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A STUDY OF THE STABILITY OF SOME STOCKS DESCRIBED BY SELF-REGENERATING STOCHASTIC MODELS[1]

A. Laurec[2], A. Fonteneau[3], and C. Champagnat[4] †

INTRODUCTION

As Cushing (Gulland, 1977b) emphasizes, the integration of stock-recruitment relations in studies of population dynamics now appears to be more and more necessary. Therefore interest is moving from models simply describing the recruited phase towards self-regenerating models. Essentially the models used up to now have been deterministic.

However, one need only examine an experimental stock-recruitment diagram to become convinced that a strong random component exists. In addition, especially in connection with hydrological phenomena, the catchability of a number of stocks can fluctuate significantly from one year to another. These two domains appear to be the ones where the random dimension of the phenomena is most important. If we imagine the establishment of models aimed, *a posteriori*, at explaining the evolution of a stock, we can imagine a reduction in the significance of the random component by carefully examining the impact of hydrological factors and interspecific relations. Still, the random aspect remains important, at least with respect to hydrological factors as long as we are not able to predict hydrological phenomena, and thus, practically, climatic ones, in projecting the evolution of a stock in the future.

Therefore it is understandable that the integration of random components has aroused growing interest in recent years. This interest, which seems to be particularly important within the framework of surplus production models (Doubleday, 1976), has appeared equally in connection with structural self-regenerating models. In this respect salmon stocks have been the object of particular attention (Allen, 1973; Walters, 1975; Peterman, 1977).

This article is not intended in any way to exhaust the subject of stochastic self-regenerating models, but very modestly to prolong a debate. It does so first by presenting several fundamental points in the construction of such models, then it studies the possible deviations in conclusions between deterministic and stochastic models on an essential problem recently advanced by Clark (1974), Gulland (1977a), and Peterman (1977), namely stock stability.

CONSTRUCTION OF STOCHASTIC SELF-REGENERATING MODELS

STANDARD DETERMINISTIC MODELS

We have had recourse to a traditional structural model, distinguishing a recruited phase, described simply by a Ricker exponential model (1958) and a stock-recruitment relation.

Modelling the recruited phase

The exponential model used takes the year as a step in time. Animals are recruited when one year old. The number of age classes taken into consideration is variable and denoted *NB*. The natural mortality is presumed constant and denoted *M*, as is customary. The individual weight is grouped in the vector *W*, where W_i is the weight of an animal of age *i*. In the basic model, F_i, the mortality suffered by a cohort between the ages *i* and $i+1$, is proportional to nominal fishing effort, *f*, and to the corresponding catchability.

Since the accent is put on problems of stock stability, it has seemed useful to envisage the possibility of variations in catchability with stock size. The importance of this phenomenon has actually been demon-

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[2] CNEXO, Centre Océanologique de Bretagne, B.P. 337 29273, Brest Cédex, France.

[3] ORSTOM, Centre Océanologique de Bretagne, B.P. 337 29273, Brest Cédex, France.

[4] Formerly with ORSTOM, Centre de Recherches Océanographiques, B.P. V 18, Abidjan, Côte d'Ivoire. † Deceased 1979.

The order of the co-authors has been determined by a Monte Carlo method.

strated by Fox (1974) and Gulland (1977a). The factor to take into consideration has been presumed to be the biomass exploited, equal to the sum of the weight of all age classes exploited, even partially. This biomass will be denoted *Be*. Following Fox (1974) in this, we have presumed that for a nominal effort f and exploited biomass Be, the effective fishing effort fe would be equal to $f\,c/(Be^d)$, d being constant[5]. By convention it was decided that $f = fe$ for $Be = Bo$ at the level of original stock abundance. This implies that $c = Bo^d$. Therefore there exists a single parameter d. We are reduced to the simple model for $d = 0$. For d we envisage only positive or zero values. At the worst, Be varies throughout a fishing year where f is constant, and this means that fe must evolve. For simplification we have presumed that fe retained its initial value throughout the year. This is only an approximation which may introduce some bias. This bias could easily be reduced by operating with a time fraction less than a year.

Finally the spawning biomass must be predicted for the needs of the stock-recruitment relation. It is assumed that the eggs are laid at the beginning of the year. Therefore the total fecundity must be calculated at this time. If the abundance of class i at this moment is N_i, with the individual weight being W_i, a corrective factor fcr_i will be used making the contribution of class i to total fecundity $N_i \times W_i \times fcr_i$, with fcr_i being called relative fecundity. This is a factor which may involve the sex ratio, and the relative degree of maturity. It is obviously zero for the immature classes. Concretely it is possible to reduce $N_i \times W_i \times fcr_i$ to the number of eggs laid by class i, as Garrod and Jones (1974) have done, if we acknowledge that there is no compensatory mechanism before the eggs are laid. If such mechanisms exist, the fecundity calculated is only a potential fecundity.

Total fecundity, S, equivalent for us to a spawning biomass, will therefore be given by

$$\sum_{i=1}^{NB} N_i \times W_i \times fcr_i.$$

Noting that $fca_i = W_i \times fcr_i$, with fca_i thus designating absolute fecundity, total fecundity will be given by

$$S = \sum_i N_i \times fca_i.$$

Stock-recruitment relations

We shall not go into detail with respect to maturation phenomena and survival of eggs and larvae. We shall simply presume that there is a relation between the spawning biomass S and the recruitment derived from it a year later, denoted R, as is customary.

Ricker base relation

As a basic model we used the traditional Ricker (1958) stock-recruitment relation $R = \alpha S e^{-\beta S}$. We have not had recourse to relations of the type of Beverton and Holt (1957), because in general we are dealing with the left portion of the stock-recruitment curves, considering high levels of exploitation capable of putting the stock in danger. In this left portion the curves of Ricker and of Beverton and Holt are close. We know that in the Ricker relation maximal recruitment is reached when $S = 1/\beta$, and is then equal to α/β. We can better grasp the concrete meaning of α by referring to the concept of fecundity per recruit (Suda, 1966; Le Guen, 1971), estimated, if it is assumed that the stock is in equilibrium and that the exploitation regime is invariable in time, by dividing total fecundity S by recruitment. Then it is easily verified (cf. Laurec, 1977, for example) that the minimal fecundity per recruit under which the stock no longer survives, is equal to $1/\alpha$. Maximal recruitment is achieved when fecundity per recruit is equal to e/α.

INTRODUCTION OF AN INFLECTION POINT IN THE ASCENDING PORTION

A simple method has been used: it consists of multiplying a simple Ricker function, $\alpha S\, e^{-\beta S}$ by $(1-e^{-\delta S})$. A supplementary parameter δ is thus introduced. When δ tends toward infinity, the tendency is toward the ordinary Ricker relation.

The introduction of an inflection point corresponds to giving consideration not only to compensatory phenomena in stock-recruitment relations, but also depensatory phenomena, assumed to be preponderant at low stock levels.

With respect to problems of stock stability, the most important point is not so much the inflection point, as the point where the tangent to the stock-recruitment curve passes through the origin (Gulland, 1977a). The slope of this particular tangent corresponds to the inverse of the minimal fecundity per recruit which can support the stock in a lasting way. At this stock level the recruitment per unit of fecund biomass, R/S, is maximal. If S diminishes, R/S does not increase, which would eventually have permitted the stock to survive. It is intuitively true that the stock cannot continue to resist exploitation which tends to reduce its biomass to a value below the threshold mentioned.

The corresponding level of the stock can be calculated in a relatively simple way: if the stock-recruitment relation is given by $R = \alpha S\, e^{-\beta S}(1-e^{-\delta S})$, it is equal to $(1/\delta)\log(1+\beta/\delta)$.

[5] When Be tends toward 0, q tends toward infinity. This paradoxical fact should not be the rule. For a given range of values of Be, excluding very small values, the formalism used still probably constitutes a useful approximation.

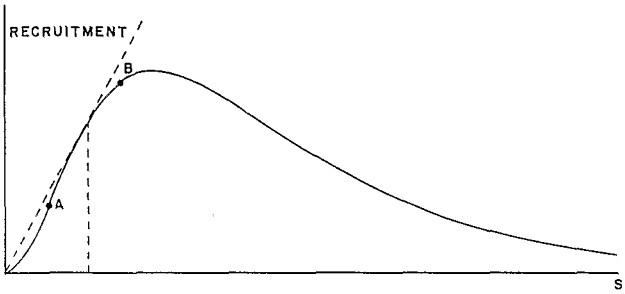

Figure 1. Ricker stock recruitment curve modified, with inflection; $\alpha = 1{\cdot}47$, $\beta = 0{\cdot}006$, $\delta = 0{\cdot}01$.

Figure 1 presents a stock-recruitment curve of the type used. This figure corresponds directly to Figure 1 in Gulland (1977a), where, however, the stock-recruitment relation has been given an exact mathematical formulation. This author gives a discussion of the differences between points A and B; only point B corresponds to a stable stock equilibrium.

INTRODUCTION OF RANDOM COMPONENTS

In the recruited phase

Basic model: catchability independent of the stock size

At this level, as mentioned in the introduction, catchability can be made random from one year to another. Then it will be supposed that $\bar{q}$ corresponds to mean catchability, which can be multiplied each year by a corrective random factor q_a, which is expected to equal 1. It only remains to choose a distribution for q_a. It has seemed useful to us to have recourse to a dissymmetric distribution, opposing the possibility of very high but not very probable catchability to the possibility of more mediocre catchability but with a relatively higher frequency. In this sense we used a log-normal distribution; log (q_a) then follows a normal law with a standard deviation marked σq and a mean qm. The expectation of q_a is equal to $\exp[qm+(\sigma q^2/2)]$. For q_a to have a mean equal to 1, it is necessary for qm to be equal to $-\sigma q^2/2$. Therefore only a single parameter remains to be chosen, σq, which will actually define the importance of the random variations in catchability. It is possible to refer to the variance of q_a to understand this variability. It is preferable to refer to the complete distribution, and in Figure 2 we have presented the probability density of q_a, associated with increasing values of σq.

Note the deviation between the modal value and the mean value of these distributions, connected with their dissymmetry. This dissymmetry is important at the level of population dynamics: it corresponds to the fact that some years of very intense exploitation are countered by more years of exploitation with an intensity moderately below the mean.

It has been acknowledged that catchability could vary in a random way from year to year, but would remain constant within one year. In addition it has been presumed that the random variations were independent from one year to another. The random factors q_a thus form an annual series which is presumed to constitute white noise. This can only correspond to a primary approximation. There must necessarily exist variations within the year, and in addition there must be a certain amount of continuity in time, not a disruption at the beginning of each year. In any event it is necessary to consider a process continuous in time to describe the random variations in catchability. We have to some extent rendered such a process discrete. The process, and the hypothesis of independence of variations in various time intervals, must be rethought for each stock. The same is true for the nature of the random distributions retained. The simple framework defined appears sufficient to us for a general survey of the problems.

Variable catchability according to stock level

Catchability was multiplied by a random factor q_a presumed to be independent of stock level.

Thus, with *Be* being the biomass exploited at the beginning of the year, real stock catchability during this year will be given by: $(c/Be^d)q_a$, with log (q_a) following a log-normal law with a standard deviation σq, with expectation $-\sigma q^2/2$.

The hypothesis according to which the variance of log (q_a) does not depend on the stock condition does not necessarily follow. In particular it is possible to imagine situations where σq would tend to increase when the stock became scarce. Here again the simple hypothesis must be re-examined for each particular case.

Random stock-recruitment relations

We shall essentially refer to the case where the basic model is provided by Ricker's stock-recruitment relation. Two methods can be envisaged for extending this deterministic model into a random model:

For any stock level it is possible suddenly to interject a random residual of zero expectation, or a multiplicative factor of expectation 1, which will be added or multiplied by the mean value predicted by the deterministic model, $\alpha S \exp(-\beta S)$. The second approach consists of considering the parameters α and β of Ricker's law as random ones. Allen (1973), for example, uses a procedure of this type.

The second approach can be considered more satisfactory from the theoretical point of view. If we were

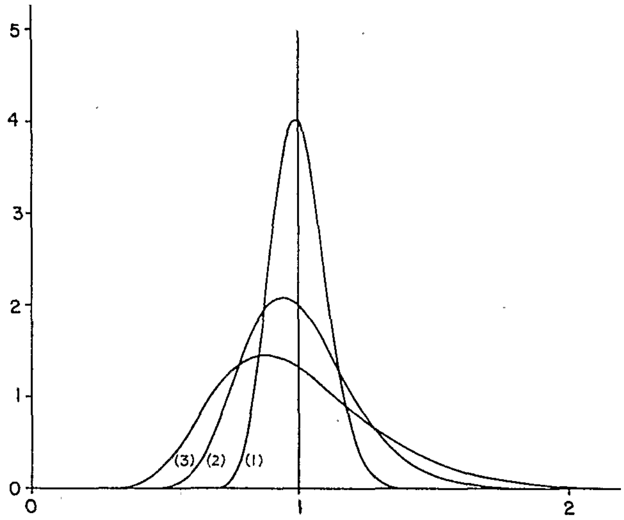

Figure 2. Distribution of q factors (log-normal law). (1) $\sigma q = 0{\cdot}1$, (2) $\sigma q = 0{\cdot}2$, (3) $\sigma q = 0{\cdot}3$.

able, for example, to connect the values of α and β to rates of development or to the abundance of food, a random factor, because it is dependent for instance on temperature, we could even deduce α and β from the temperature distribution.

In this sense it would be interesting to reexamine the models devoted to the survival of eggs and larvae (Jones, 1973; Cushing and Harris, 1973; Lett et al., 1975).

Because of a lack of sufficiently detailed knowledge and because we have no inclination to study a given stock, we followed the first approach; it would be interesting with an exact stock to recall, at least, the second approach, even if we did not follow it strictly. We have considered that a random multiplicative factor r_a also intervenes at every level S of total fecundity, if the mean recruitment value is equal to $\alpha S \exp(-\beta S)$.

It has been acknowledged that the values taken by r_a are independent from one year to another. Here again this hypothesis must be questioned for each precise stock. Everything actually depends on the causes of the variability in recruitment. If, for example, it is related to the abundance of a long-lived predator, this will imply a certain amount of continuity from year to year. Even if the question concerns plankton, it is known that the multiyear variations do not necessarily constitute white noise (Colebrook, 1972). It we come back to the primary causes, such as hydrological variations, the existence of more or less long-term variations is frequently mentioned. Here again, if we continue initially with the simplest model, it may be necessary to adapt this basic model to each stock.

To specify the stochastic model, the major traits of which have been qualitatively described, it is necessary to choose the distribution of r_a for each level of parental stock S.

Here it seemed useful to have recourse to a dissymmetric distribution and we chose a log-normal distribution. Log (r_a) therefore follows a normal law of the standard deviation $\sigma r\ (S)$, capable as we shall see of varying with S. It is necessary to choose a mean of log (r_a) equal to $-\sigma r^2(S)/2$ for r_a to have an expectation of 1.

It is still necessary to fix the variations in the standard deviation of log (r_a) with S. If we simply assume that this standard deviation is constant, the recruitment variability tends to diminish too quickly in the left branch of the stock-recruitment curve, when reference is made to the majority of cases known.

In order to remedy this, it is necessary to increase $\sigma r(S)$ when S diminishes. The simplest procedure is to set $\sigma r(S) = b/S$. This time it is on the right that the variability appears too weak. The respective merits of the two previous solutions can be combined by setting $\sigma r(S) = a + b/S$.[6] This is illustrated in Figure 3, with $a = 0{\cdot}2$ and $b = 30$.

It is obviously possible to envisage more complex variations of $\sigma r(S)$ according to S. The formula proposed is the simplest which is not in obvious contradiction with known facts. As an example we can verify that the stock-recruitment diagram presented by Garrod and Jones (1974) seems to fit the framework defined in this way. In a more general way it takes into consideration very great variability in the left limb of the curve. This makes very significant recruitment possible, even when the mean recruitment is mediocre. Perhaps these are the terms which should be used to interpret the opinion sometimes advanced that excellent recruitment can precede a drop in recruitment. Actually it is possible within the framework of the model to reconstitute analogous situations by simulation. The stochastic model proposed could also be used for estimating stock-recruitment relations on the basis of experimental diagrams. The traditional adjustment by least squares is an optimal procedure only within the framework of an exact stochastic model, where the random residuals are additive, normally distributed, and with a variance independent of the stock size. The unsuitability of this model is obvious, and it would be interesting to examine

[6] For a low value of S, the variability becomes very important. It may appear too high, in which case it would be preferable to use a relation such as $r(S) = 1/[(a+b)/S]$. With the relation used in this paper, the very high variability at low levels of the stock, associated with a log-normal distribution, means that when the stock is very depleted, a good, and even a very good, recruitment may occur, but with a very small probability. In most cases one gets only poor recruitments; in practice we are very close to a situation where an absorbing state exists at low stock levels.

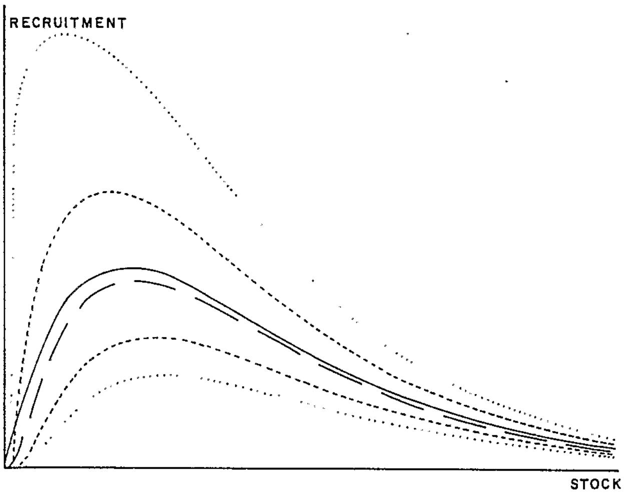

Figure 3. Stochastic stock-recruitment relation derived from Ricker's curve. $\alpha = 1{\cdot}47$, $\beta = 0{\cdot}006$, $a = 0{\cdot}2$, $b = 30$. Solid line, average; long broken line, median; short broken lines, quantiles, 25%; dotted lines, quantiles, 16·6%.

its effects on an estimate of the parameters of the mean stock-recruitment relations.

While the reasoning followed was made with reference to a mean recruitment stock relation according to Ricker, we followed the same procedure exactly in the relations involving an inflection point in the left limb. For a parental stock of level S, the mean recruitment is $\alpha S \exp(-\beta S) \times [1 - \exp(-\beta S)]$. This is complicated by a random multiplicative factor r_a. Log (r_a) follows a normal law of which the standard deviation is equal to $a + b/S$ as previously.

Finally the stock-recruitment relation and catchability can be presumed to be random. The corresponding random factors have been presumed to be independent. This could be discussed for each case: it is conceivable that recruitment and catchability are subject to the same hydrological phenomena. In this case independence, *a priori*, cannot be admitted. A model including a dependence between variability of recruitment and catchability would also be of interest, because it can bring out the importance of the random phenomena: if, for example, an abnormally great catchability is associated with mediocre recruitment, the dangers entailed by this could be grasped intuitively.

STABILITY OF STOCK AND STOCHASTIC MODELS

While the problems of stability are not the only ones which merit study within the framework of stochastic models, they do have particular importance. The concept of equilibrium is different in a stochastic context: the conditions of equilibrium can also be different. The most famous example in this respect is provided by the model of Lotka–Volterra which, when it is completed by random components, systematically predicts the final extinction of one or the the other of the two populations involved (cf. for example, Bartlett, 1960). Other examples can be found in May (1974).

This discussion of the problems of stability will begin with several generalities. In this second stage we shall be interested in the so-called basic model which combines a Ricker stock-recruitment relation with a Ricker exponential model, where catchability does not depend on stock size. We shall end with the influence of the complications discussed by Gulland (1977a): the presence of an inflection point in the stock-recruitment relation and variations in catchability according to stock size.

GENERALITIES

Studies of equilibrium and transition situations

Within the framework of a deterministic self-regenerating model, the definition of a stable equilibrium is simple. A stock is in equilibrium when it remains in the same condition year after year, apart from any external disturbance. Equilibrium is stable if, when the stock is slightly displaced from its equilibrium condition, it tends to return to it spontaneously, as long as the disturbance is sufficiently slight for the stock to remain in a so-called attraction domain encompassing the equilibrium condition. The more or less great attraction of the equilibrium condition corresponds to the concept of elasticity. For more detail, in an area exceeding the fishing framework, one can refer, for example, to Orians (1975).

If a level of stock exploitation is considered, the first stage consists of studying whether or not there is a state of equilibrium corresponding to this exploitation level. This is not sufficient. It is necessary to study the transition situations to find out if a stock is endangered by fishing in the short term or in the long term. This is even more true because it is inconceivable that an exact model would remain satisfactory for a stock over a very long period of time. In this sense we have not so much accented the fact of knowing whether there might or might not be extinction at the end of a possibly very long period, but in relation to the future of the stock for several decades. More exactly we limited the study to 50 years of a given fishing pattern. While the evolution throughout these 50 years has been studied, particular attention has been accorded to the situation after 20 years.

In order to be complete a study of exploited stock stability should include an investigation of stock recuperation with reduced exploitation. Actually this restoration could be of various degrees of difficulty, according to the stock-recruitment relation and according to possible variations in catchability with stock size (Fox, 1974; Gulland, 1977a).

Here again the stochastic dimension of the phenomena complicates the model. In order to limit the size of the present document, we have postponed this research for future studies.

Equilibrium and pseudo-equilibrium in stochastic models

If we exclude the possibility of extinction of the stock for the moment, we can easily transpose the idea of equilibrium as defined with respect to deterministic models. It is no longer a question of the stock remaining identical; but if the condition of the stock undergoing random fluctuations is described by a stationary annual series, we can speak of a state of equilibrium. This corresponds to the existence of a stationary distribution: concretely, if some changes are possible from year to year, they do not reveal any evolution (May, 1973).

If extinction is possible, it is even more probable the longer one waits. Thus it is possible to evaluate the probability of extinction for a given delay. Naturally this probability continues to rise as years elapse.

It is also possible to become interested in the distribution of situations by excluding cases where extinction has occurred. In certain stochastic models (monotype branching processes), it is demonstrated that the distribution of these situations stabilizes (Yaglom, 1974; in Lebreton, 1978), and we then speak of quasi-stationary distributions. Lebreton (1978), using a population of storks as an example, finds that this remains true for a multi-type branching process. The processes studied are not branching processes. It would still be interesting to examine whether or not a phenomenon close to the quasi-stationary states mentioned is found.

Without entering into a mathematical study, the complexity of which is beyond us, it is still interesting to study the evolution of the probability of extinction with the passage of years and the evolution of the distribution of remainders (excluding extinction). Finally, in order to obtain a complete picture of what the stochastic dimension involves, several typical evolutions should be envisaged.

Practical study by the Monte Carlo method

The complexity of the stochastic models used is sufficient for an explicit resolution of them to exceed our mathematical ability. Therefore we have had recourse to simulation according to the Monte Carlo method, using an algorithm generating pseudorandom numbers.

Considering effort f, we shall begin with a stock at the level corresponding to the virgin stock in the deterministic model. For 10 years the stock will evolve without any exploitation. During the next 10 years the stock is subjected to exploitation at level $f/2$. It is not until the 21st year that the effort stabilizes at level f. The stage at level $f/2$ aims at reducing discord which can create too sudden a variation in effort.

For each value of effort f, the simulation was repeated 100 times, the limitation corresponding to the necessary calculation time. More precisely we followed the evolution of the spawning biomass S. For a given year we did not consider absolute extinction, corresponding to an absolutely zero stock, but a virtual extinction. In effect we considered that if the spawning biomass was less than 1/50 of what it was in the virgin stock, the stock was "virtually" extinct. This is the sense in which the frequencies of extinction presented below must be interpreted. Since the Monte Carlo method is used, these frequencies are probability estimates based on samples of size 100. It is easy to construct confidence intervals. We have not added them to the figures in order not to overburden the graphs.

Theoretical stocks taken as examples

Two stocks were studied, differing essentially in their longevity. This factor appears essential, *a priori*, because a stock of great longevity should be more capable of correcting random variations.

We shall speak of stocks 1 and 2, which respectively entail 8 and 3 age classes. Stock 1 will be followed with particular attention. For the recruited phase we were guided by the example of the yellowfin (*Thunnus albacares*) for stock 1 and that of the Ghana sardine (*Sardinella aurita*) for stock 2. We do not make any pretence of describing these stocks, the stock-recruitment relation and structure of which remain largely unknown.

For stock 1 the vectors indicating the weight increase, the relative and absolute fecundity and catchability are compiled in Table 1. Table 2 is similarly associated with stock 2. In both cases the age at first capture is less than maturity. This has the purpose of augmenting the problems of stability and also corresponds to observations.

For the stock-recruitment relation we used the basic model $\alpha = 1{\cdot}47$ and $\beta = 0{\cdot}006$ for stock 1, according to previous notations in Ricker's formula. Within the framework of the deterministic model this corresponds

Table 1. Fundamental characteristics of stock 1. $NB = 8$, $M = 0{\cdot}7$, $\alpha = 1{\cdot}47$, $\beta = 0{\cdot}006$

Age	1	2	3	4	5	6	7	8	9
Weight at age i	1	2·7	10·5	30	50	76	99	100	100
Relative fecundity at age i	0	0	0·57	0·666	1	0·79	0·61	0·60	–
Absolute fecundity at age i	0	0	6	20	50	60	60	60	–
Catchability between age i and age $i+1$	0·1	0·1	0·1	0·1	0·1	0·1	00·1	0·1	–

to a minimal fecundity per recruit of 0·68. The corresponding effort is essentially equal to 810. It can be verified that the total mortality can scarcely exceed twice the natural mortality.

In the basic model for stock 2, $\alpha = 0{\cdot}45$ and $\beta = 0{\cdot}0025$. In the deterministic model framework the limiting fecundity per recruit is 2·22 for an effort of 1500. Thus the stock can support a total mortality as high as 2·5 times the natural mortality rate.

BASIC MODEL

Influence of recruitment variability

Stock 1

As we have said, the limiting effort in the deterministic model is essentially equal to 810. If we consider virtual extinction in the sense defined earlier, this essentially corresponds to the effort leading to virtual extinction in 50 years. To reach virtual extinction in 20 years, a level of effort equal to 900 is needed.

The stock-recruitment relation has been rendered random according to the procedure indicated in the first part of this paper, with $a = 0{\cdot}2$ and $b = 30$. Therefore refer to Figure 3 to judge recruitment dispersion by quantiles. The conclusions relative to stability obviously depend on the variability, and especially on b, which controls this variability at low levels of abundance. Depending on whether b is strong or weak, the features directly related to the random component will be marked or slight.

Table 2. Fundamental characteristics of stock 2. $NB = 3$, $M = 1$, $\alpha = 0{\cdot}45$, $\beta = 0{\cdot}0025$

Age	1	2	3	4
Weight at age i	5	40	80	120
Relative fecundity at age i	0	0·6	0·5	–
Absolute fecundity at age i	0	24	40	–
Catchability between age i and age $i+1$	0·1	0·1	0·1	–

Figure 4 shows the virtual extinction frequencies in 20 and 50 years for different effort levels. The sigmoid curves obtained in this way are to be compared with the "step" curves found in the deterministic model. If virtual extinction in 50 years is considered, this seems possible from an effort of 600. At the 650 level it is relatively frequent. At the 800 level, or approximately that of extinction in the deterministic model, extinction is quasi-systematic. Therefore the deviation is practically in a uniform direction: the random component renders unstable stocks which the deterministic model would consider as stable. The range of efforts concerned is not negligible, since for an effort equal to 650 (or 20% lower than the critical deterministic effort), the risk of extinction in 50 years is significant.

As May (1973) notes, for an equilibrium to exist in a random framework it is necessary that the power of attraction of the equilibrium situation over neighbouring situations be sufficiently strong. In other words elasticity must be sufficient. This deserves to be refined mathematically, but can intuitively assist in showing that in practice there is no equilibrium possible if the fecundity per recruit is too close to the limit.

On a theoretical basis this again demonstrates that it is not necessary systematically to attribute stock decline either to fishing activity or to hydrological or climatic accidents. There is interaction when a hydrological accident intervenes in a stock previously thinned out by fishing; this stock would have survived

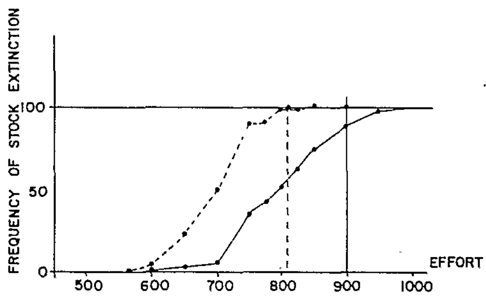

Figure 4. Frequency of virtual stock extinction with random recruitment for stock 1. Solid line, after 20 years of full exploitation; broken line, after 50 years.

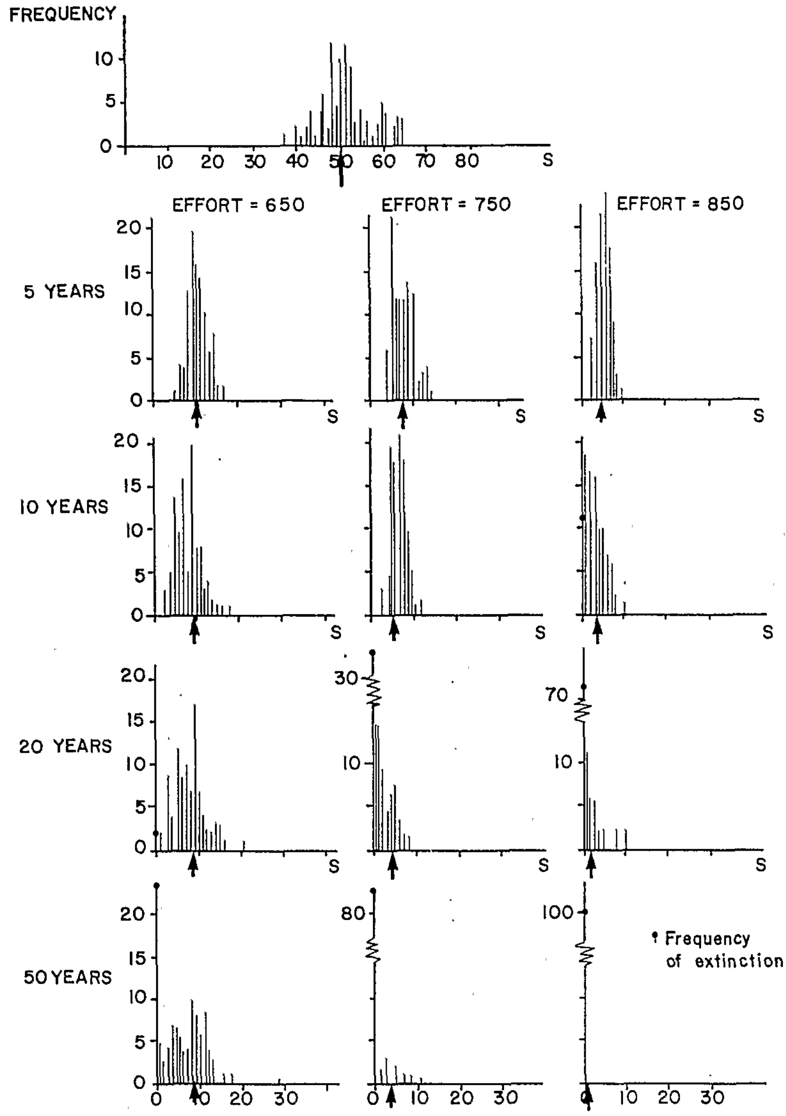

Figure 5. Histograms of spawning stock biomass S for stock 1, after 50 years for a virgin stock and after 5, 10, 20, and 50 years of full exploitation, with a fishing effort equal to 650, 750, and 850. The arrows indicate the values predicted by the deterministic model.

without this accident, but equally it would have been able to endure the accident if fishing had not thinned it out.

If the probabilities of extinction in 20 years are of interest, we come to analogous conclusions. We can even note that in the stochastic model it is possible to extinguish in 20 years a stock which the deterministic model predicts as stable for the effort under consideration. This is particularly true for level 750.

If interest goes beyond extinction probabilities, reference can be made to Figure 5. This figure presents histograms of the values of the spawning stock biomass S after 5, 10, 20, and 50 years of full exploitation. On the abscissa the unit is equal to 1/50 of the spawning stock biomass of the virgin stock in the deterministic model. The class farthest to the left thus defines what we have called virtual extinction. These histograms are given for three effort levels: 650, 750, and 800. With respect to the last level, we can see that extinction is relatively rapid and tolerates almost no exceptions. As we have seen, chance can scarcely assure survival of a stock condemned by the deterministic model. If we consider level 750, we see cases appear after 20 years where the stock is not only not extinct, but is at a level of relatively high abundance, comparable on the whole to that predicted by the deterministic model. However, after 50 years, survival is much less probable.

Level 650 is even more interesting, because we can clearly see the divergence of cases of extinction and cases where it maintains itself at a high level, or even at a very high level in certain cases. If we consider the distribution of non-extinguished stocks, we see that this distribution has scarcely evolved between the 20th and 50th years, while the frequency of extinction has increased. This can be compared with the existence of quasi-stationary distributions mentioned in the generalities. The evolution of the stocks, within the framework of our hypotheses, does not seem to proceed by a systematic decrease year after year. In a number of cases the stocks maintain themselves without any notable evolution, but gradually as time passes there are more and more frequent breaks. Therefore it is relatively normal for a stock to be able to maintain itself for a greater or lesser period of time, despite exploitation, and then suddenly to collapse. This does not necessarily imply a definitive evolution of the environment (for example, one related to a multispecific phenomenon), but a simple accident where the stock diminished by fishing is not capable of recovering.

Stock 2

The coefficients a and b were chosen in such a way as to obtain a relative variability comparable to that of stock 1. Thus, for this variation to be the same for high levels of abundance, we kept the same value for a, i.e., 0·2. In order for the relative variability to be the same at the mean maximal level of recruitment, we chose the value 72 for b instead of 30. Thus the variability is the same to the point where, if the analog of Figure 3, corresponding to stock 1, were plotted for stock 2, we would get the same curves, including the quantiles, by changing the abscissa scale.

As could be understood from the generalities, with an equal variability the differences between the deterministic and stochastic models become clearer for stock 2 with respect to stock 1. This appears in Figure 6, the analog of Figure 4, where the frequencies of virtual extinction are presented. This time, in 50 years, extinction appears a number of times, beginning with level 800, instead of 1500 in the deterministic model. The frequency of extinction is very significant beginning with effort 1000 (66% of the critical level in the deterministic model). From effort 1200 on, extinction is practically systematic.

Analogous conclusions are drawn if the situation after 20 years of full exploitation is considered.

If, as for stock 1, we follow the evolution of the spawning stock biomass by means of histograms, we see even more clearly a divergence appearing between

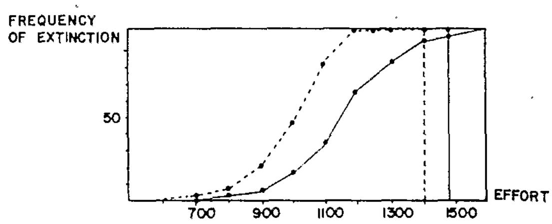

Figure 6. Frequency of virtual stock extinction with random recruitment for stock 2. Solid line, after 20 years of full exploitation; broken line, after 50 years.

the cases of extinction and the cases where a relatively abundant stock would survive. This appears in Figure 7 where, if we compare the situation after 5, 10, and 50 years of exploitation with the effort of 1000, the situation is again reminiscent of quasi-stationary distributions.

This can be seen better if we refer to several typical cases. These cases are presented in Figure 8, where we can follow in one column the evolution of effort, spawning-stock biomass, recruitment, weight of catches, and catches per unit of effort. The fishing is analysed for 70 years with 10 years of no fishing effort, followed by 10 years of fishing effort equal to 500 units of effort, followed by 50 years of effort equal to 1000 units. The left-hand column corresponds to the deterministic model; the centre column corresponds to a favourable case where the stock is maintained at a high level after 50 years of high fishing effort; the right-hand column corresponds to a case where sudden extinction occurred rapidly after 22 years of exploitation. If reference is made, for example, to the c.p.u.e., a sudden drop of strictly random origin can be seen in the unfavorable case.

Examination of these two cases shows very well how the destiny of two stocks governed by the same stochastic model can differ, depending upon whether recruitment has been above or below the mean. Note in passing that excellent recruitment preceded the collapse in the unfavourable cases.

Random catchability

Deterministic recruitment, random catchability

The typical deviation of the logarithm of q_a was chosen as equal to 0·2. Here again, depending upon whether σq is increased or reduced, the originality of the random model is marked to a greater or lesser degree.

If we consider stock 1, we can again study the frequency of virtual extinction in 20 and 50 years, depending on the effort levels. These frequencies are shown in Figure 9. This can be compared with Figure 4, relative to the case where recruitment was random. The originality of the stochastic model appears this time as much less marked.

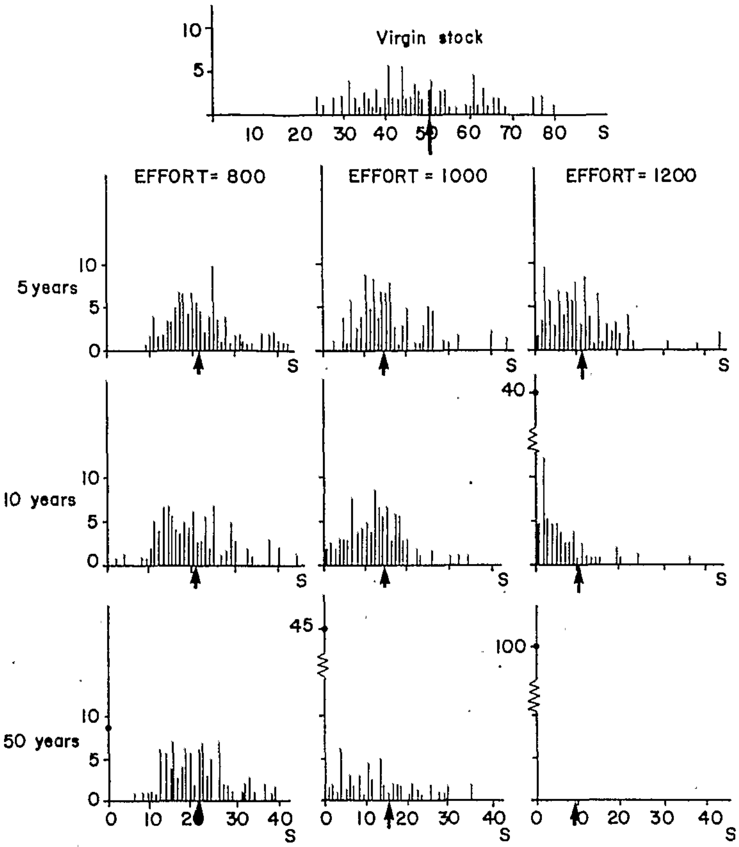

Figure 7. Histograms of spawning stock biomass S for stock 2, after 50 years for a virgin stock and after 5, 10, and 50 years of ful exploitation, with a fishing effort equal to 800, 1000, and 1200. The arrows indicate the values predicted by the deterministic model

If we are interested in the frequency of extinction in 20 years, an effort level of 850 must be achieved for it to result. The risk of extinction is not propagated in any significant way by efforts below the critical effort in the deterministic model. In addition it can also be seen that, beyond the limiting effort of the deterministic model, the stock may have a chance of survival in the stochastic model. This time the deviation is not systematic. In the cases studied there is even quasi-symmetry.

If we go beyond the probabilities of extinction to study the distribution of survivors, we can again see empirical histograms with variations reminiscent of a quasi-stationary distribution.

The originality of the stochastic model is again clearer if we return to stock 2. However it is much less marked than when recruitment is random (Fig. 10, compared with Fig. 6).

Random recruitment and catchability

Whether stock 1 or stock 2 is considered, there does not appear to be any dangerous synergic effect. Essentially the same results are found as when recruitment alone was random. This is illustrated as regard the frequencies of extinction for stock 1 in Figure 1l and for stock 2 in Figure 12.

Naturally this is only true if the random components of recruitment and of catchability are indepen dent. If the cases of extinction are removed, we cai equally well find the phenomenon of quasi-stabilization of the stock level again.

In summary the random fluctuations of recruitmen are more important than those of catchability witl the hypotheses, and especially the distributions, chosen and with the values retained for the parameter characterizing the various variabilities. In addition in the cases studied the random fluctuations o catchability can just as well save a stock condemned by the deterministic model as endanger a stock considered as stable by the deterministic model. Likewise there is always the unavoidable progressive increase in the frequency of extinction as the years pass forming a contrast with an apparent stabilization o the distribution of survivors. Therefore in all cases wc

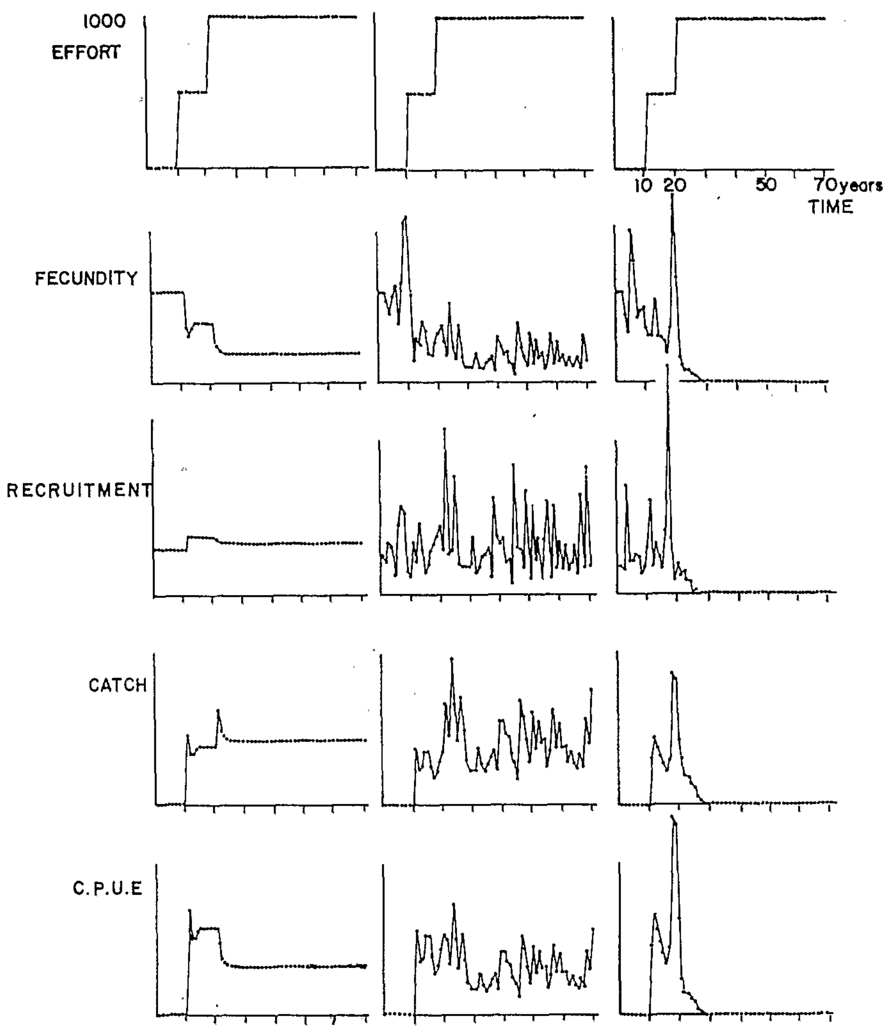

Figure 8. Examples of the temporal evolution for: fishing effort, spawning stock biomass, recruitment, catch, and catch per unit of effort for stock 2. Left-hand column, deterministic model; centre column, stochastic model, favourable case; right-hand column, stochastic model, unfavourable case.

will tend to witness sudden drops rather than progressive reduction if a stock can be extinguished.

IMPACT ON THE SOPHISTICATED MODELS

We shall successively examine the interaction of the random phenomena with the two sophistications discussed by Gulland (1977a): the introduction of an inflection point in the stock-recruitment relationship and the variation in catchability according to stock size. Finally we shall make several remarks on the unstabilizing effect of the random components.

Introduction of an inflection point in the stock-recruitment relation

We chose 0·01 as the value for δ. The values of α and β were modified so that extinction would occur at the same effort level as in a simple Ricker relation.

Essentially we shall study the interactions with the random component of recruitment. In this case, therefore, the deterministic model predicts extinction if effort exceeds 805. The introduction of a random component does not significantly increase the danger in the case of lower effort levels: the increase is much less than with a simple Ricker relation (Fig. 13).

Variations in catchability with stock size

In principle these variations are an important unstabilizing factor. Actually a random reduction in stock entails an increase in catchability which increases mortality and also accents the effect of reduction. Still the interactions with the random fluctuations of recruitment and catchability are not very great.

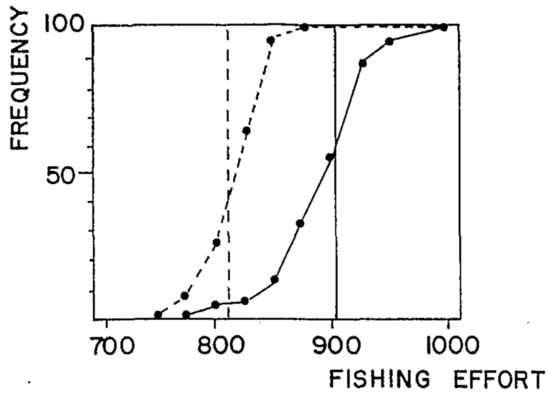

Figure 9. Frequency of virtual extinction for stock 1. Random catchability. Solid line, after 20 years of full exploitation; broken line, after 50 years.

Notes on the destabilization caused by the random components

If we consider an exploitation leading to a stable equilibrium in a deterministic framework, as has been mentioned already, this stability is not necessarily preserved in a stochastic model. There exist conditions for it to be preserved. The first condition has already been mentioned: it is necessary that there be an attraction force sufficient to pull back the system displaced by a random fluctuation toward the point of equilibrium. This may be quantified within the framework of surplus production models, or equivalently in populations limited to a single age class (May, 1973). Thus we end with local conditions, calling on the derivations of the state variables at the point under consideration. These strictly local conditions are necessary, but not sufficient. Near one state there may exist a domain such that, if the system is brought there by a random fluctuation, it tends to remain there. This is particularly true when the domain leads to extinction. This remains true even when it includes other points of equilibrium (Peterman, 1977).

Referring to the two criteria (local and connected with the proximity of a danger), we can try to analyse the destabilization phenomena by random fluctuations, such as have appeared in the basic and sophisticated models. The latter models include domains where attraction toward extinction is great. One may, *a priori*, think that the proximity of these domains can propagate destabilization toward moderated effort levels, associated with high stock levels. In our simulations this has not been very noticeable. The introduction of random phenomena entails rather fewer new facts than the basic models. This can be understood intuitively by referring to the so-called local conditions of stability. At low stock levels equilibrium, as noted, is weakly stable. In the basic models there is a relatively wide range of efforts leading to equilibrium for low stock levels in the deterministic framework. This equilibrium is easily upset by random fluctuations. On the other hand, in the more sophisticated models which have been discussed in this paragraph, we can pass very quickly from a high stock level to extinction with a slight increase in effort (Gulland, 1977a). There is only a reduced range of efforts leading to weakly stable equilibrium, according to local conditions. These considerations can *a posteriori*, help in having one result acknowledged. The fact remains that it is extremely difficult to judge the greater or lesser destabilizing effect of random fluctuations without calculations. The facts found could not be generalized anyway. On the other hand in such circumstances it is always useful to keep in mind the existence of local stability conditions and of conditions associated with the proximity of a dangerous domain.

Finally, leaving the basic deterministic model, it may be of interest to compare the effect of the introduction of the complications discussed in this paragraph with the effect of the introduction of a random component in recruitment. With respect to the first point, as we have said, following Gulland (1977a) it is possible to arrive at stock extinction in the sophisticated models at the cost of a slight increase in fishing effort. The introduction of random components produces a not identical, but similar, result: with a slight increase in effort we do not pass, this time, from favourable situations to systematic extinction but to exploitation regimes involving considerable danger

CONCLUSIONS

Undoubtedly the conclusions reached depend to a large degree on the basic hypotheses relating to the models, and the values used for the different para

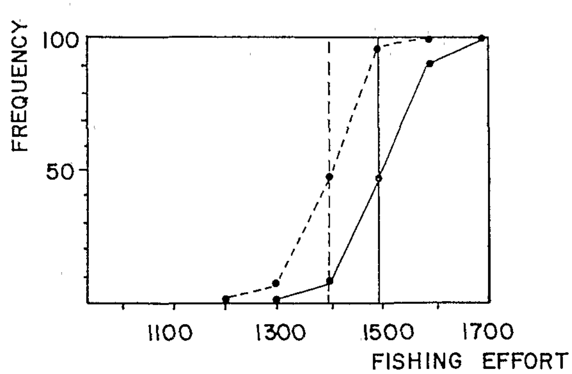

Figure 10. Frequency of virtual extinction for stock 2. Random catchability. Solid line, after 20 years of full exploitation broken line, after 50 years.

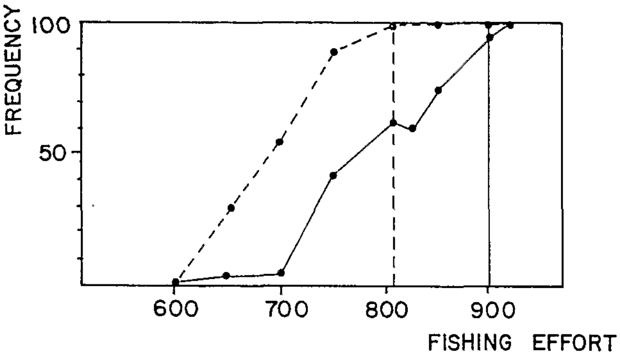

Figure 11. Frequency of virtual extinction for stock 1. Random recruitment and random catchability. Solid line, after 20 years of full exploitation; broken line, after 50 years.

meters. However, if there were any need, this study confirms that the stochastic models can lead to conclusions, in the matter of stock stability, quite different from those provided by the deterministic models. This is particularly true with respect to random recruitment fluctuations.

In addition, a very important characteristic appears in the stochastic models used: for a moderate increase in fishing effort, we can rapidly pass from a favorable situation, where recruitment is maintained[7] at high levels with equilibrium, to situations involving considerable risk of fishery collapse.

If collapse occurs, the manner in which it takes place within the framework of our models is of equal importance. With the passage of years we cannot see a systematic decline except when overexploitation is very marked, but rather a divergence between cases where extinction takes place and those where, on the contrary, stock maintains itself at a satisfactory level. Collapses then tend to occur relatively abruptly and without being systematic. If we consider recruitment involving a random component, precisely in accord with the risk of recruitment, we may have the illusion of equilibrium for at least a limited period of time, or on the contrary may witness collapse of the stock.

In terms of fishery management, the major dangers appear to be connected with two facts which have been mentioned:

a) The risks of collapse can arise from a moderate increase in effort.
b) The dangers do not necessarily appear very rapidly, and can be masked throughout favourable periods by good recruitment of random origin.

We have pointed out that we make no claim to systematic extrapolation of the results obtained within the framework of our simulations. At the level of stock-recruitment relations, the results relating to questions of stability are extremely sensitive with respect to the variability which the model attributes to recruitment at low stock levels. As an example, by using a random stock-recruitment relation of the type suggested by Allen (1973) and used by Walters (1975) and Peterman (1977), the risks of destabilization brought about by random fluctuations are much more reduced. This indicates the danger there would be in hastily generalizing our conclusions. This also shows that the care with which we discussed the construction of random models in the first paragraphs of this study is absolutely indispensable. With constant respect to the random stock-recruitment relationships and their discussions, it appears to us that the general formulations defined in this study can be a useful basis.

In practice the habit should be acquired of debating stock management within the framework of stochastic models. This should not be limited to problems of stability, but to a treatment of all the consequences of various possible choices, as has been shown by Walters (1975) and Lett and Benjaminsen (1977). In most cases the conclusion will be complex models in which exact mathematical resolution exceeds the capacity of most of those studying population dynamics. It is important to attract the attention of specialized mathematicians to such problems. In the immediate future the Monte Carlo methods of simulation should permit most researchers concerned to reach the essential conclusions. Effort must in the immediate future be brought to bear on the construction of realistic stochastic models, i.e., adapted to each particular case.

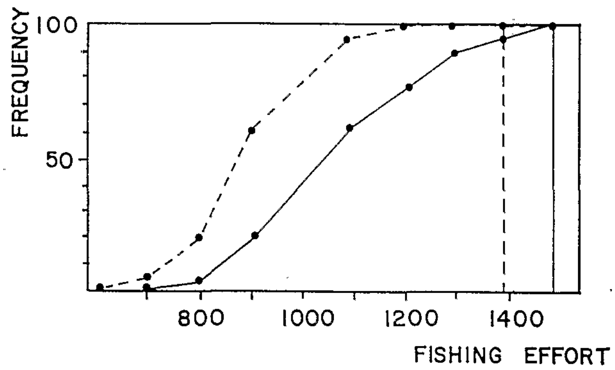

Figure 12. Frequency of virtual extinction for stock 2. Random recruitment and random catchability. Solid line, after 20 years of full exploitation; broken line, after 50 years.

[7] When no "growth overfishing" is possible, because the growth slows down fast (stock 2), this means that good catches are maintained. When growth overfishing is possible (slow growth and low natural mortality), the appearance of such overfishing may protect the stock against the more dangerous "recruitment overfishing".

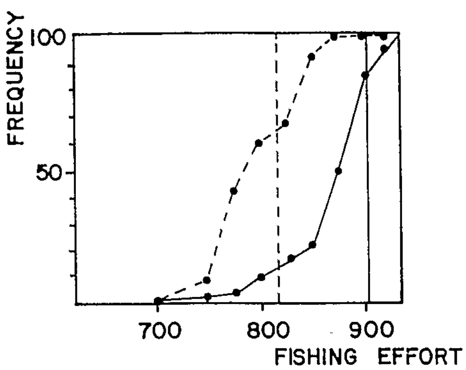

Figure 13. Frequency of virtual extinction for stock 1. Random recruitment, combined with an inflection point in the basic stock recruitment curve. Solid line, after 20 years of full exploitation; broken line, after 50 years.

SUMMARY

Deterministic self-regenerating models appear to be useful for investigating the basic facts in population dynamics. In a second stage it appears that such models give only rough approximations and that stochastic models are more realistic. They are also more complicated; one should first wish to know whether or not they are necessary in the sense that they would have a significantly different behaviour from deterministic models. This paper does not try to answer this question in all its generality, but aims to highlight some basic facts about an especially important point, fish stock stability.

While this paper is especially interested in stability problems in stochastic models, it also pays considerable attention to the construction of such models. This is the purpose of the first part. Basically a self-regenerating model will be considered where recruitment is obtained from a spawning stock with a Ricker stock-recruitment curve. This model can first be randomized at the level of recruitment. For a given stock it is considered that if the Ricker curve gives an average value, there exists a random multiplicative factor (*ra*); this factor is considered to follow a log-normal distribution. The variance of log (*ra*) can change with the level of the parental stock: var $(\log(ra)) = a + b/S$. The catchability may also be affected by a random component. It is assumed that this corresponds to a multiplicative factor (*qa*) which affects the fishing mortality vector. It is also assumed that this factor *qa* follows a log-normal distribution with a mean equal to 1. The variance of log(*qa*) is considered to be constant (independent of the level of stock and of fishing mortality).

The second part of this paper is devoted to the study of some basic facts about fish stock stability problems in stochastic models constructed as shown in the first part. Two hypothetical stocks are considered ε examples, with a different life span (8 and 3 year: and different natural mortality (0·7 and 1·0). Und the assumption of the model, and given our data, appears that a moderate fishing effort associated wit random variability of recruitment will produce significant number of stock collapses.

This difference between deterministic and stochast: models is greater with a 3-year-class stock. Stoc which have not yet collapsed appear to be in a sem stationary state, fluctuating in the neighbourhood the situation predicted by the deterministic model.

The effects of a random catchability are less sign ficant than the previous ones. There is danger collapse with effort slightly smaller than the critic: deterministic effort, but also some opportunity sustain a fishery with efforts slightly greater than th level.

Combining variabilities of recruitment and catcl ability does not produce any dangerous synergy an gives results similar to those of random recruitme alone.

Possible effects of a random variability upon Ricker stock-recruitment curve with an inflectic point on the left have been briefly explored. Differe ces between stochastic and deterministic models a pear to be relatively small, because in such mode there are fewer subcritical situations that can becon critical with a stochastic component.

A model assuming increasing catchability with d creasing stock, as described in Fox (1974), has al been explored and shows minor differences betwe deterministic and stochastic models.

All of these results are provisional ones, dependi on the assumptions of the model and on the dat However, they indicate that variability of recruitme produces a danger of collapse which must be careful estimated in the management of a stock, especial a pelagic stock.

RESUME

Les modèles déterministes autorégénérants sont util pour explorer dans un premier temps les règles base de la dynamique des populations. Dans u deuxième étape il semble que les modèles stochastiqu peuvent apporter des conclusions plus réalist L'emploi de ce deuxième type de modèles étant pl complexe, il est nécessaire de déterminer si les de catégories arrivent à des conclusions divergentes ceci dans quelles conditions. Cette note a pour se ambition de dégager certaines différences de ba principalement dans le domaine important de stabilité des stocks de poissons. Cet article prête to d'abord une certaine attention à la construction c modèles stochastiques. Fondamentalement un sim modèle autorégénérant est employé, dans lequel le recrutement est calculé à partir d'une courbe stock-recrutement de Ricker. Ce modèle peut être rendu aléatoire tout d'abord en ce qui concerne le recrutement: pour chaque niveau du stock, le recrutement est multiplié par un facteur aléatoire *ra* de moyenne égale à 1, qui suit une loi log-normale. La variabilité du recrutement est accrue aux niveaux décroissants du stock pour tenir compte des faits observés. La capturabilité du stock peut aussi varier aléatoirement grâce à un facteur multiplicatif du vecteur des mortalités par pêche qui suit aussi une loi log-normale de moyenne 1.

La deuxième partie de cette note est consacrée à l'analyse de certains résultats de base. Deux stocks hypothétiques l'un à 8 classes d'âges et $M = 0{\cdot}7$, l'autre à 3 classes et $M = 1{\cdot}0$ ont été employés. Les modèles et les données employées conduisent aux conclusions suivantes: le danger d'extinction des stocks est accru par l'introduction d'un recrutement stochastique. On constate ainsi, pour des efforts inférieurs au niveau critique en régime déterministe, qu'un certain nombre de stocks demeurent un certain temps dans un régime quasi-stationnaire alors que d'autres stocks s'effondrent. La fréquence des effondrements s'accroît avec la durée de l'exploitation. Les divergences entre les conclusions des régimes déterministes et stochastiques sont particulièrement importantes dans le cas du stock à 3 classes d'âge.

Les effets d'une capturabilité aléatoire du stock sont moins significatifs et semblent être tantôt positifs, tantôt négatifs pour l'effondrement des stocks. La combinaison d'un recrutement et d'une capturabilité aléatoires n'introduit par de synergie notable dans la dynamique du modèle et donne des résultats comparables à ceux obtenus avec la variabilité du recrutement seule.

Les effets d'une variabilité du recrutement dans la relation de Ricker modifiée par l'introduction d'un point d'inflexion, sont jugés peu importants. Il en est de même dans le modèle où la capturabilité du stock est accrue quand le stock décroît. Ceci peut s'expliquer simplement par le fait que dans ces deux modèles il existe moins de situations subcritiques que l'introduction d'une composante aléatoire pourra rendre instable. Toutes ces conclusions sont provisoires et dépendent à la fois du modèle employé et des données de base. Ils semblent indiquer que la variabilité du recrutement introduit pour une pêcherie en exploitation une probabilité d'extinction des stocks non négligeable. Dans ces conditions il serait important d'appliquer ce modèle (ou des modèles dérivés) à l'analyse de la dynamique de certains stocks précis, spécialement les stocks de pélagiques côtiers qui semblent les plus sensibles aux dangers d'un effondrement brutal.

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Note: The computer program (FORTRAN IV), corresponding to the models described. can be furnished by the authors on request.

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