On the stock-recruitment relationships in fish population models*

SUZANNE TOUZEAU[1] AND JEAN-LUC GOUZÉ[1]

[1] *INRIA – Comore*
BP 93 – 06 902 Sophia Antipolis Cedex – France
E-mail: `Jean-Luc.Gouze@sophia.inria.fr`

The framework of this article is modelling applied to fisheries. It aims at relating some classical stock-recruitment curves to a dynamic structured model, consisting of the adults stages of the stock and a pre-recruits stage (i.e. eggs, larvae, juveniles). The main result is that no functional stock-recruitment relationship can be found, unless further restrictive assumptions are added to the model (slow-fast dynamics and uniformity). Among the curves thus obtained, is the Beverton–Holt curve, but not Ricker's.

Keywords: population dynamics, fishery, stage-structured model, stock-recruitment relationship.

1 Introduction

The use of population dynamics models is essential to provide assessment of the fish abundance and advice on management and strategies for the fisheries. Because the data on a fish population mainly concern the *stock*, i.e. the harvested fraction of the population, most studies concentrate on the evolution of the stock instead of looking at the entire life cycle.

There exist two different types of dynamic models to represent the stock: the global models and the structured models. In a global model, all the individuals are aggregated in a single variable. Whereas in a structured model, the evolution of each stage or age class is described separately [1, 2]. In this paper, we will use the second approach.

Thus we need to express the corresponding recruitment, i.e. the input in the exploitable phase [3]. Some models consider a constant or purely stochastic recruitment. This means taking an exogenous function as input and assessing that the environmental fluctuations have a predominant influence. Recruitments of this type are called open loop inputs. Indeed, there are examples where the recruitment is actually governed by the environment (cases with strong food limitations or limitations on the spawning habitat). However, it is generally difficult to deny any connection between the spawners, the subsequent juveniles and the recruitment. Other models therefore use a stock-recruitment

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relationship, that is an equation linking the recruitment to the number or biomass of mature females, i.e. the spawning stock. This allows the loop to be closed and respects the biological bonds between consecutive generations (cf. figure 1).

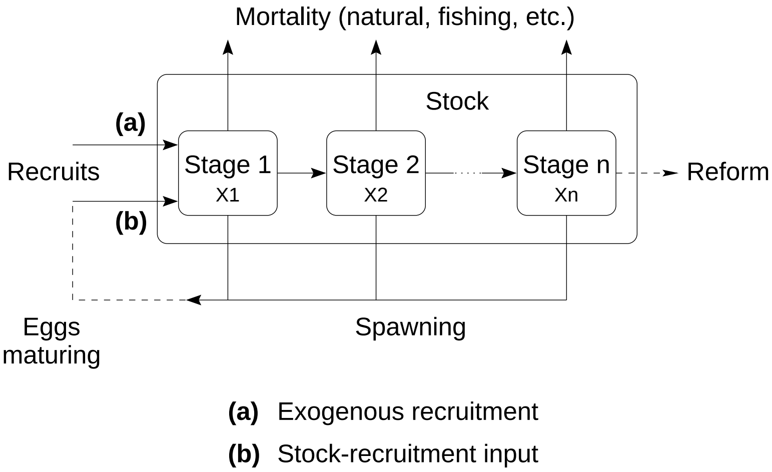
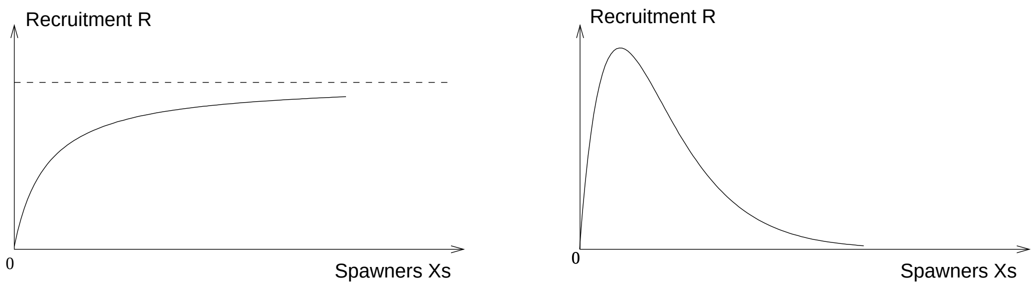


Figure 1: Representation of a stage structured stock.

Stock-recruitment relations are commonly used because they are practical and synthetic: they don't require data concerning the stages preceding recruitment, data which are rarely available. The two classical relations have been established by Beverton–Holt [4] and Ricker [5] (cf. figure 2). They both derive from the integration of an ordinary differential equation representing the dynamics of the juveniles over a small time period. This process is described by Clark [1, pp217–218,229–230] and more briefly by Hilborn and Walters [3, pp257–261].



(a) Beverton and Holt $R = \frac{aX_s}{b+X_s}$ (b) Ricker $R = X_s e^{a(1-X_s/b)}$

Figure 2: Classical stock-recruitment relationships.

Unfortunately, comparisons between these models and the experimental data are often disappointing (cf. figure 3) [3, pp 241–296]. A reason for the disagreement between the curves and the data may be the environment: physical or biological parameters, as well as interactions with other species, may influence the growth of larvae [7]. Furthermore, data are not perfect. The link between the spawning stock and its offspring may then be

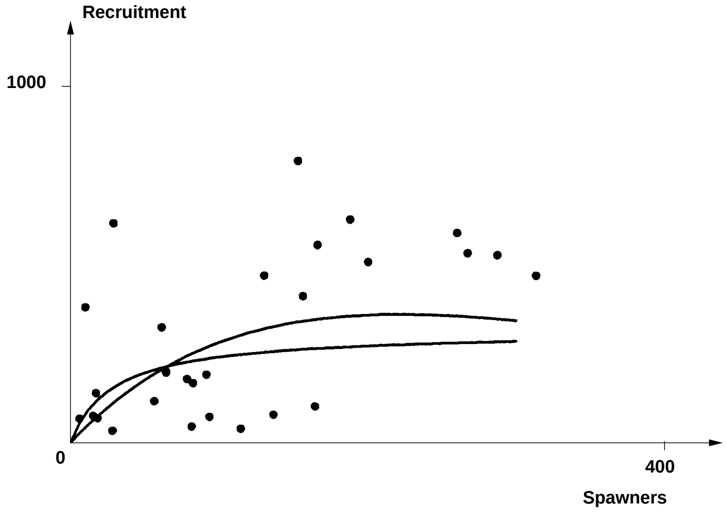


Figure 3: Example of a Ricker and a Beverton and Holt curve fitting Icelandic summer spawning herring data (data from Jakobsson 1980 [6]); adapted from [3, p276].

hidden, which leads to the "stock-recruitment paradox" [8] where no empiric relation is observed.

In fact there is a relation between the spawning stock, related to the number of eggs, and the recruits, corresponding to the eggs that have survived and grown old and big enough to enter the stock. But a stock-recruitment relation might not be able to express it, because there is an evolution between those two stages.

In order to understand better the phenomena involved, it is necessary to introduce the pre-recruits (eggs, larvae, juveniles, etc.) in the model. Paulik studied the eggs and larvae stages in a static way [9]. Fisher examined the egg survival and the growth of larvae, and introduced these static functions in a discrete dynamic model [10].

To study the interactions between the juveniles and the stock, static approaches are not really appropriate. So we chose to add a pre-recruits stage to the stock model. The dynamics of this stage are defined by taking into account the hypotheses made by Ricker and Beverton–Holt to build their stock-recruitment relations. The model obtained is simple, with rough dynamics for the stock, but includes a more detailed and realistic approach of the juveniles dynamics. A concept of slow-fast dynamics, presented in the next section, is introduced to study the evolution of the system. The pre-recruits stage and the introduction of two time scales constitute the originality of the model.

We first present the model and its properties: positivity of the variables, equilibria and slow-fast dynamics. In the second section, we then try to relate it to the classical stock-recruitment relationships. We show that no stock-recruitment function can be extracted from the model, unless further restrictive assumptions are added. These results are discussed in the following section, and then more general conclusions are drawn.

2 Model and properties

The model we have built is a continuous time stage-structured model. It includes $(n+1)$ stages represented by their abundance, stage 0 being the pre-recruits stage as shown in figure 4. Each stage in the stock $(i = 1, \ldots, n)$ is characterized by its fecundity, mortality and predation rates. In addition, we will consider a constant fishing effort, included in the global mortality term. The mathematical formulation of the model is the following:

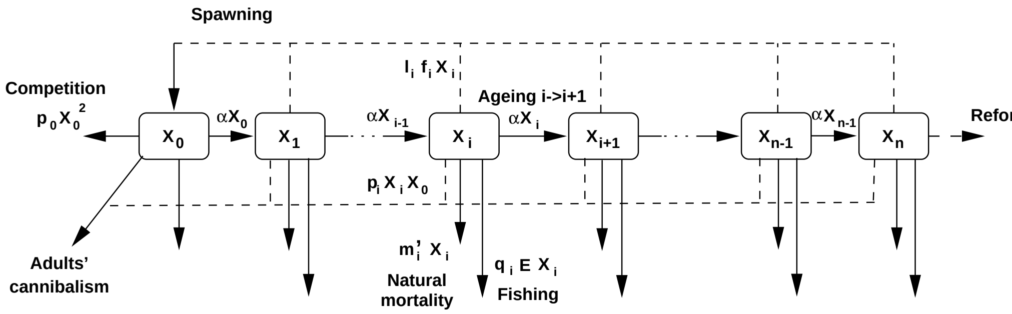


Figure 4: Structure of the model with a pre-recruits stage (1,2).

$$\dot{X}_0(t) = \underbrace{-\alpha X_0(t)}_{\text{ageing}\rightarrow 1} + \frac{1}{\varepsilon}\Big[\underbrace{-m_0 X_0(t)}_{\text{lin. mort.}} + \underbrace{\sum_{i=1}^{n} f_i l_i X_i(t)}_{\text{eggs } i\rightarrow 0} - \underbrace{\overset{[*]}{\sum_{i=1}^{n}} p_i X_i(t) X_0(t)}_{\text{predation of } i\rightarrow 0} - \underbrace{p_0 X_0(t)^2}_{\text{competition}}\Big] \quad (1)$$

$$\dot{X}_i(t) = \underbrace{\alpha X_{i-1}(t)}_{\text{ageing } i-1\rightarrow i} - \underbrace{\alpha X_i(t)}_{\text{ageing } i\rightarrow i+1} - \underbrace{m_i X_i(t)}_{\text{lin. mort.}} \qquad (i = 1, \ldots, n) \quad (2)$$

m_i:	linear mortality rate
α :	linear ageing coefficient
p_0 :	juvenile competition parameter
f_i :	fecundity rate of class i
l_i :	reproductive rate of class i
p_i :	predation rate of class i on class 0
ε :	$\varepsilon = 1$ (one time scale) or $0 < \varepsilon \ll 1$ (two time scales)

A continuous time modelling is seldom used for fisheries, but appears with parasitoids [11] or plankton [12, 13, 14, 15], etc. Its main inconvenience is the numerical spread due the ordinary differential equations it is composed of: a pulse of juveniles as initial condition will produce a small amount of adults instantaneously. It would be consequent if, for instance, our goal was to study the evolution of a cohort and its outbreak in each stage. However, our system represents the entire population with a spawning feedback (as opposed to a single cohort) and evolves away from the axes (stable non-zero equilibrium), so we can neglect this artefact. Furthermore, in order to observe the interactions between juveniles and adults, we need a small time step. So if we were using a discrete time modelling, we would have to implement a time step smaller than the stage duration, which would increase the number of variables. The results obtained would be quite similar with discrete or continuous time modelling, but the model is much simpler in the continuous case and the tools available more practical.

After a brief description of the model, its main properties are presented: positivity of the variables, analysis of the equilibria and introduction of the two time scales.

2.1 Description of the model

Each stage i is subject to "external" mortality, due to fishing or "natural" causes, i.e. anything except intra-specific effects. We assume this mortality rate to be linear, which means that the proportion of fish in class i dying from "external causes" per unit of time is independent of time (constant rates m_i). The ageing process is also assumed linear: the fish go in and out of each stage i ($i = 0, \ldots, n$), with a constant rate α. In this case, the rate doesn't depend on i. So the mean residence time in a stage ($\frac{1}{\alpha}$) is the same for all stages $i = 0, \ldots, n$. In other words we could consider the stages 0 to n to be age classes, though no cohort can be identified stepping from one class to another (continuous reproduction assumption).

The dynamics of class 0 are more complicated. From the very simple linear system described above, we add to the pre-recruits stage a spawning term and non-linear terms. The non-linearities are due to specific mortalities. They reflect the assumptions made by Ricker (cannibalism) and Beverton and Holt (competition among the juveniles) when elaborating their stock-recruitment models. The cannibalism term ($p_i X_i X_0$) is expressed as a Lotka-Volterra predation term between class i and class 0. The term ($p_0 X_0^2$) can be interpreted as an intra-stage competition for food and space in a limited environment.

The spawning term being related to the number of eggs, some assumptions have to be made on the laying of eggs. We will assume it to be continuous in time. This assumption seems reasonable, as the spawning season of a species is sometimes badly known. It may occur more than once a year or even during the whole year (case of the tropical seas, where there are almost no seasons). The total number of eggs introduced in the 0-stage is equal to the sum of the eggs produced by class i: ($f_i l_i X_i$) (per unit of time); where f_i represents the proportion of mature individuals in stage i and l_i the mean number of eggs produced by such an individual per unit of time .

When $\varepsilon \ll 1$, the terms in the square brackets $[*]$ in (1) evolve faster than the rest of the system. This slow-fast behaviour defines two time scales for the system. If $\varepsilon = 1$, the model is a classical differential system with a single time scale.

2.2 Positivity of the variables

This model makes no sense for negative values of X_i. The structure of the model however ensures that if the initial abundances are non-negative, they will remain non-negative in the course of time. For example, let us consider that at time t, the abundance of stage i: X_i, is zero and that the other abundances are non-negative. Its derivative, given by (2), is then:

$$\dot{X}_i(t) = \alpha X_{i-1}(t)$$

If $X_{i-1}(t) = 0$, as long as X_{i-1} remains zero, X_i will remain zero too. But if $X_{i-1}(t) > 0$, X_i increases and becomes positive. So at time $t + \delta t$ (δt being small), either X_i remains zero, or it is positive. In neither case it becomes negative.

2.3 Equilibria

The existence of a positive and stable equilibrium is necessary to avoid the extinction of the population. There is at least one trivial equilibrium: $X_0^* = X_1^* = X_2^* = \cdots = X_n^* = 0$. But it corresponds to an extinct population and is therefore not very interesting. A non-trivial equilibrium may exist under the following assumptions:

$$\left| \begin{array}{l} p_0 + p_1 + p_2 + \cdots + p_n \neq 0 \\ \sum_{i=1}^{n} f_i l_i \pi_i > \alpha\varepsilon + m_0 \\ \qquad \text{with: } \pi_i = \frac{\alpha^i}{\prod_{j=1}^{i}(\alpha + m_j)} \end{array} \right.$$

where the non-linear coefficients are the p_i $(i = 0, \ldots, n)$. In other words, if there is at least one non-linearity in the system and the spawning coefficient are big enough so as to avoid extinction, the following positive equilibrium occurs:

$$\left\{ \begin{array}{lcl} X_0^* & = & \frac{\sum_{i=1}^{n} l_i f_i \pi_i - m_0 - \alpha\varepsilon}{p_0 + \sum_{i=1}^{n} p_i \pi_i} \\ X_i^* & = & \pi_i X_0^* \end{array} \right.$$

Under further but not very restrictive assumptions [16], it is possible to prove the stability of this non-trivial equilibrium, locally as well as on a larger domain, which ensures the survival of the population. The zero equilibrium is then unstable.

2.4 Slow-fast dynamics hypothesis

When ε is small compared with 1 ($\varepsilon \ll 1$), two time scales coexist. The system can be considered as the superposition of the fast dynamics (1) and the slow one (2). The processes bounded to the juveniles, except the ageing in stage 1, are faster and bigger than those of the stock. This corresponds to the fact that the pre-recruits mortality is high, the competition and predation during a time unit are important and a large number of eggs is laid. Since the juveniles are more vulnerable than the adults and that the spawn is large, this assumption sounds reasonable. The behaviour of the system is then the following:

1. *Rapid phase:* First, the fast dynamics are predominant, so the fast state variable (X_0) hurries towards the so-called "slow surface" ($[*] = 0$). It corresponds to the equilibria of the subsystem (1), the stock variables X_i ($i \neq 0$) being fixed. The global positive equilibrium belongs to this surface.

2. *Slow phase:* Then there is a slow evolution in the neighbourhood of the slow surface, governed by the slow dynamics. A good approximation of this evolution is given by (2) and the equation of the slow surface:

$$\left[p_0 X_0(t)^2 + \left(m_0 + \sum_{i=1}^{n} p_i X_i(t) \right) X_0(t) - \sum_{i=1}^{n} f_i l_i X_i(t) \right] = 0 \tag{3}$$

The equation (3) gives $X_0(t)$ as an implicit function of the $X_i(t)$s. The pre-recruits stage is not static, but its evolution along time directly depends on the other stages. Because of the structure of the model, X_0 only appears in $\dot{X}_1$. So provided we know this equation (3), we only need to study the reduced linear system (2) (one dimension less), with a non-linear feedback input $X_0(t)$ on the first stage of the stock.

The mathematical background of these results is referred to as the *singular perturbation* field [17]. The validity of this approximation can be proved thanks to Tikhonov's theorem [16]. It allows the simplification of the initial system, reducing its dynamics of one dimension.

3 A stock-recruitment relationship?

From the model described above, we try to extract a stock-recruitment function and compare it with the reference forms. The recruitment is the input to the first class of the stock X_1. Remember that a stock-recruitment relationship links this input to the number of mature females, i.e. the spawning stock. So we need to represent the instantaneous recruitment:

$$R(t) = \alpha X_0(t)$$

as a function of the spawning stock at this same time:

$$X_s(t) = \sum_{i=1}^{n} f_i X_i(t)$$

Recruitment is said to be instantaneous here because it is a number per unit of time, i.e. an input flow.

We first take a simple numerical example showing that we cannot extract a single stock-recruitment function from this particular model, so we then try to refine our hypotheses in order to recover well known stock-recruitment shapes.

3.1 In general: no stock-recruitment function

For a given set of parameters (cf. table 1), we first run a few simulations so as to plot $R(t)$ as a function of $X_s(t)$. The choice of the parameters was made in order to get a realistic example. In particular, mortalities m_i are set to 0.2 for the stock but m_0 is bigger as the juveniles are more vulnerable than the adults. The fecundity rates are 0.5 or 0, which means that in mature stages, half of the fish are females ready to breed. The other coefficients just make sense. We chose a very simple scheme:

Class 0: juveniles.

Class 1: young immature adults; no reproduction, no cannibalism.

Classes 2,3,4: mature adults; same predation rate on class 0, same proportion of mature females but different reproductive rates ($l_2 < l_4 < l_3$).

For $\varepsilon = 0.01$, we can consider that there are two time scales. But the simulations are made with the complete system (1,2). All the curves we obtain, first rapidly go (fast

Table 1
Parameter values of the model (1,2), associated with the figures 5, 7 and 8.

	Pre-recruits	Stock			
Stage i	$i = 0$	$i = 1$	$i = 2$	$i = 3$	$i = 4$
m_i	0.5	0.2	0.2	0.2	0.2
p_i	0.2	0	0.1	0.1	0.1
f_i	–	0	0.5	0.5	0.5
l_i	–	0	10	20	15
α			0.8		
ε			0.01		

phase) towards a certain region of the graph, the slow surface, and then slowly evolve (slow phase) in this area. This is consistent with the slow-fast dynamics described in the previous section. The trajectories also tend towards a non-trivial equilibrium, which indicates its stability.

A typical example of the curves such obtained is shown in figure 5. They all are parameterized by time. The following points are made:

- The "stock-recruitment relationship" is not a mathematical function: a given spawning stock corresponds to several possible recruitments; $R = \varphi(X_s)$ is not defined in a unique way.
- It strongly depends on the initial conditions; several repartitions in the stock stages allow the same initial point on the (X_s, R), but lead to different evolution of the spawning stock and the recruitment.

This example demonstrates that it is generally impossible to extract a stock-recruitment function from the model with a pre-recruits stage.

N.B.: Figure 6 shows that even with $\varepsilon = 1$, the behaviour of the system is very close to the slow-fast dynamics described previously.

3.2 How can we find a stock-recruitment function?

The only way to extract a stock-recruitment function, in a strict mathematical sense, is to make the following very strong assumptions:

(i) very fast and significant pre-recruits dynamics ($\varepsilon \ll 1$);

(ii) for each $i \in \{1, \ldots, n\}$: $\left| \begin{array}{ll} \text{(Case a)} & f_i = f,\ l_i = l \text{ and } p_i = p; \\ \text{(Case b)} & f_i = l_i = p_i = 0; \end{array} \right.$

i.e. for a given age i, either the fecundity, reproductive and predation rates are zero (case b) or they take the common values f, l and p (case a). So we need to consider the evolution of the system in the slow phase only and the stock has to be separated in two superclasses: the pre-recruits interactive ages (a) and the neutral ages (b).

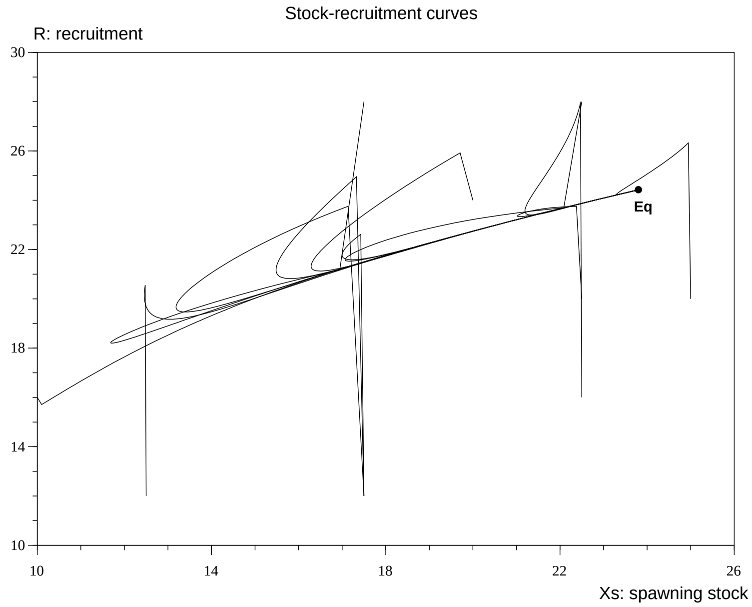


Figure 5: Stock-recruitment curves obtained with model (2,1) and the parameters of table 1. The trajectories projected on the stock-recruitment plane differ in their initial condition $X_i(0), i = 0, \ldots, n$. They all converge towards the positive equilibrium (**Eq**).

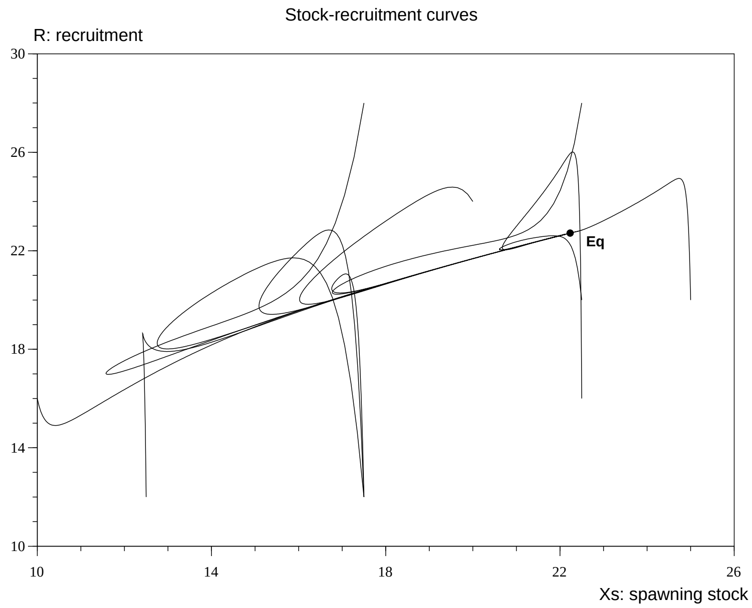


Figure 6: Stock-recruitment curves equivalent to those of figure 5, but obtained with $\varepsilon = 1$ (one time scale). The positive equilibrium (**Eq**) has therefore a slightly different value.

We assume that l and f are not zero, otherwise there is no breeding and the population becomes extinct. Depending on the values of p_0 and p, we can obtain different stock-recruitment forms.

1. If $p \neq 0$ and $p_0 = 0$, we get an exact representation of a Beverton and Holt's curve (cf. figure 2):
$$R = \frac{lX_s}{m_0 + \frac{p}{f}X_s}$$
We note that if $m_0 = 0$, there is constant recruitment.

2. If $p = 0$ and $p_0 \neq 0$, the recruitment doesn't saturate anymore. It is a square root-like increasing function.
$$R = \frac{\alpha}{2p_0}\left(-m_0 + \sqrt{m_0^2 + 4p_0 lX_s}\right)$$

3. If $p \neq 0$ and $p_0 \neq 0$, we obtain a curve which is similar to the Beverton and Holt's model: a strictly increasing and bounded curve.
$$R = \frac{\alpha}{2p_0}\left(-m_0 - pX_s/f + \sqrt{(m_0 + pX_s/f)^2 + 4p_0 lX_s}\right)$$

4. If $p = 0$ and $p_0 = 0$, pre-recruits are only submitted to linear mortality and the system becomes entirely linear, making the stock-recruitment relation linear as well.
$$R = \frac{\alpha l}{m_0}X_s$$

We will discuss these results and compare them with the classical shapes in the following section.

4 Discussion

4.1 Comments

Under the hypotheses related to our model, there is no functional stock-recruitment relationship. This doesn't mean there is no relationship at all between those two entities. Summarizing the juvenile part of the fish's life cycle, from the egg until the recruitment, which is what a stock-recruitment function does, actually implies strong uniformity assumptions. In our case, it requires two scales of time and almost reduces our stock to two groups of individuals:

Superclass a: The spawners who also predate their progeny ($l_i = l, f_i = f, p_i = p$).
Superclass b: The others who don't interact with the juveniles ($l_j = f_j = p_j = 0$).

The stages among the superclasses only differ in their mortality rates m_i. The simplest model would be composed of two or three stages: the pre-recruits, the mature adults and possibly an immature but recruited (i.e. susceptible of being caught) stage in between. Having more than $n = 2$ adult stages could introduce some heterogeneity among the matures or/and immatures thanks to the m_i rates; it could also allow fish to grow from an immature to a mature phase, and then again become immature.

We discuss below the different types of curve we obtain under these assumptions, in the same order as previously in subsection 3.2:

1. With *cannibalism and no competition*, we exactly obtain a Beverton and Holt's curve. These assumptions actually reflect the ones made by Ricker for his stock-recruitment model.

2. With *competition and no cannibalism*, i.e rather Beverton and Holt's hypotheses, there is no upper bound on the recruitment, which steadily increases with the size of the spawning stock. This doesn't correspond to any classical stock-recruitment curve.

3. With *competition and cannibalism*, the curve is similar to that of Beverton and Holt.

4. With *no competition and no cannibalism*, the relationship between spawning stock and recruitment is linear. This could correspond to unlimited habitat and food for the pre-recruits (no competition), and separate territories for the adults and the juveniles (no cannibalism).

In conclusion, we note that in order to obtain an increasing and bounded stock-recruitment relationship, we need to have cannibalism on the pre-recruits. The introduction of limitations on food or habitat only slows down the recruitment, but does not bound it. Besides, in none of the cases mentioned do we obtain a Ricker-like stock-recruitment curve (cf. figure 2). There is no way to find a decreasing recruitment for high values of the spawning stock from the pre-recruits modelling we chose.

We would like to point out that the perturbations due to the environment and their influences on the recruitment have been neglected in this model. But it is still possible to obtain an apparently "randomly" distributed pattern of stock-recruitment points (X_s, R), as shown in figure 7, proceeding from a deterministic time continuous model. To obtain this figure we did some measurements of the spawning stock and the recruitment at discrete times, for several simulations taken from figure 5.

Figure 7 does not show deterministic chaos as it sometimes happens in discrete or continuous dynamic models [18, 19]. But it corresponds to the projection of various trajectories, stemming from a "simple" almost linear system, on a particular plane. Figure 8 shows the evolution of the abundance of stage 2 versus time for some simulations used in figure 5. We note that these trajectories are not chaotic.

4.2 Extensions to the model

We intend to improve the model by adding a control term to the system and trying to adjust it on structured data. In order to integrate the fishing aspect in a more dynamic way, it is possible to introduce an external control on the mortality, in terms of a fishing effort $E(t)$, such that:

$$m_i = m'_i + q_i E(t)$$

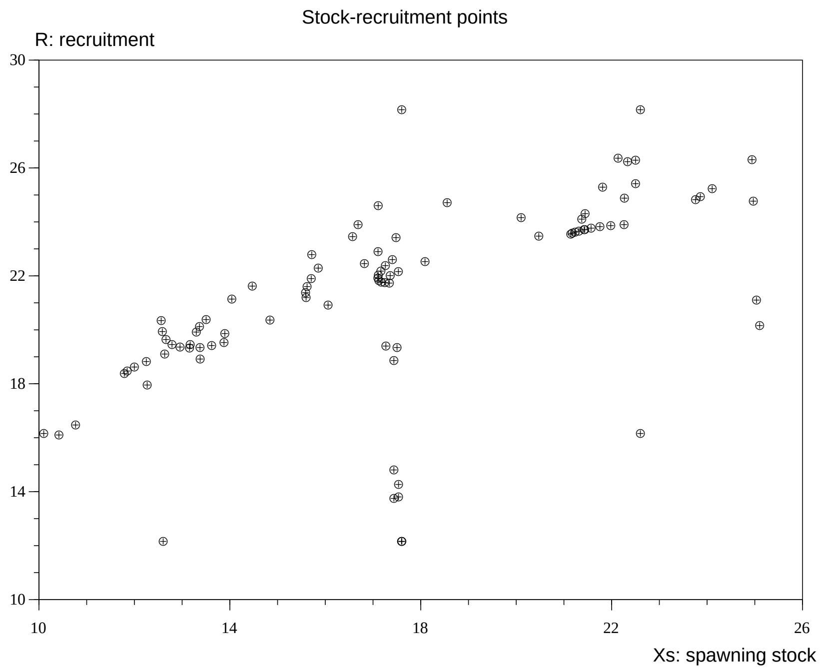


Figure 7: Stock-recruitment points obtained from figure 5.

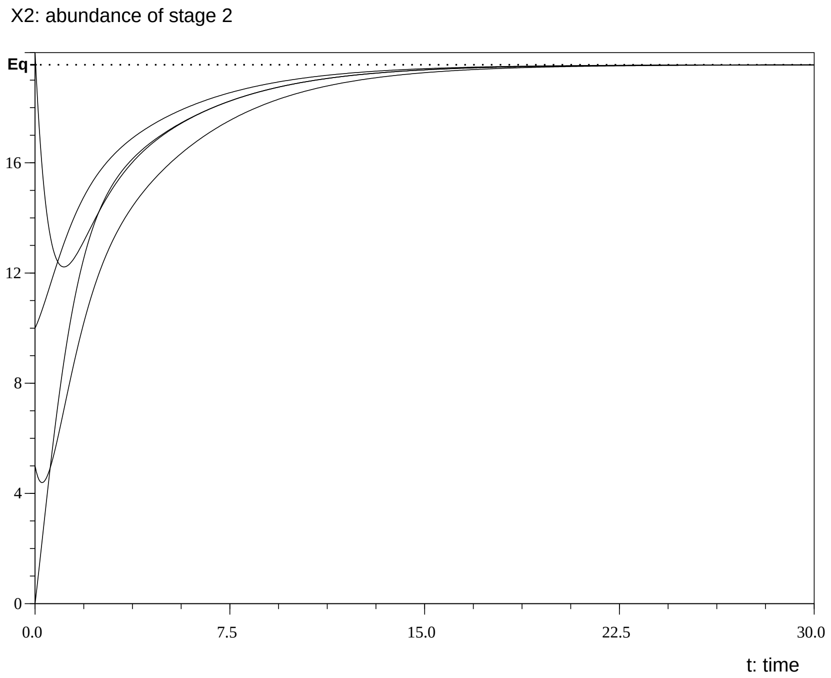


Figure 8: Abundance of stage 2 for some simulations used in figure 5.

where m_i' is the natural mortality rate and q_i the catchability of stage i.

Moreover, it would be straightforward to improve the model by introducing a seasonal effect on the spawning terms, by the means of an exogenous periodic variable, allowing the eggs to be laid only during a certain period of the year. Outside this period, there would be no entry in the pre-recruits stage 0.

5 Conclusion

We have developed a time continuous stage structured model of a harvested marine population. Unlike the usual models, the whole life cycle is represented, by the means of a pre-recruits stage (eggs, larvae and juveniles) added to the adults stages of the stock. The pre-recruits being particularly vulnerable, their mortality is more detailed (competition, cannibalism).

Such a model is not restricted to fisheries. It could be used for any aquatic or land population with sensitive first development stages. The addition of a control term on the mortality would suit harvested or harmful populations.

The assumptions made on the pre-recruits mortality stem from the hypotheses made by Ricker and Beverton–Holt for their stock-recruitment relationships. Anyhow, we have shown that generally we cannot extract a stock-recruitment function from the model with a pre-recruits stage. Such a relation is indeed a static summary of the juveniles development. This study proves that the heterogeneity of the spawning stock and the interactions between juveniles and adults may actively influence the recruitment, but cannot be expressed in a stock-recruitment function.

To conclude, we would like to stress the fact that a stage submitted to important interactions with other variables (e.g. other stages) should no be suppressed without further precautions. Indeed it may provoke a loss of generality. One should rather express the entire dynamic model and then study the possible simplifications.

Moreover, seemingly chaotic behaviour should be treated with care. The apparent randomness of distributed data may not only be caused by fluctuations due to a stochastic environment, but may result from a dimension reduction, as for instance the projection of deterministic trajectories in the stock-recruitment plane.

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