$

The relationship given by replacing $N_{i(t)}$ in equation (2) allows us to calculate the parental egg production directly from the previous recruitments:

$$S_{(t)} = \sum_{i=1}^{nc} R_{(t-i+1)}.e^{-(i-1).M}.W_i.a_i. \tag{6}$$

When the dynamics converges to a stable fixed point, both recruitment and parental egg production become constant, so:

$$S = \Gamma.R \text{ where } \Gamma = \sum_{i=1}^{nc} e^{-(i-1).M}.W_i.a_i. \tag{7}$$

Γ, called the coefficient of reproductive potential per recruit, corresponds to the average number of eggs laid by one female during one breeding season. $\Gamma_i = e^{-(i-1).M}.W_i.a_i$, defined as the contribution that age class i brings to this potential, stands for the average number of eggs laid by a i year-old female.

Basic Analytical Properties—Usefulness of Graphical Tools

Mathematical aspects of the model's dynamics for a population of nonoverlapping generations are similar, apart from the notations, to those discussed by several authors in the middle of the seventies [11–16]. Briefly, if $\ln(\alpha.\Gamma) > 0$, (6) always possesses a nontrivial equilibrium that is a stable fixed point provided

$$\alpha.\Gamma < e^2. \tag{8}$$

Beyond the threshold $\alpha.\Gamma = e^2$, the stable equilibrium point becomes unstable and the dynamic behavior of the model "bifurcates" into a succession of very different regimes that can be displayed using graphical tools.

Bifurcation diagram

The effects of parameter's variation on existence and stability properties of steady states in equation such as the Ricker SR relationship are often represented on a bifurcation diagram. This is a powerful tool that allows to sum up the different dynamic behaviors of the model along an X-axis for a range of the key-parameter values (here the product $\alpha.\Gamma$). Y-axis represents the magnitude of steady state of the equation (here S, the parental egg production). The same scale for all the bifurcation diagrams is used: $\alpha.\Gamma$ increases from 1 to 20 on the horizontal axis, and for the vertical axis, S varies from 0 to 9000. For each value of the product $\alpha.\Gamma$, the model is run long enough for it to converge to its dynamic regime, and then the next 100 values of the total egg production S are plotted.

Attractor diagram

For a given value of $\alpha.\Gamma$, it is possible to visualize the behavior of the model using another phase plan, displaying the dynamic trajectories of the runs by plotting $S_{(t+1)}$ versus $S_{(t)}$. Those trajectories help to identify the type of attractor governing the dynamics of the model. An attractor is an object that attracts initial conditions from a region around it called the basin of attraction [25]. Trajectories that start off on the attractor remain on it forever; trajectories initially off the attractor approach it in time to an arbitrary degree of closeness [26]. An attractor is either a fixed point or a cycle (with entire or nonentire periods) or neither of the two. In that particular case, it is called a "strange attractor."

Simulation Principles

Some mathematical properties of the model will be explored by running simulations of "fictitious" populations. To work with more realistic life-history parameters for each species, some constraints like "sigmoid-shaped" growth for vector $\mathbf{W}$ were used. The natural mortality rate M was linked to the life span nc, making the exponential decrease of the numbers comparable whatever the life span of the simulated species is. This is expressed by the relation:

$$M = \frac{\ln(100)}{nc}. \tag{9}$$

By this relation, it is assumed that the number of the last age class equals 1% of the 1-year-old's number (the recruitment). The relative degree of fecundity's coefficients a_i are equal to zero for all the immature age classes.

For populations with overlapping generations, the product $\alpha.\Gamma$ represents the basic parameter of the dynamics. For any species, Γ is fixed by the life-history parameters. α will then vary from $1/\Gamma$ up to $20/\Gamma$. To explore model's sensitivity to variations in life-history parameters, we have defined several "life-tables" (regrouped in Table 1), each one representing a fictitious fish species.

3. SIMULATIONS OF MULTIPLE-AGE SPAWNING POPULATIONS

Introducing Example: From Nonoverlapping to Overlapping Generations

The bifurcation diagram standing for the basic case of nonoverlapping generations is represented on Figure 2 (see Table 1a: the life-history parameters of the corresponding species denoted species a). Beyond the first bifurcation threshold, a new stable cycle of period 2 arises. Then, for increasing values of the product $\alpha.\Gamma$, this period-two cycle grows in amplitude but remains stable until a new threshold of $\alpha.\Gamma$ from where, by a succession of pitchfork bifurcations, stable harmonics of period $2n$ occur. Finally a "chaotic" regime, in which cycles of arbitrary period and

Table 1. Tables for 11 simulated sets of life-history parameters values, from Table 1a to Table 1k.

Table 1a. $M = 4.6$, $nc = 1$, $\Gamma = 5.00$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	10	0.5	1

Table 1b. $M = 2.3$, $nc = 2$, $\Gamma = 8.26$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	20	0.02	0.05
2	80	0.98	0.95

Table 1c. $M = 1.54$, $nc = 3$, $\Gamma = 6.13$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	10	0	0
2	40	0.5	0.7
3	80	0.5	0.3

Table 1d. $M = 1.54$, $nc = 3$, $\Gamma = 6.13$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	10	0	0
2	40	0.3572	0.5
3	80	0.8330	0.5

Table 1e. $M = 1.54$, $nc = 3$, $\Gamma = 6.13$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	10	0	0
2	40	0.3536	0.495
3	80	0.8414	0.505

Table 1f. $M = 1.15$, $nc = 4$, $\Gamma = 7.22$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	10	0	0
2	40	0.1900	$\dfrac{1}{3}$
3	80	0.3000	$\dfrac{1}{3}$
4	100	0.7580	$\dfrac{1}{3}$

Table 1g. $M = 0.77$, $nc = 6$, $\Gamma = 6.00$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	5	0	0
2	15	0	0
3	35	0.2000	$\dfrac{1}{4}$
4	70	0.2160	$\dfrac{1}{4}$
5	100	0.3265	$\dfrac{1}{4}$
6	110	0.6410	$\dfrac{1}{4}$

Table 1h. $M = 0.66$, $nc = 7$, $\Gamma = 10.00$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	5	0	0
2	15	0	0
3	40	0.1872	$\dfrac{1}{5}$
4	75	0.1931	$\dfrac{1}{5}$
5	110	0.2548	$\dfrac{1}{5}$
6	130	0.4171	$\dfrac{1}{5}$
7	140	0.7494	$\dfrac{1}{5}$

even totally aperiodic but bounded population fluctuations can occur. This diagram is similar to the one related to the logistic equation that was first described by May in 1976 [13]. As a first step, a very small perturbation to the basic nonoverlapping generations' model is added by splitting the reproduction process into two age classes. A species (species b) living three years is simulated. The maturity begins during the second year, just after the recruitment. The youngest age class contributes hardly to the spawning process: Γ_1 represents only 5% of the eggs laid each breeding season. while Γ_2 represents 95% of this total (see Table 1b). The corresponding bifurcation diagram (Figure 3) shows something like a superimposition of a set of new values on the classic bifurcation diagram represented on Figure 2. The first bifurcation arises for a value of $\alpha.\Gamma$ slightly greater than e^2. A set of attractor diagrams included on Figure 4 help to identify the

Table 1 (Continued). Tables for 11 simulated sets of life-history parameters values, from Table 1a to Table 1k.

Table 1i. $M = 0.51$, $nc = 9$, $\Gamma = 12.00$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	5	0	0
2	15	0	0
3	30	0	0
4	50	0.1847	$\dfrac{1}{6}$
5	80	0.1923	$\dfrac{1}{6}$
6	120	0.2135	$\dfrac{1}{6}$
7	160	0.2666	$\dfrac{1}{6}$
8	180	0.3946	$\dfrac{1}{6}$
9	190	0.6226	$\dfrac{1}{6}$

Table 1j. $M = 0.46$, $nc = 10$, $\Gamma = 14.00$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	5	0	0
2	15	0	0
3	30	0	0
4	50	0.1590	$\dfrac{1}{7}$
5	80	0.1574	$\dfrac{1}{7}$
6	120	0.1662	$\dfrac{1}{7}$
7	160	0.1975	$\dfrac{1}{7}$
8	180	0.2781	$\dfrac{1}{7}$
9	190	0.4173	$\dfrac{1}{7}$
10	195	0.6441	$\dfrac{1}{7}$

Table 1k. $M = 0.38$, $nc = 12$, $\Gamma = 18.37$.

i	W_i	a_i	$\dfrac{\Gamma_i}{\Gamma}$
1	5	0	0
2	10	0	0
3	20	0	0
4	40	0	0
5	70	0.1500	$\dfrac{1}{8}$
6	110	0.1396	$\dfrac{1}{8}$
7	150	0.1497	$\dfrac{1}{8}$
8	170	0.1931	$\dfrac{1}{8}$
9	180	0.2667	$\dfrac{1}{8}$
10	187	0.3754	$\dfrac{1}{8}$
11	190	0.5403	$\dfrac{1}{8}$
12	190	0.7899	$\dfrac{1}{8}$

different dynamic regimes. Beyond the first birfurcation, there is a range of key-parameter $\alpha.\Gamma$ values for which the attractor is a limit cycle of nonentire period (case $\alpha.\Gamma = 8.5$ on Figure 4a). Then it goes through a period 4 cycle, and then the period is doubling (the period equals 8 for $\alpha.\Gamma = 15$, Figure 4b). From those 8 points emerge 8 strange attractors ($\alpha.\Gamma = 15.5$, Figure 4c) that grow when larger value of $\alpha.\Gamma$ are used (Figure 4d).

This first example suggests that the dynamics may be very sensitive to the reproductive strategy of the species. In the next paragraph, some more detailed explorations of the effects of sharing out the reproductive process into several age classes are undertaken.
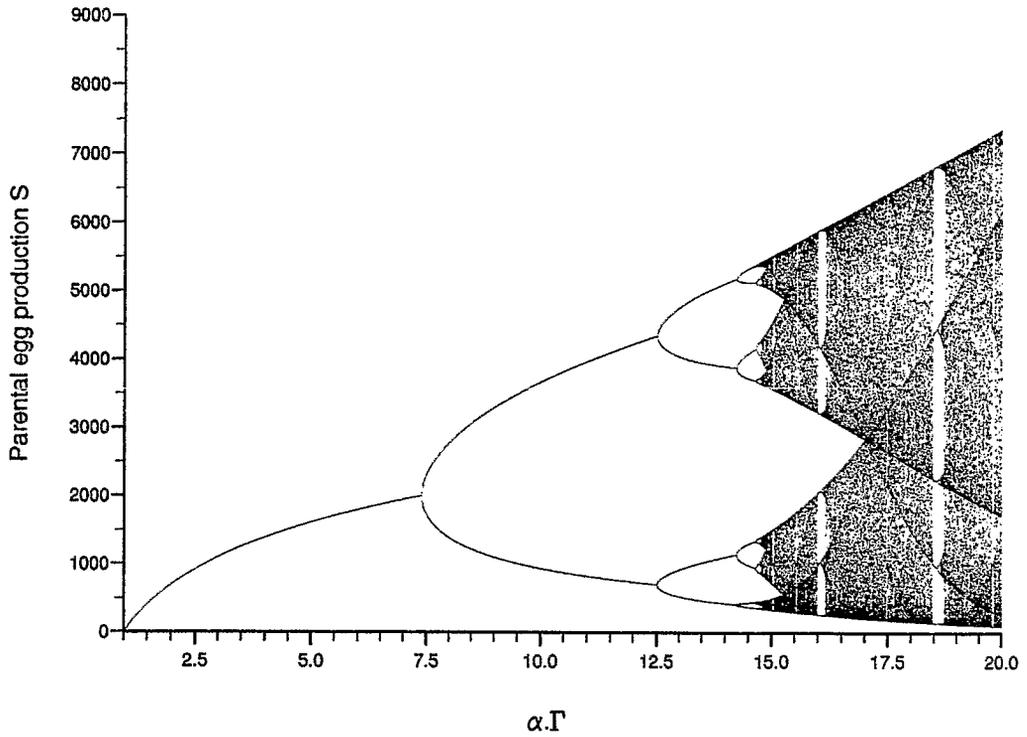
Figure 2. Bifurcation diagram corresponding to the dynamics of a population with nonoverlapping generations (see Table 1a).
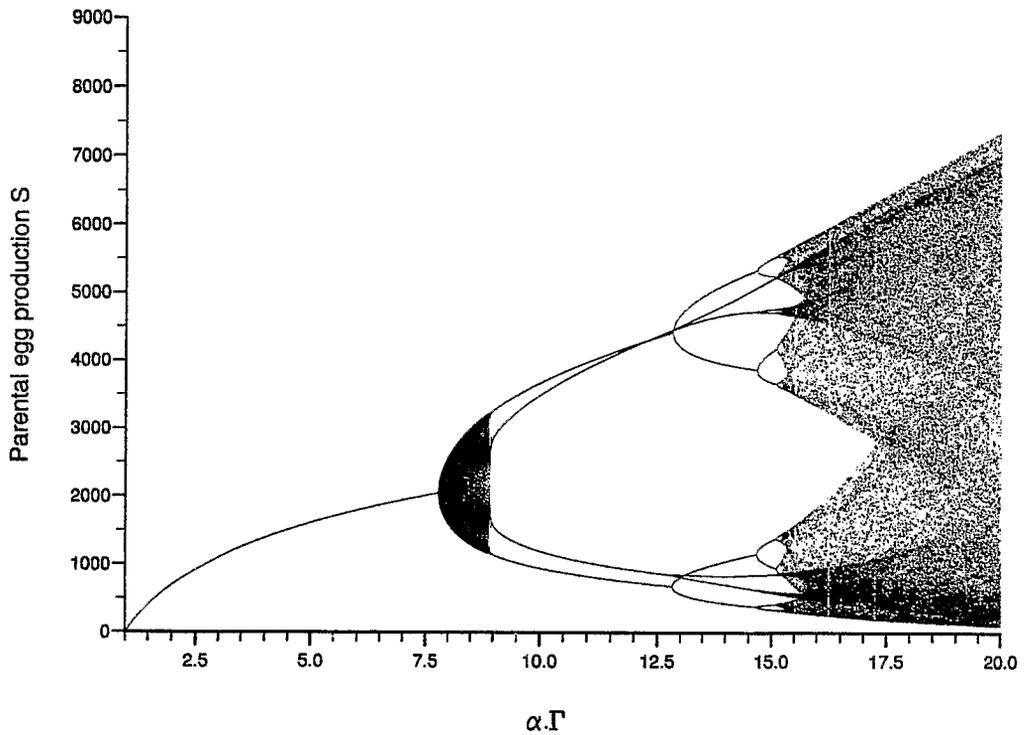

Figure 3. Bifurcation diagram corresponding to the dynamics of a population with two adult age classes, the first one laying 5% of the annual amount of eggs and the second one 95% (see Table 1b).

(a) $\alpha.\Gamma = 8.5$

(b) $\alpha.\Gamma = 15$

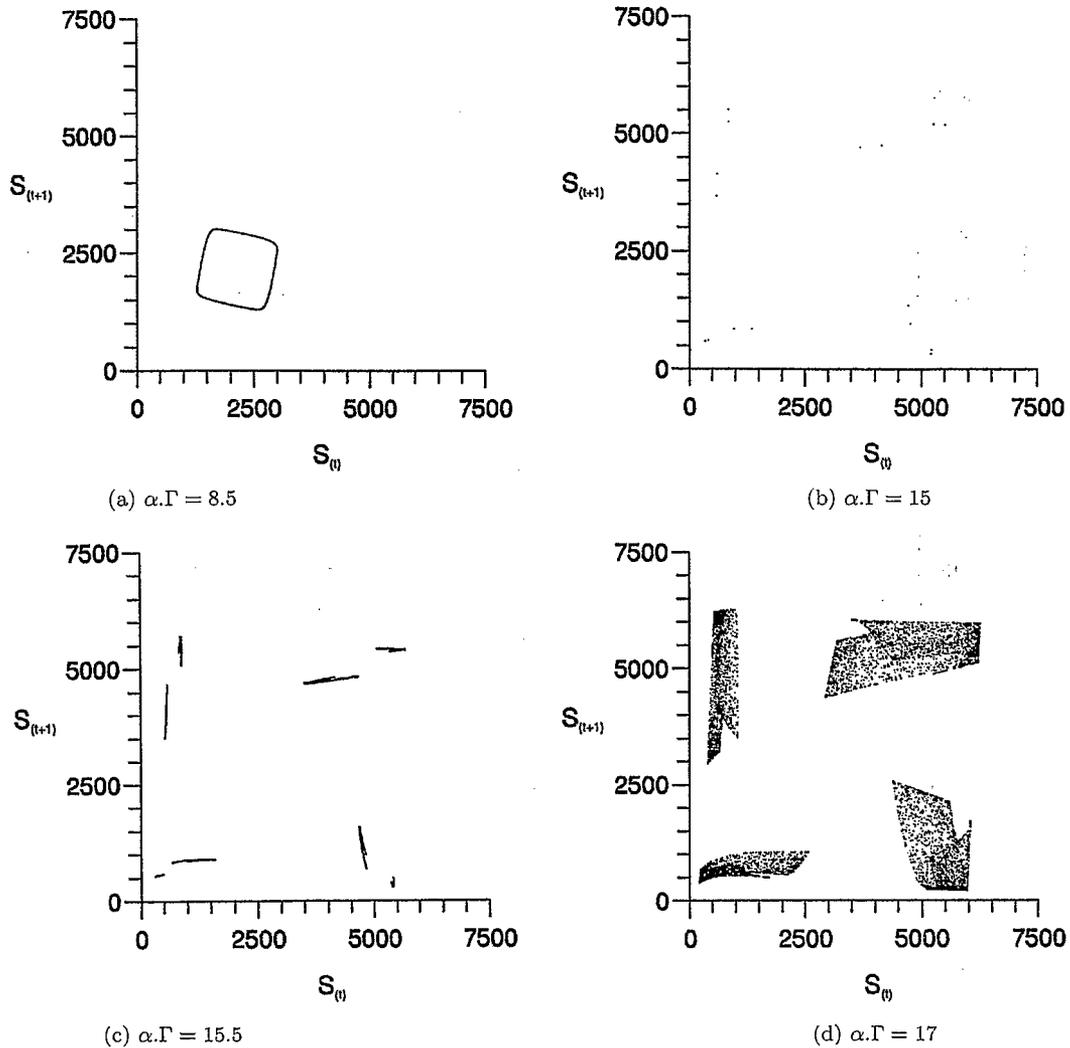(c) $\alpha.\Gamma = 15.5$

(d) $\alpha.\Gamma = 17$

Figure 4. Attractors governing the dynamics of a population with two adult age classes, the first one laying 5% of the annual amount of eggs and the second one 95% (see Table 1b). 4 attractors are drawn at relevant levels of key parameter.

Dynamic Behavior Characterization of the Overlapping Generations' Model

The dynamics of a species c living 4 years was simulated, the fish becomes mature at 2 and each adult age class has the same relative degree of fecundity (see Table 1c). The contribution of the two cohorts of spawners is less thrown off balance: Γ_2 represents 70% of the reproductive potential and Γ_3 30%. A roughly similar pattern appears on the corresponding bifurcation diagram (Figure 5): for growing values of $\alpha.\Gamma$, the attractor is first a steady state point, then a limit cycle of nonentire period (see on Figure 6a the case $\alpha.\Gamma = 10$), then the limit cycle seems to lose its regular shape and some "high-presence" densities appear ($\alpha.\Gamma = 14$, Figure 6b). They lead to a period-9 cycle, then each of the 9 points becomes a limit cycle of nonentire period ($\alpha.\Gamma = 17$, Figure 6c), and finally each of them evolves in a strange attractor ($\alpha.\Gamma = 18.5$, Figure 6d).

Similar dynamic evolutions are obtained for species living longer: the first stable equilibrium seems to always give way to a nonentire-period limit cycle, that is chaos. Focusing on model sensitivity to variations in the age-dependent relative degree of fecundity, it will be shown that this characterization may become unsuitable in some particular case.
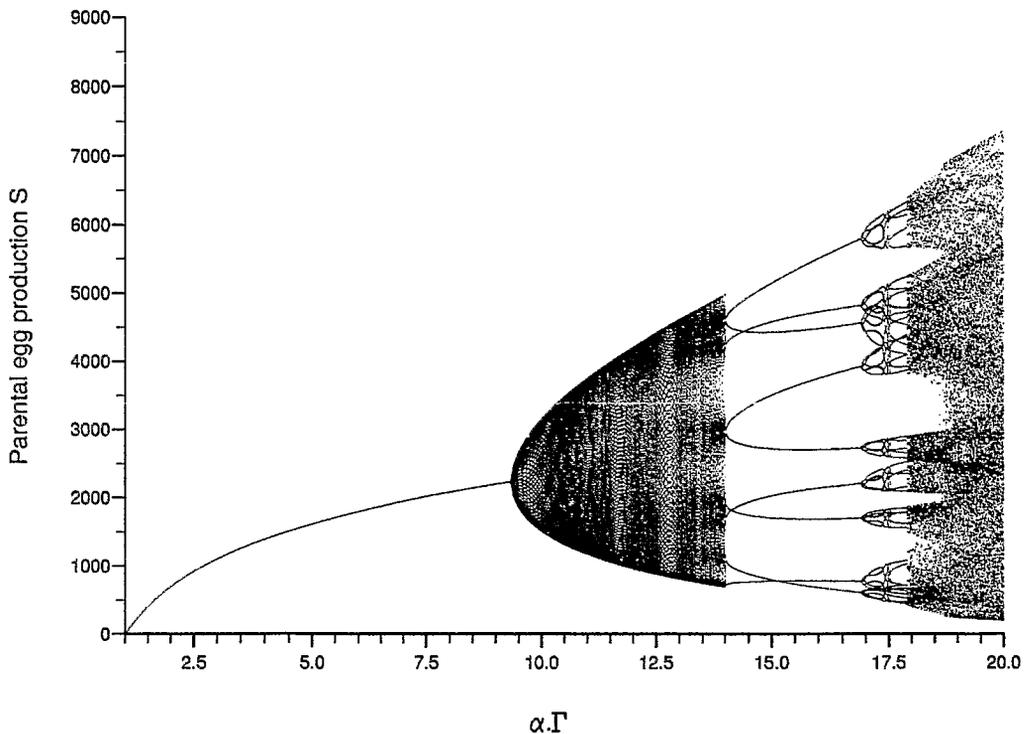
Figure 5 Bifurcation diagram corresponding to the dynamics of a population with two adult age classes, the first one laying 70% of the annual amount of eggs and the second one 30% (see Table 1c).

Model Sensitivity to the Age-Dependent Relative Degree of Fecundity

For any simulation, the synthetic parameter Γ summarizes the reproductive strategy of the species. Γ represents the average number of eggs laid per year by one female. α being fixed, does this synthetic parameter embrace the dynamic behavior of the model? Trying to answer this question, we simulate two very close species that have the same reproductive potential (Γ), being only different by the sharing out of this potential among the mature age classes. A possible way to do so is to modify the relative degree of fecundity with age. In particular, to make the distribution of the reproductive potential uniform, the relative degrees of fecundity are increased with age. In a way, this higher rate of fecundity offset the exponential decrease of the oldest fish's numbers. Thus, each of the adult age classes brings the same contribution—in term of eggs laid—to the reproductive process. Species d, that has exactly the same life-history parameters—except the relative degree of fecundity—than species c, is then simulated: it lives 4 years, has 2 mature age classes and the same reproductive potential $\Gamma = 6.13$, but this time, $\Gamma_2 = \Gamma_3 = \Gamma/2$ (see Table 1d). This particularity seems to give an extraordinary power of stabilization to the population dynamics (see the corresponding bifurcation diagram Figure 7). The phase of a limit cycle with nonentire period disappears, the dynamics passing directly from the regime governed by the steady state point to the entire period cycle regime. To test if the stability factor is really the uniformity of the reproductive potential distribution among mature age classes, a species e, with quite the same relative degrees of fecundities as species d, is defined. This time, Γ_2 represents 49.5% of the reproductive potential and Γ_3 50.5% (see Table 1e). The corresponding bifurcation diagram (Figure 8) tends toward the confirmation of this hypothesis: an arising phase of nonentire limit cycle appears again. This feature is not a numerical peculiarity as similar results for species with more mature age classes are obtained. Those results are summarized in Table 2. They are qualitatively the same from a species with 2 mature age classes (described above) up to a species with 8 mature age classes: in the case of a uniform reproductive potential distribution

(a) $\alpha.\Gamma = 10$

(b) $\alpha.\Gamma = 14$

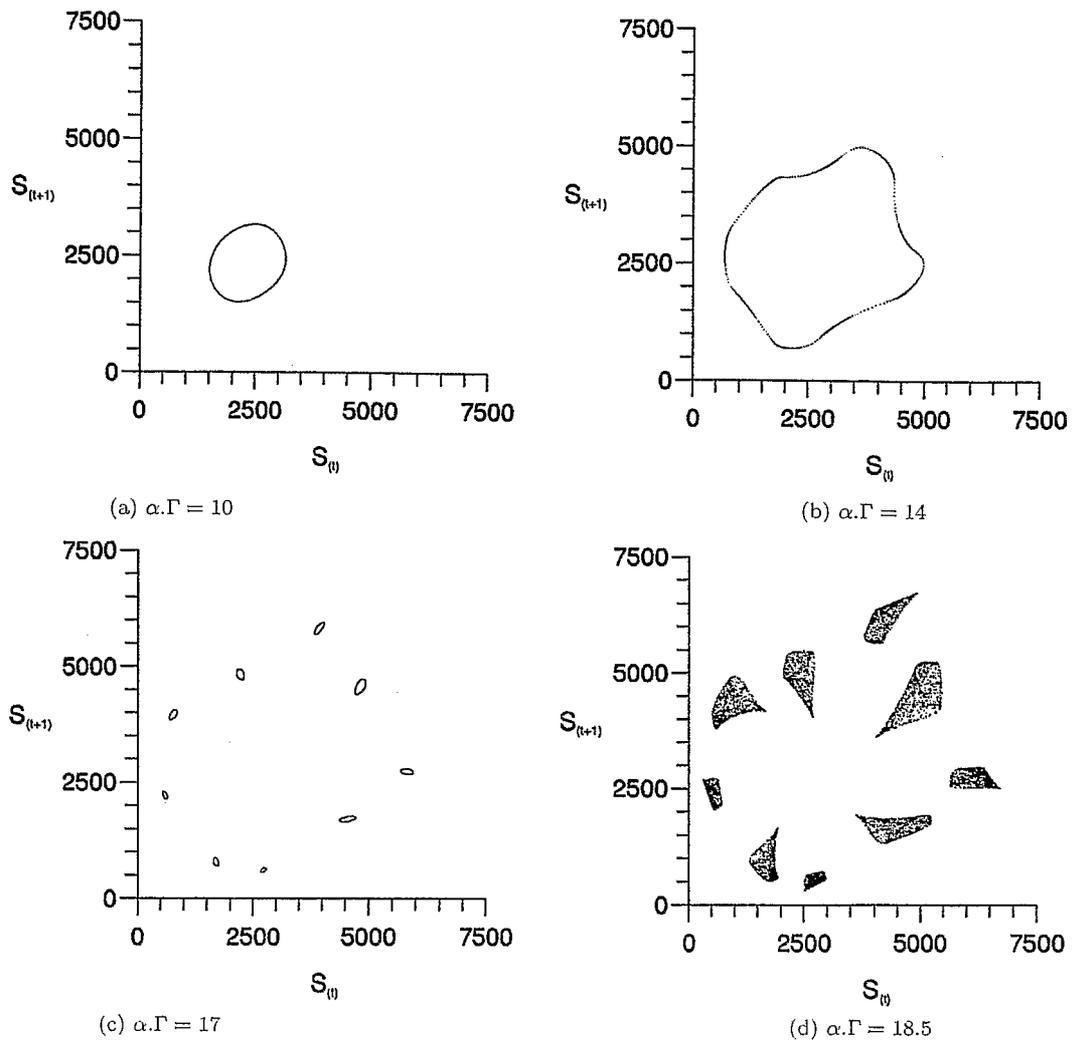(c) $\alpha.\Gamma = 17$

(d) $\alpha.\Gamma = 18.5$

Figure 6. Attractors governing the dynamics of a population with two adult age classes, the first one laying 70% of the annual amount of eggs and the second one 30% (see Table 1c). 4 attractors are drawn at relevant levels of key parameter.

Table 2. Summary of several bifurcation diagrams corresponding to populations with adult classes that bring the same contribution to the reproductive process. The $\alpha.\Gamma$ threshold at first bifurcation corresponds to the end of the stable fixed point's area.

Life table number	Number of adult age classes	$\alpha.\Gamma$ threshold at first bifurcation	chaotic area's disappearance	limit cycle period
1d	2	9.37	Yes	5 then 3
1f	3	12.14	Yes	6 then 3
1g	4	10.86	Yes	9 then 5
1h	5	12.68	Yes	10 then 6
1i	6	11.49	Yes	13 then 7
1j	7	12.83	Yes	14
1k	8	11.83	Yes	17

among adult age classes, the chaotic behavior disappears. This impressive property is related to an increase of fecundity with age that gives the same reproductive importance to all the mature age classes. In the next section, those results are placed in a biological perspective.
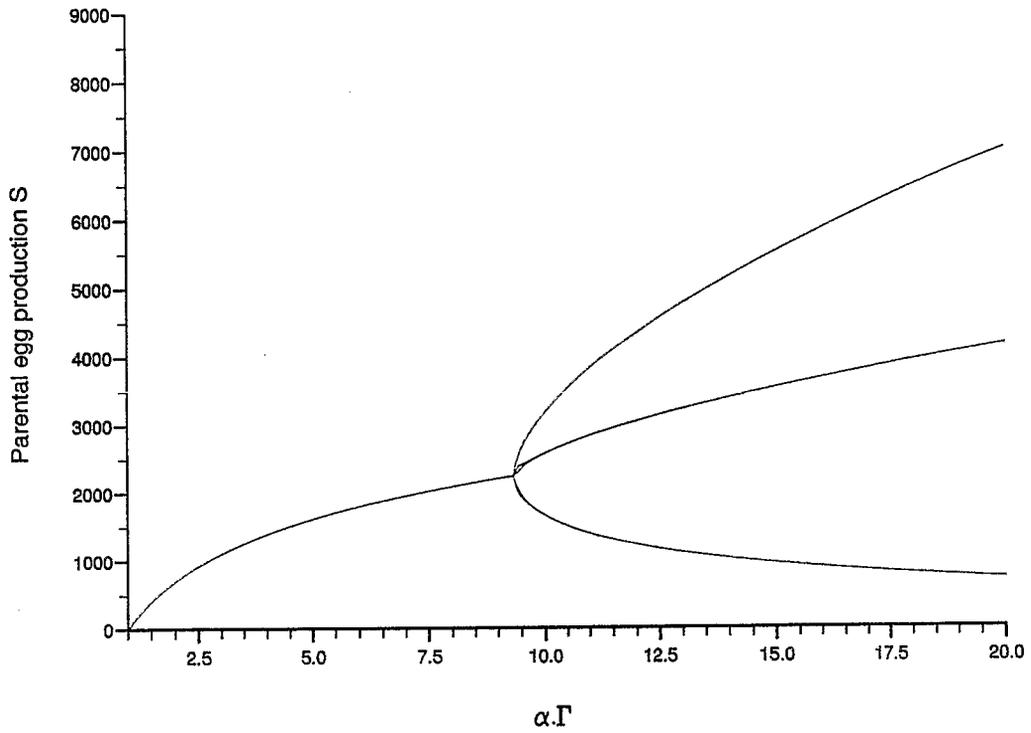
Figure 7. Bifurcation diagram corresponding to the dynamics of a population with two adult age classes, both laying 50% of the annual amount of eggs (see Table 1d).
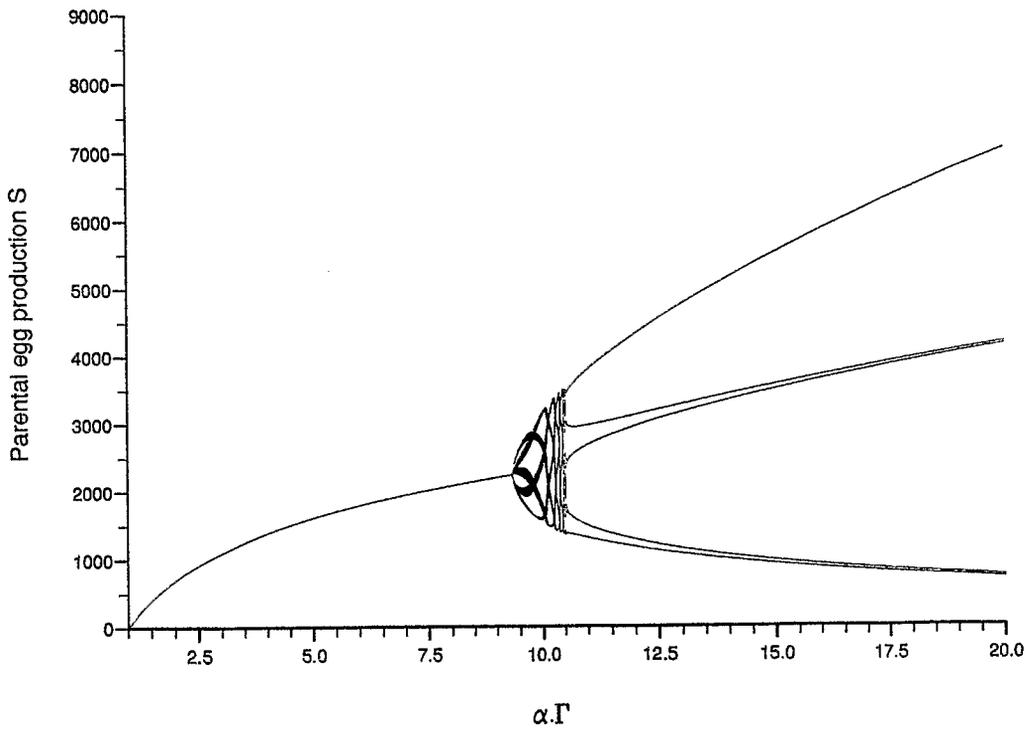

Figure 8. Bifurcation diagram corresponding to the dynamics of a population with two adult age classes, the first one laying 49.5% of the annual amount of eggs and the second one 50.5% (see Table 1e).

4. DISCUSSION

The Ricker SR relationship is frequently used in fisheries and includes a strong density dependence effect at high stock levels. It was combined with an analytical simulation model in order to explore the dynamics of a self-regenerating model with different age-structured populations. The distribution of the fecundity among age classes leads to chaotic dynamics. However when considering the same reproductive importance for all the mature age-classes, this can be reached by increasing the relative degree of fecundity with age, it has a dramatic power of stabilization as chaotic behavior disappears. In the wild, the total annual fecundity was found to be heavily age-dependent. For example, off California, the northern anchovy (*Engraulis mordax*) females that are 4+ year-old produce nearly 5 times as many eggs per unit of weight as 1 year-olds [27]. The importance of the age-specific fecundity is of greater significance for population models than previously thought. Stability versus instability in natural population is a central debate in ecology [28,29]. Recent trends in ecology suggest that stability may not be a necessary condition to characterize evolutionary stability [30], and chaos theory provides a new way for exploring the complex behavior of nonlinear equations like the Ricker's model [31]. More numerical simulations and exploratory analysis are needed to better understand the demographic consequences of life-history parameters like the age-dispersion of the reproductive potential. A collaborative effort between mathematician and ecologist will provide some resolution and certainly some new insights in understanding nonlinear dynamics and drastic changes that appear in biological systems.

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