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A generalized stock-recruitment relationship fitted to the observed yield: implications for the recruitment dynamic

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Abstract

The present study presents a method of assessing and fitting a stock-recruitment relationship. The method is based on a combination of an equilibrium production model and a yield per recruit model. It does not use recruitment data which are, in general, highly dispersed, but production data. Thus, the relationship obtained is not of the parametric form of classical stock-recruitment relationship such as those of the Beverton and Holt (1957) and Ricker (1954), however, in some cases, the resulting stock-recruitment curve resembles models currently used in fisheries science. It is interpreted as an expectation of the recruitment conditionally to stock spawning biomass and stock demographic structure. However, for some realistic values of the parameters, the curve thus obtained describes a loop which suggests that two different recruitment levels may be expected from the same stock spawning biomass level. This theoretical property is illustrated with simulations. As an illustrative example, the method is applied to North-West Atlantic gadoid stocks. The significance of the method, its originality, the validity of the underlying assumptions and their conceptual consequences are discussed.

Keywords: Fisheries management, population dynamic, stock-recruitment relationship, fitting, recruitment variability, Gadidae.

Une relation stock-recrutement généralisée ajustée à la production observée et ses implications sur la dynamique du recrutement.

Résumé

Cette étude propose une méthode d'estimation et d'ajustement d'une relation stock-recrutement fondée sur la combinaison d'un modèle global et d'un modèle de rendements par recrue. La méthode n'utilise donc pas de données de recrutement (en général fortement dispersées) mais des données de production. La relation obtenue n'est pas une relation paramétrique classique comme les modèles de Beverton et Holt (1957) ou de Ricker (1954) bien que dans le cas courant elle ressemble aux modèles utilisés en halieutique. Elle est interprétée comme une espérance du recrutement conditionnellement à la biomasse féconde et à la structure démographique. Pour certaines valeurs réalistes de ses paramètres, la courbe obtenue décrit une boucle permettant d'envisager deux niveaux de recrutement possibles pour une même biomasse féconde. Cette propriété théorique est illustrée à l'aide de simulations. La méthode est, à titre d'exemple, appliquée à des stocks de Gadidés de l'Atlantique Nord-Ouest. L'intérêt de la méthode, son originalité, la validité des hypothèses sous-jacentes et leurs conséquences conceptuelles sont discutées.

Mots-clés : Dynamique des populations, relation stock-recrutement, variabilité du recrutement.

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INTRODUCTION

The stock-recruitment relationship is a useful tool both for assessment and management of fish stocks: it is indeed a theoretical means which may help to define recruitment overfishing. It is also significant from a conceptual point of view for it allows us on the one hand to consider stock collapses for very low biomass levels, and on the other hand to explain the resilience of fish populations. However, in most cases, the observed recruitment is too variable to allow precise identification of a stock-recruitment model or to choose between different given models. As mention Myers *et al.* (1994), "the relationship between spawning biomass and recruitment is notoriously variable and the underlying theoretical relationship is never known in practice". At the same time, variation around a yield curve is often considerably less. A reason for this is that the observed yield (Y) depends on several cohorts and hence on several recruitments and so the variations of year-class recruitment are smoothed out. This smoothing is often sufficiently great that a curve can be fitted to the observed yield. That is Ye, the equilibrium yield curve from production models. These can be interpreted as a conditional expectancy with given values of effort and biomass which implicitly include in heuristic formulation the effects of recruitment, mortality and growth (Gulland, 1977; Sissenwine and Shepherd, 1987; Laloë, 1995). The principle of the present approach is to isolate, by means of a yield per recruit model, the smoothed component of the recruitment expressed in a production model and then incorporate the two models so as to obtain a stock-recruitment relationship.

METHOD

Principle

The suggested principle is to isolate the density dependence phenomenon implicitly included in production models by using a yield per recruit model (Y/R(F)). As a matter of fact, using the classic assumption that most of the density dependence phenomenon expressed by the production model results from the pre-recruited stages density dependence (Cushing, 1975; Iles, 1980 in Laurec *et al.*, 1981; Shepherd *et al.*, 1982; Sissenwine *et al.*, 1987; Myers *et al.*, 1993), we can easily calculate the variations of the recruitment at equilibrium Re (*i.e.* the theorical recruitment in an equilibrium state with the stock spawning biomass for a given fishing effort (Moran, 1950 in Gulland, 1977) depending on fishing mortality.

In this way, using the yield per recruit as an equilibrium state $\left(\frac{Y}{R}(F) = \frac{Y_e(F)}{R_e(F)}\right)$, we can write:

$$Y_e(F) = \frac{Y}{R}(F).Re(F) \quad (1)$$

hence:

$$Re(F) = \frac{Ye(F)}{\frac{Y}{R}(F)} \quad (2)$$

By analogy with the yield per recruit model, the stock spawning biomass per recruit can be expressed as a function of the fishing mortality F. The stock spawning biomass at equilibrium $SSBe$, which corresponds to the recruitment at equilibrium Re, is then deduced:

$$SSB_e(F) = \frac{SSB}{R}(F).Re(F) \quad (3)$$

Knowing the recruitment at equilibrium $(Re(F))$ and the spawning biomass at equilibrium $(SSBe(F))$, which are both functions of the same fishing mortality, we can plot point by point the curve of the recruitment at equilibrium versus the spawning biomass at equilibrium. This parameterized curve corresponds to the stock- recruitment relationship implicitly included in the fitted production model (Fig. 1).

Let us now consider recruitment as resulting from a combination of a stock-recruitment relationship, intrinsic to the population under consideration, and of extrinsic permanent environmental noises (both biotic and abiotic). In most cases, the environmental noise is so great that it seems to determine the recruitment evolution; hence the stock-recruitment relationship remains « concealed ». In such circumstances, the evolution of recruitment and spawning biomass to steady states Re and $SSBe$ would never be observed in practice and therefore, the equilibrium stock-recruitment relationship is only of theoretical interest. Nevertheless, by definition, the equilibrium recruitment $Re(F)$ covers the stock-recruitment relation curve when fishing mortality F varies (Moran, 1950 in Gulland, 1977) (Fig. 2). The resulting equilibrium recruitment curve is then also the stock-recruitment relation curve (R/SSB).The stock-recruitment relationship thus determined does not refer anymore to any equilibrium with the fishing mortality. This equilibrium only served to cover the theoretical equilibrium recruitment curve.

Consequently, one can consider this stock-recruitment relationship as the recruitment intrinsic expectation with respect to the fecund biomass.

Application

The method presented above is applied to some real data. These are taken from various CIEM working groups (anon., 1993; 1994) which use cohort analysis to assess stocks. The effective effort is assessed as the arithmetic average of the fishing mortalities per age calculated by the working groups. The fitting of production models is carried out with effort data transformed by the method of Fox (1975).

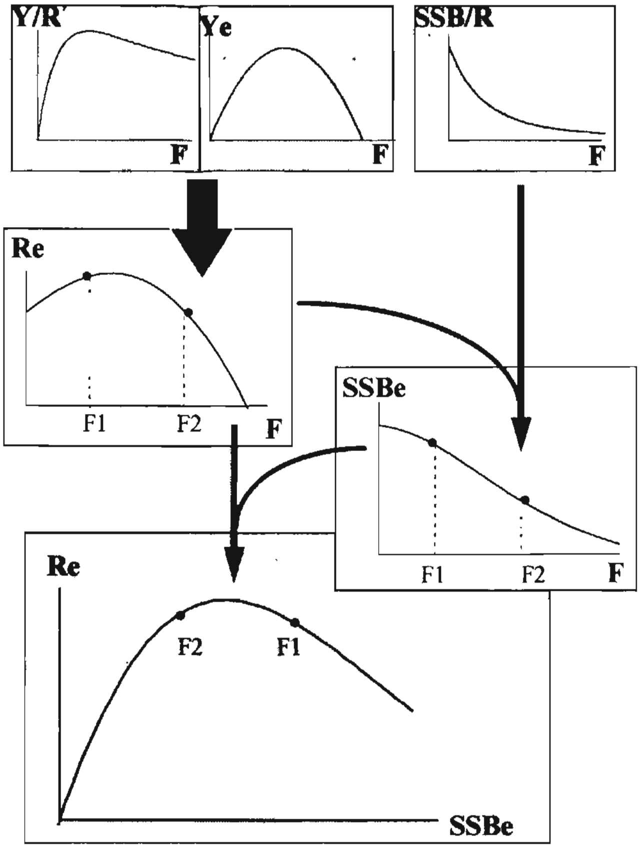

Figure 1. – Synthetic presentation of the stock-recruitement curve determination method (see text). Equilibrium recruitment model is calculated with yield per recruit model and surplus production model. Stock/equilibrium spawning biomass model is then calculated with stock spawning biomass per recruit model and equilibrium recruitment model. Stock/equilibrium spawning biomass model and equilibrium recruitment model are used to plot point after point the recruitment at equilibrium (Re) against the stock spawning biomass at equilibrium ($SSBe$) for each level of fishing mortality (F) (two levels of fishing mortality F1 and F2 are represented on the differents models). The equilibrium recruitment-stock model is drawn by joining those points.

The equilibrium production model used here is a generalized production model (Pella and Tomlinson, 1969):

$$Ye(F) = F.\left(\frac{K}{H} + \frac{F}{H}\right)^{\frac{1}{m-1}}$$

where F is the effective fishing effort applied to the whole stock and K, H and m, are the parameters of the model.

The yield per recruit curves – $Y/R(F)$ – as well as the stock spawning biomass per recruit curves – $SSB/R(F)$ – are calculated using a model close to Thomson and Bell model (1934):

$$Y/R(F) = \sum_{a=1}^{n}\left(\left(\prod_{i=1}^{a} e^{-(F_i+M_i)}\right) \times \frac{F_a.W_a}{(F_a+Ma)}\left(1-e^{-(Fa+Ma)}\right)\right)$$

and

$$SSB/R(F) = \sum_{a=1}^{n}\left(\left(\prod_{i=1}^{a} e^{-(F_i+M_i)}\right).Wa.\phi a\right)$$

where F is the vector of fishing mortality; n is the maximum number of age groups; F_a, the fishing mortality at the age a; M_a, the natural mortality at the age a; W_a the weight at the age a and ϕ_a, the fecundity rate at the age a. The theoretical stock-recruitment curve is then calculated point by point using an effort multiplier of the reference vector [F] varying from 0 to 10 by step of 0.025.

To investigate theoretically the properties of the determined stock-recruitment relationship, the adjustment parameters (production model, fecundity rate...) are progressively modified from real examples.

Simulations

In classical models of stock-recruitment relationships, recruitment is assumed to be a deterministic function of the stock spawning biomass ($R = f(SSB)$). On the contrary, for the stock-recruitment relationship model we propose, the expectation of the recruitment is a deterministic function of the total biomass ($E(R) = f(B)$) because the production model express itself the expectation of the production as a function of the total biomass. The recruitment is then expressed as a function of the stock spawning biomass by means of a relationship linking biomass and stock spawning biomass. This non-linear relationship is a function of the age structure of the population and then of the fishing pattern.

Various simulations are used to clarify the implications of recognizing a biomass density dependence of the recruitment. One of these simulations, the most illustrative, is presented here. The simulated population has 4 age class. Its growth is governed by a Von Bertalanffy model (Table 1) with $L_\infty = 25\,\text{cm}$ and $K = 0.9$. (*Weight*$=10^{-4}.L^3$ at length follows an allometric relation of length and fecundity rate equals 1 at ages 0, 1 and 2 and equals 0 at age 3. The stock number at age is calculated with natural mortality rate equals 0.2 at all ages and fishing mortality rate equals 0.08 for ages 0 and 1 and equals 0.8 for ages 2 and 3. Those caricatural ogive maturity and fishing patterns are used to favour a loop-shaped stock-recruitment relationship (see results).

The stock recruitment relationship used is a Ricker model (1954) modified to allow a density dependence of biomass:

$$E(R) = a.SSB \cdot e^{-b.B} = f(B, SSB) \qquad (4)$$

with recruitment expectation $E(R)$, biomass B, stock spawning biomass SSB, a and b, the parameters. The equation (4) allows us to take into account two important a phenomena: the proportionality

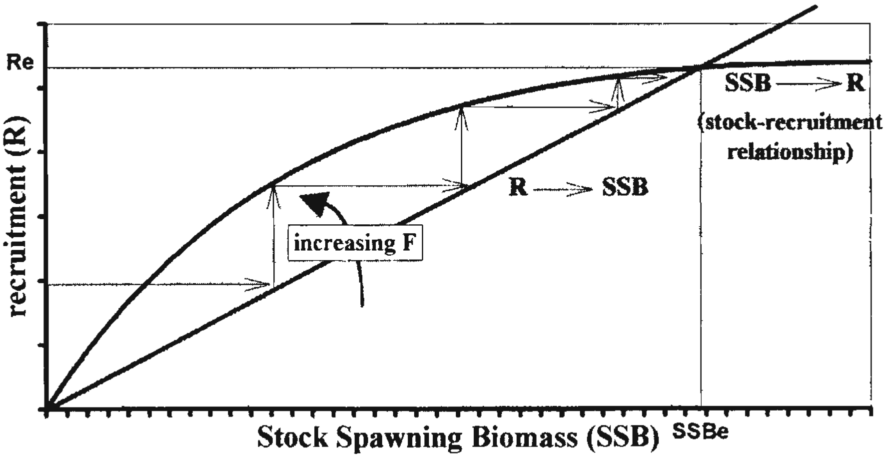

Figure 2. – Theoretical relationship between the stock-recruitment relationship and equilibrium recruitment $Re(F)$ defined as the intersection of the stock-recruitment relationship and the line $R \rightarrow SSB$ (Gulland, 1977). The increase of the fishing mortality causes the slope of the line $R \rightarrow SSB$ to increase. The recruitment at equilibrium is hence translated along the stock-recruitment relationship and covers the whole stock-recruitment at equilibrium curve.

Table 1. – Values of the parameters used in the simulation (see text).

Age	Fishing mortality	Fecundity
0	0.08	1
1	0.08	1
2	0.8	1
3	0.8	0
Natural mortality	0.2	
L_∞	25 cm	
K	0.9 year^{-1}	

of the numbers of eggs spawned to the stock spawning biomass and the negative density dependent component of the recruitment function of the whole biomass. This model is hence more realistic than a model expressing recruitment as a function of only the biomass or only the stock spawning biomass.

(Simulations were also realised with a modified Beverton and Holt model (1957) and results were the same as with modified Ricker model.)

Stock dynamics is simulated over 250 years. In order to cover different age structure, fishing mortality is multiplied by an effort multiplier which slowly (to approach an equilibrium) increases from 0 to 25 during the whole period (steps equal 0.1).

RESULTS

Stock-recruitment relation obtained in the general case

For most of the tested species, the stock-recruitment relationship derived by the above method has a maximum. Two examples (Fig. 3), selected for their high observed dispersion of recruitment, are presented here as an illustration: the 1991 assessment of cod (*Gadus morhua*) in the CIEM zone VIIa and of saithe (*Pollachius virens*) in zone VIa (Tables 2-3-4-5). For calculating the effort, Fox's method was applied on 5 years for the cod and 8 years for the saithe.

For cod, the production model fitted is a Schaeffer model ($m = 2$ in the Pella and Tomlinson generalized model):

$$CPUE = -21\,158.mF + 29\,358$$

with mF an effort multiplier of the averaged F 1990-1992, and with the catch per unit effort (CPUE) in tonnes/mF. The determination coefficient $R^2 = 0.608$.

For saithe, the production model fitted is a Fox model ($m = 1$ in the the Pella and Tomlinson generalized model):

$$CPUE = 23\,532\,e^{-3.0584.mF}$$

with mF an effort multiplier of the fishing mortality averaged on 1990-1992 and with the catch per unit effort (CPUE) in tonnes/mF. The determination coefficient $R^2 = 0.959$.

For both stocks, the natural mortality is supposed to be equal to 0.2 at all ages. Maturity ogive, weight in the catch and fishing pattern are given in Tables 2-3-4-5.

The interesting feature of this method is that it is possible to fit an intrinsic stock-recruitment relationship to apparently erratic recruitment data, expressing simultaneously an « intrinsic » trend and « extrinsic » environmental disruptions. Figure 3 shows the satisfactory aspect of the stock-recruitment relationships in spite of the difficulty, *a priori*, of choosing and fitting a meaningful curve to the observed recruitment.

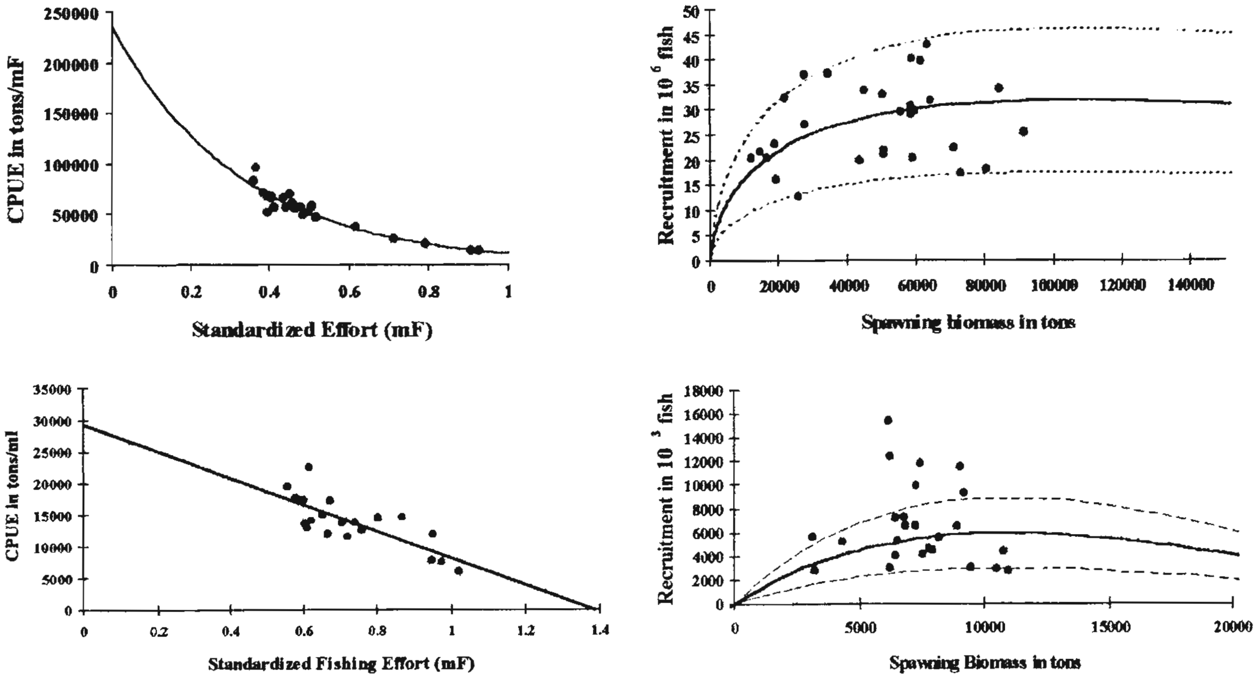

Figure 3. – Application to the West Scotland zone real data in 1991: at the top, saithe of CIEM zone number VIa and at the bottom, cod of CIEM zone number VIIa. The fitting of the production models is carried out on the CPUE expressed in relation to the effort transformed by the method of Fox (on the left, the points represent the observed CPUE and the line the fitted model). The stock-recruitment models obtained are plotted on the right (curves) as well as the observed recruitment (points). The dotted line schematizes the effect of the extrinsic phenomena.

Table 2. – Observed values of stock spawning biomass, recruitment, effort multiplier and landings used for the COD VIIa (anon., 1993).

Years	SSB observed (tonnes)	R observed (age 1) (thousands)	$mF1\text{-}7_{(90\text{-}92)}$	Landings Y (tonnes)
1868	8 191	5 587	0.623 8	8 541
1969	6 766	7 314	0.742 5	7 991
1970	6 192	12 475	0.577 5	6 426
1971	7 539	4 201	0.532 9	9 246
1972	9 042	11 546	0.473 9	9 234
1973	10 934	2 731	067.2 9	11 819
1974	9 186	9 341	0.578 3	10 251
1975	9 480	2 983	0.69.8 9	9 863
1976	7 918	4 453	0.684 7	10 247
1977	7 798	4 600	0.666 8	8 054
1978	7 281	9 938	0.485 7	6 271
1979	7 423	11 800	0.615	8 371
1980	7 221	6 638	0.617 6	10 776
1981	10 474	2 934	0.657 8	14 907
1982	10 743	4 391	0.777 2	13 381
1983	8 905	6 510	0.729 2	10 015
1984	6 801	6 622	0.721 8	8 383
1985	6 521	5 371	0.761 8	10 483
1986	6 141	15 411	0.785 0	9 852
1987	6 414	7 273	0.888 9	12 894
1988	6 210	3 073	0.971 6	14 168
1989	6 411	4 053	1.071 9	12 751
1990	4 285	5 265	0.965 5	7 379
1991	3 159	5 689	0.861 3	6 714
1992	3 234	2 863	1.173 2	7 173

Table 3. – Maturity ogive, weight at age and fishing pattern used for yield per recruit calculation for the COD VIIa (anon., 1993).

	Age maturity (year)	Weight in the catch (kg)	$F\ mean_{90\text{-}92}$
1	0.00	0.836	0.350 8
2	0.17	1.830	0.810 0
3	0.85	3.710	1.177 8
4	1.00	5.575	1.170 8
5	1.00	6.956	1.075 2
6	1.00	8.469	1.061 8
7	1.00	11.384	1.061 8

Deformation of the curve for some values of the parameters

For some realistic values of the parameters, the curve is so deformed that it forms a loop (Fig. 4). For a range of values of stock spawning biomass there are then two possible values of the equilibrium recruitment.

The stock-recruitment relationship is a parameterized curve *i.e.* a set of (SSB, R) points where $SSB = f(F), R = g(F)$ where f and g are both functions of the same variable F. The necessary condition for it to form a loop is that f is a non monotonous function of effort F (then the curve of equilibrium spawning biomass against effort passes through a maximum for a non nul effort). Then, for

Table 4. – Observed values of stock spawning biomass, recruitment, effort multiplier and landings used for the SAITHE VIa (anon., 1993).

Years	SSB observed (tonnes)	R observed (age 1) (thousands)	mF1-7$_{(90-92)}$	Landings Y (tonnes)
1863	12 147	30 710	0.390	6 594
1964	16 831	20 435	0.468	13 596
1965	22 074	20 435	0.763	18 395
1966	19 159	32 326	0.517	18 584
1967	27 704	23 121	0.508	16 034
1968	27 897	37 028	0.332	12 787
1969	34 303	27 014	0.371	17 124
1970	44 983	37 250	0.254	14 536
1971	50 221	33 952	0.380	19 863
1972	64 206	33 290	0.306	29 219
1973	84 051	31 778	0.405	33 832
1974	91 307	34 172	0.503	35 973
1975	73 146	25 548	0.462	30 800
1976	80 528	17 370	0.598	41 747
1977	58 857	10 069	0.553	27 210
1978	71 004	20 341	0.535	31 370
1979	58 173	22 366	0.420	21 604
1980	59 432	30 977	0.392	22 102
1981	61 174	29 961	0.387	23 574
1982	58 734	39 676	0.416	23 884
1983	63 319	40 358	0.441	28 890
1984	50 537	43 157	0.324	21 641
1985	58 386	21 879	0.395	26 595
1986	55 384	29 205	0.718	39 886
1987	50 429	29 517	0.680	31 369
1988	43 457	21 153	0.919	34 178
1989	25 721	20 023	0.977	25 577
1990	19 314	12 656	0.956	19 865
1991	14 722	16 020	1.194	16 995
1992	10 747	21 657	0.850	11 803

$F = F$ max, we have $SSBe(F) \geq SSBev$ with the virgin state ($F = 0$) noted v.

By definition:

$$SSB_e(F) = \frac{SSB}{R}(F).Re(F)$$

Thus, the condition for the stock-recruitment curve to form a loop is the existence of $F_{\max}$ such as:

$$\frac{SSB}{R}(F) \geq \frac{SSB_{ev}}{Re(F)} \qquad \text{for} \quad F = F_{\max} \tag{5}$$

Two cases are likely to favour the realization of (5):

– a curve $SSB/R(F)$of flat form (its asymptote is close to $(SSB/R)v$) (Fig. 4)

– a curve $Re(F)$ giving high values or having a steep slope at the origin and hence a curve $SSBev/Re(F)$ presenting small values or having a steep negative slope at the origin.

These conditions favour a loop-shaped stock-recruitment relation but they are not necessary conditions. Biologically, they will be achieved if either:

– sexual maturity is precocious;

Table 5. – Maturity ogive, weight at age and fishing pattern used for yield per recruit calculation for the SAITHE VIa (anon., 1993).

	Age maturity	Weight in the catch (kg)	F mean$_{90-92}$
1	0.00	0.546	0.007
2	0.00	0.794	0.110
3	0.00	0.984	0.443
4	0.00	1.252	0.807
5	1.00	1.871	0.750
6	1.00	2.534	0.877
7	1.00	3.678	0.980
8	1.00	5.043	0.927
9	1.00	6.566	0.880
10+	1.00	8.989	0.880

– sexual senescence exists (or a shift of old fish sex-ratio decreasing the number of females (Fig. 4));

– growth rate is low, especially in old fish;

– natural mortality is high;

or:

– the potential for production is high,

– productivity of the stock for small fishing efforts is high (high slope at the origin for the production model).

The various biological characteristics presented above are those of many pelagic fish.

Simulated inferences from a biomass density dependence

It is the non-linearity of the relationship linking biomass and fecund biomass that allows us to consider stock-spawning biomass curves presenting a maximum and hence loop-shaped stock-recruitment relationships (Fig. 4). Actually, in the generalized production model we use, density-dependence is a function of the stock biomass but not of the stock spawning biomass. This density-dependence is assumed to be expressed at the level of the recruitment at equilibrium. Hence, the decrease of the biomass at equilibrium due to an increase of effort could lead to an increase of the recruitment which would cause an increase of the stock spawning biomass (annex 2). Stock spawning biomass and biomass at equilibrium do not necessarily vary in parallel (Fig. 4). A curve with a maximum used as a model for the stock spawning biomass as a function of effort is hence realistic and is particularly comprehensive when the fecundity rate decreases for old fish.

Let us consider the case where stock spawning biomass admits a maximum when effort increases (Fig. 5). As a consequence, the stock-recruitment relationship forms a 2D loop resulting from a 3D curve (Fig. 6). The simulation clearly shows that in the range where the curve forms a loop, the two possible levels of recruitment correspond with two different fishing effort multipliers and then with two different age structures of the stock (Fig. 5-6). If the fishing pattern does change, the recruitment versus stock spawning biomass curve will also be modified.

If one introduces a random perturbation ($R = a.SSB \cdot e^{-b.\varepsilon.B}$ with ε a random number) to the stock-recruitment relationship (Fig. 5), a « cloud » of extremely scattered points makes the loop impossible to detect visually. Then, one can easily understand that even if a loop shaped curve does exist, it will be very difficult to detect because of the environmental fluctuations.

Each point of the loop shaped stock-recruitment relationship is an equilibrium point function of a given effort. This equilibrium arise with realistic parameters. If we increase parameters until an unrealistic range, the system never reaches equilibrium rather limit cycles and chaos. What happens to the recruitment versus stock spawning biomass curve if parameters are increased until the simulated stock never reaches an equilibrium? Ricker stock-recruitment curve is well known to generate limit cycles and chaos for high (but unrealistic) values of the parameters (May, 1974; Lepage *et al.*, 1995). If we plot the recruitment points versus the stock spawning biomass generated by such a chaotic dynamics (we draw the discrete phase portrait of the dynamical system), the points appear in a

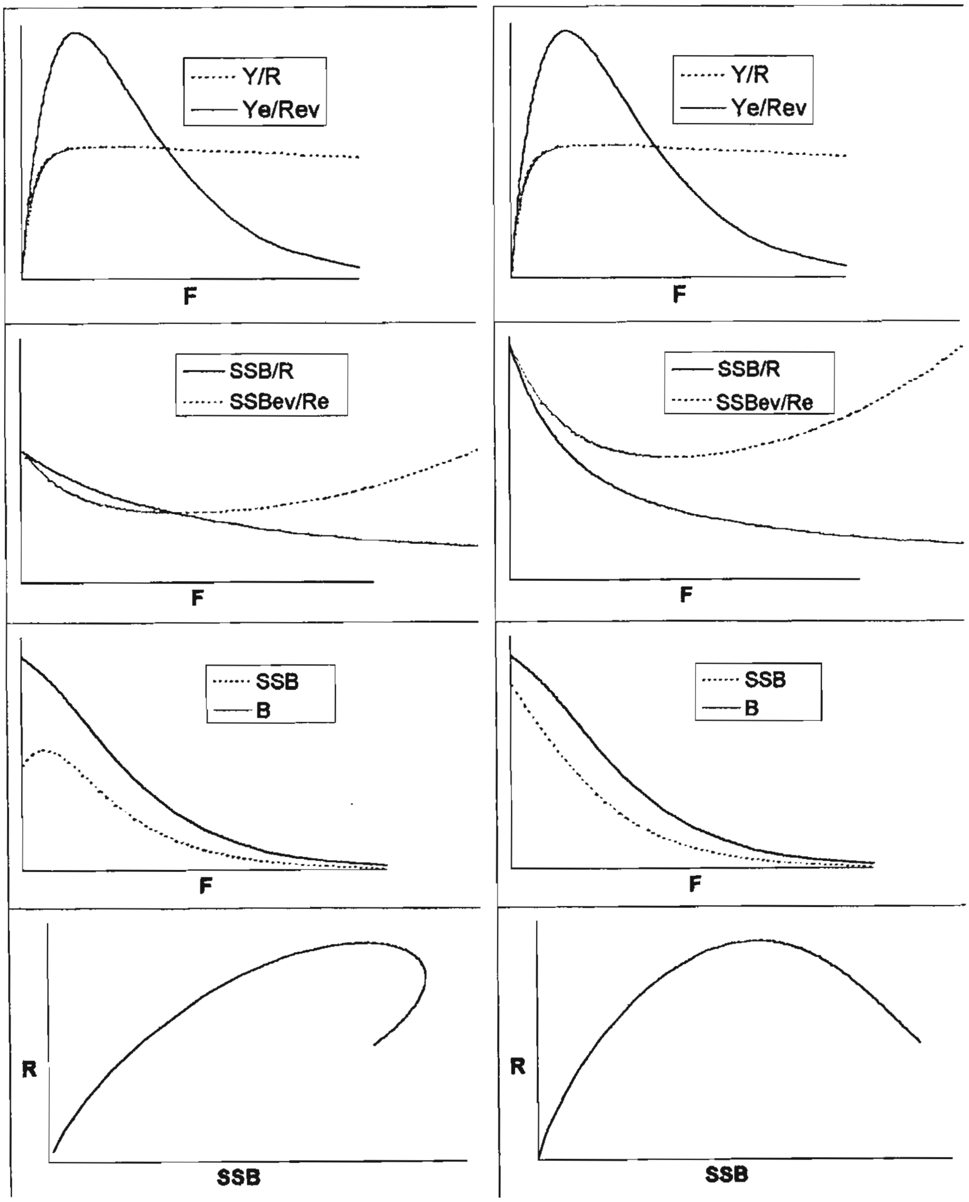

Figure 4. – Determination of the stock-recruitment relation for an imaginary stock based on the North-East Atlantic stock of mackerel. On the right, the fecundity rate is equal to one, from sexual maturity stage to death. On the left, old animals undergo sexual senescence, leading to a decrease of their fecundity rate.

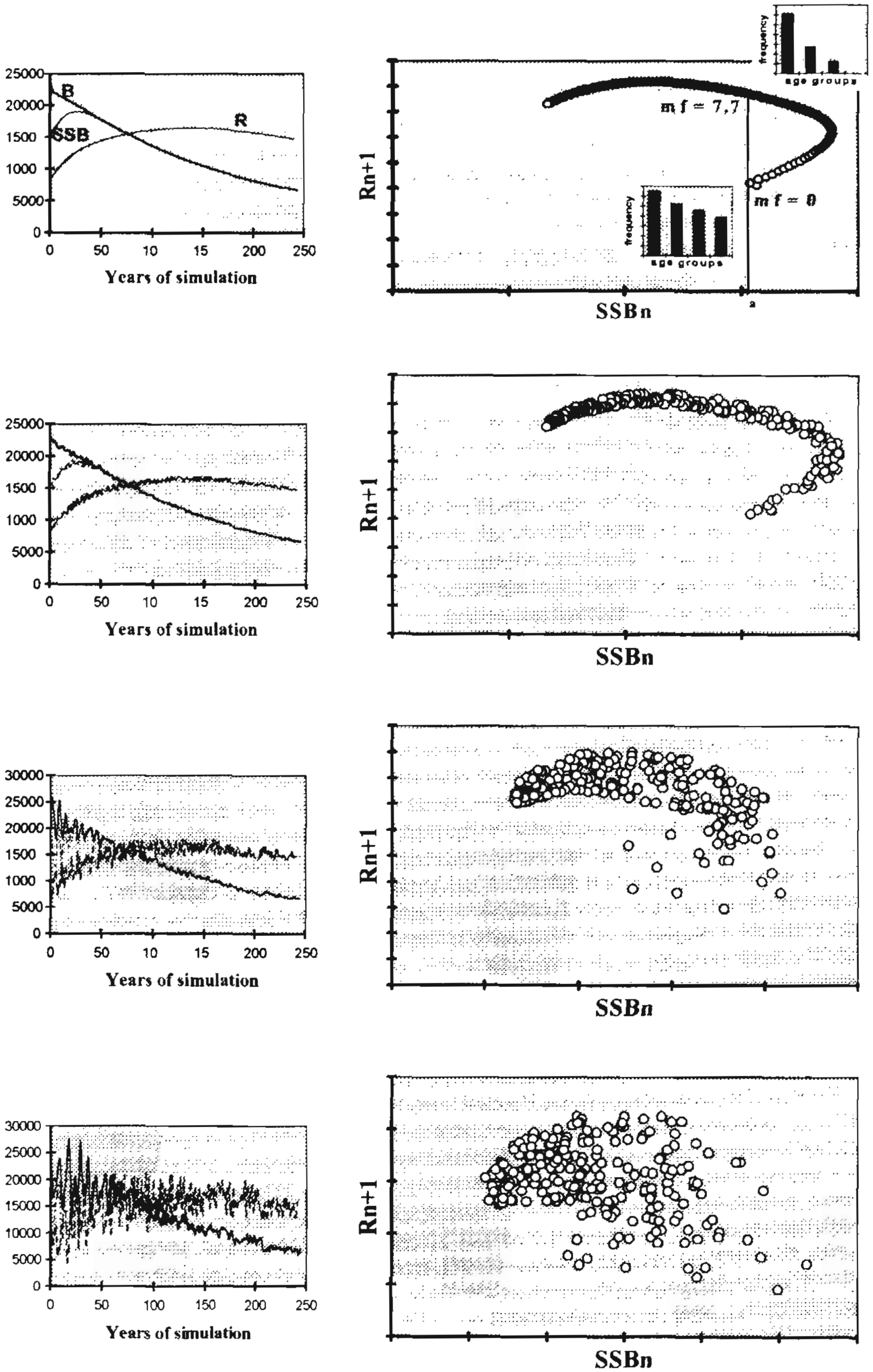

Figure 5. – The left column presents simulated evolution of recruitment, biomass and stock spawning biomass over 250 years (see text). The right column presents a loop shaped stock-recruitment relationship obtained by simulation. Effort is slowly increased from 0 (year 0) to a multiplier equals to 25 (year 250) by steps of 0. 1. Each point is almost in an equilibrium situation. For the same level of stock spawning biomass correspond two levels of fishing effort ($mf = 0$ and $mf = 7.7$) and then two different age distribution, two different biomass levels and two different recruitment levels. From line 2 to line 4, environmental random noise is added to the simulation ($R = a.SSBe^{-b.\varepsilon.B}$ with ε a random number). Line 2 $\varepsilon = 0.05$, line 3 $\varepsilon = 0.2$, at the bottom $\varepsilon = 0.5$. For relatively low levels of perturbation the loop shaped relationship is « concealed » and cannot be observed.

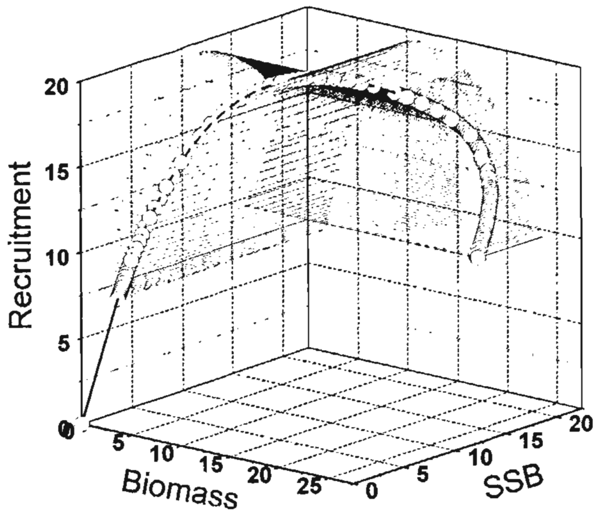

Figure 6. – Three-dimensional stock-recruitment relationship ($E(R) = f(B, SSB)$). The diagram clearly shows that the two-dimensional diagram is a projection of the three-dimensional one. It is also seen that in the case of a loop-shaped relationship $R = f(SSB)$, two different recruitment levels for the same stock spawning biomass arise for different biomass levels.

completely unpredictible order but they finally cover the Ricker curve (Fig. 7). With the modified stock recruitment model (equation (4)), the phase portrait can also be drawn in two dimensions. But because $R = f(SSB, B)$, the phase portrait requires three dimensions and the classical representation in two dimensions is not completely meaningful (Fig. 7) in terms of a stock-recruitment relationship!

DISCUSSION

A stock-recruitment relation curve: relevant or irrelevant?

Most of the stock-recruitment relationship models used in fisheries science (Ricker, 1954; Beverton and Holt, 1957; Deriso, 1978; Shepherd, 1982) are non-linear functions of the stock spawning biomass combining positive density-dependent effects (proportionality of the number of eggs on the spawning-stock biomass) and negative density-dependent effects (such as increase of the natural mortality of pre-recruited stages with their number). Those models permit us to account for the drop of recruitment for very low levels of spawning-stock biomass (a zero stock will produce a zero recruitment!) and for the obvious resilience of stocks.

Numerous authors have questioned the relevance of a deterministic stock-recruitment relationship in accounting for the fluctuations of the recruitment in teleost fish recruits (Gulland, 1983; Koslow, 1992). They argue that, in most cases, the recruitment fluctuates in such a way that it is impossible to fit a curve. The high fecundity rates of most teleost fish (10^4-10^6 eggs per female) and the high natural mortality of the pre-recruited stages induces a high natural variability of the recruitment. Actually, the natural mortality acts exponentially on the number of fish eggs. Consequently, if the number of pre-recruits is very high, even low variations in mortality induce strong variations in the number of recruits (Koslow, 1992). The strong influence of the environment on the mortality of pre-recruited stages hence often determines the evolution of recruitment (Garcia, 1983; Gulland, 1983; Cury and Roy, 1989; Fréon, 1991). It follows from this that one seldom observes a sufficiently clear stock-recruitment relationship to fit a curve. Koslow (1992) used theoretical simulations to demonstrate that even if the recruitment of teleost fishes is governed by a stock-recruitment relationship, fish fecundity amplifies the slight variations of the pre-recruited stage mortality in such a manner that it would be impossible to identify the stock-recruitment relationship from the observed recruitment.

These various considerations have often led to doubts being cast over the value, or even the very existence of a stock-recruitment relationship. In the face of recruitment variability, stock management has extensively relied on the calculation of the yield per recruit (which by definition -and it is its interest-set aside the fluctuations in recruitment). Recent examples have shown convincingly the necessity of preventing recruitment overfishing (Hilborn *et al.*, 1992; Myers *et al.*, 1995). Together with other empirical methods, a curve expressing the stock-recruitment relationship can be used to answer the crucial questions set by the follow-up and the management of the stocks (What are the risks of collapse for the stock? What is the level of exploitation that may lead to recruitment overfishing?). In this perspective, Gulland (1983) defines the stock-recruitment relationship as the curve fitted to mean recruitment as a function of the spawning-stock biomass. Around this curve is distributed the observed recruitment which is also dependent on environmental factors: « the parent stock will determine a distribution of possible recruitment; the particular value within this distribution will be determined by the various environmental factors ». Similarly, the curve of the stock-recruitment relationship can be defined as the relation between the recruitment expectation and the descriptives variables of the parent stock such as the classicaly used stock spawning biomass. Then, $R = E(R) + \varepsilon$ with $E(R) = F(SSB)$, the expectation of the recruitment and ε, a random variable of mean equal to zero. In the following of the text, the « stock-recruitment relationship » expression will be used by extension for the relation $E(R) = F(SSB)$. This relation allows the isolation of the strictly monospecific phenomenons (as well as the environmental phenomenons with constant effects on recruitment) called intrinsic, from other variable determining phenomenons (including the abiotic factors-temperature, salinity, ...– and the biotic factors -larval's food, predators abundance...–) called

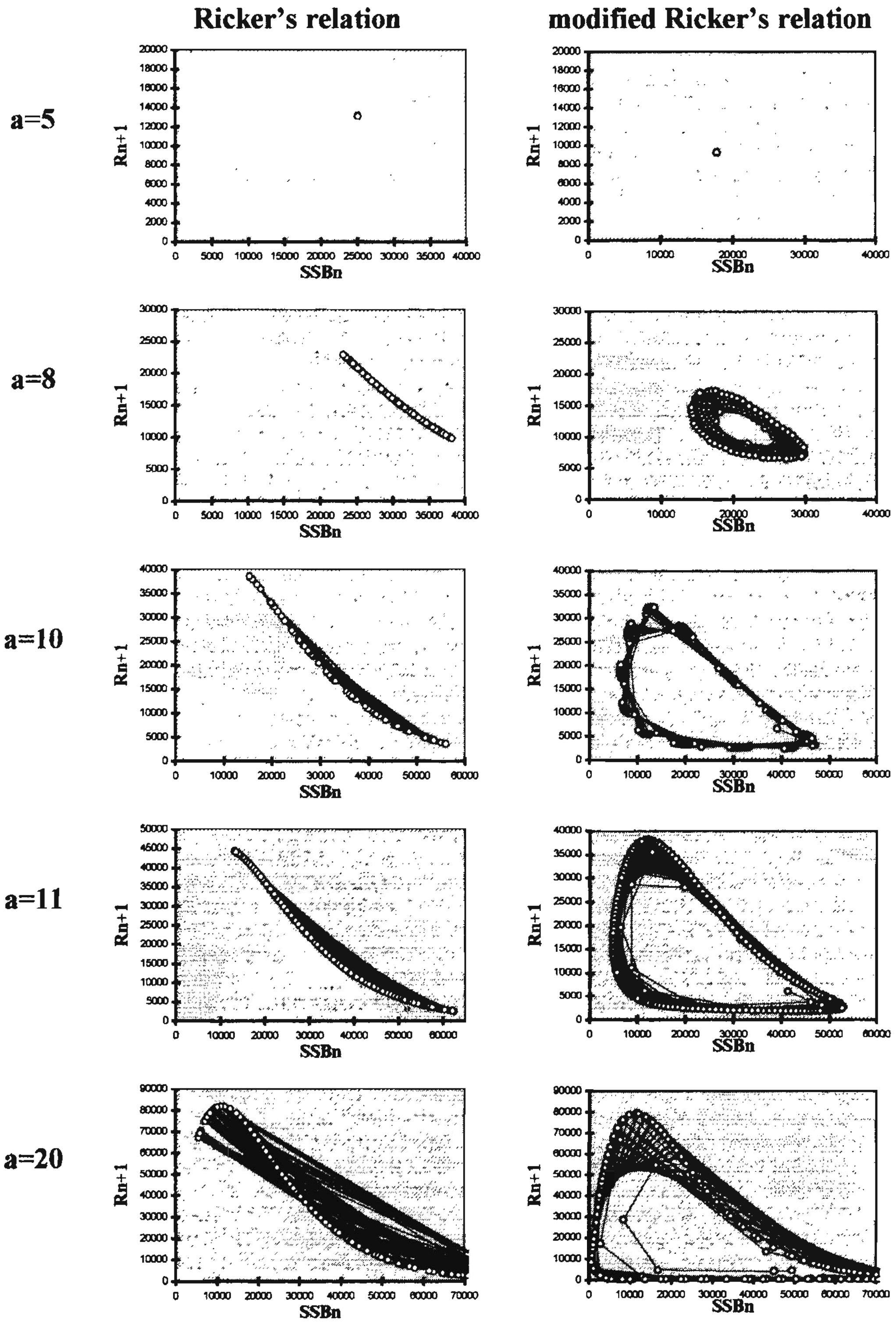

Figure 7. – Simulated comparison of the phase diagrams (recruitment at time $t+1$ function of stock spawning biomass at time t) obtained for different values of the parameters a for the Ricker model and modified Ricker model $E(R) = a.SSB \cdot e^{-b.B}$ ($b = 9.10^{-5}$ and effort equals 0 over the 250 years covered by the simulation; see Table 1 for other parameters). For $a = 5$, the dynamics stay in an equilibrium state which corresponds to the loop-shaped relationship when effort increases. For $a = 8$, both dynamics converge to a limit cycle. For high (unrealistic) values of the parameter a, dynamic is chaotic (see text). Because the modified model is a function of two variables, the 2D diagram is not very meaningful and should be replaced by a 3D one.

extrinsic. Then, the observed recruitment must be considered as resulting from a combination of the intrinsic expectation and the extrinsic factors.

The method we have applied uses the fitting of a production model associated with the knowledge of a yield per recruit curve. The production model expresses an expectation of the production conditioned by given past efforts (and biomass). The stock-recruitment relationship obtained must also correspond to a conditional expectation of recruitment.

Scientific background

By implicitly making the assumption that density-dependence compensatory phenomena are only evident in the pre-recruited stages (annex 1), various authors have proposed to associate a stock-recruitment relationship with a yield per recruit age-structured model in order to assess a production model (Beverton and Holt, 1957; Cushing, 1973; Garrod *et al.*, 1974; Shepherd, 1982; Gulland, 1983). Without making this assumption, Kimura (1988) proceeds in the same way by using a model of stock reduction analysis. The principle of the method we propose is, on the contrary, to identify in a production model the effects of recruitment by isolating them from the effects of growth and mortality by comparison with a yield per recruit model. Its main interest is to permit the determination of a stock-recruitment relationship from catches per age data.

Pauly (1979, 1982) applies a method close to ours. He uses the catches and the yield per recruit of the year a to determine the recruitment of the year a. His method is not based on a production model in an equilibrium situation leading to a stable recruitment curve (and hence to a stock-recruitment model), but on annual production data leading to the recruitment of a given year. It is therefore only applicable to cases for which the period of a cohort exploitation is short enough for recruitment to be a factor directly determining production. Furthermore, it is of value only when data are insufficient to determine recruitment by cohort analysis.

Deriso (1980) uses data of catches and effort to assess by regression all biological parameters of its model, including the parameters of stock-recruitment relationship. The method we propose uses a process conceptually close to his. Nevertheless, instead of attempting to determine biological parameters of growth and mortality, it uses them, accurately assessed by more direct methods.

The stock-recruitment relationship as defined here can be considered as a generalized stock-recruitment relationship (GSRR). It is permits us to obtain different families of curves, some of which are very close to models usually used in fisheries science (Ricker, 1954; Beverton and Holt, 1957; Deriso, 1978; Shepherd, 1982) but some forms of the model we describe exhibit other shapes such as the family of loops. The reliability of the resulting relationships depends, in particular, on the sensitivity to the choice and to the fitting of the production model. Therefore, those relations must be cautiously handled by keeping in mind, on the one hand, the production model fitting assumptions:

- constancy of the fishing pattern over the production model fitting period,
- the possibility of fitting an equilibrium model to data that are from a stock in a period of charge,

and, on the other hand, the problems linked to the sensitivity of the yield per recruit model and particularly the sensitivity to the assumption of natural mortality and the sensitivity to the tuning method of the cohort analysis. For the determination of the GSRR, it is possible to use production models adapted to different cases or to different aims; models fitted without equilibrium hypothesis, models with effects of environment (Fréon, 1991); models with an inaccessible quantity of biomass (Laloë, 1988).

The fitting that is carried out here is simply for illustration; other fits of a production model are undoubtedly possible with the same level of statistical validity (Laloë, 1995). They would lead to stock-recruitment curves of different shapes from those described here.

The crucial question of density-dependence

For the stock-recruitment relationship model we propose, the expectation of the recruitment is a deterministic function of the total biomass ($E(R) = f(B, SSB)$). From a biological point of view, it is quite defensible that the density-dependence can be a function of the total biomass. This intra-specific competition for a limited resource could emerge at different levels:

- the number of eggs spawned per unity of spawning biomass (R/SSB) (the stock spawning biomass SSB is in competition with the whole biomass B);
- the growth of the adults and hence of the level of stock spawning biomass depends on the total biomass level;
- the mortality of larvae by adult predation (fertile or not);

It is hence more realistic to take into account both biomass and stock spawning biomass as two components of the recruitment expectation as we did in the simulation.

If we admit that $E(R) = f(B; SSB)$, a 2D. diagram expressing the expectation of recruitment versus the stock spawning biomass is only a projection of the 3D graphic where R is function of B and SSB. Actually, to the same level of the total stock spawning biomass may correspond several levels of biomass depending on the fishing pattern. And therefore, to the same level of stock spawning biomass may correspond several levels of recruitment. Consequently, to each different fishing pattern (different relation between B and SSB) corresponds a different curve of $E(R) = f(SSB)$ on the $E(R) = f(B; SSB)$ surface (Fig. 8).

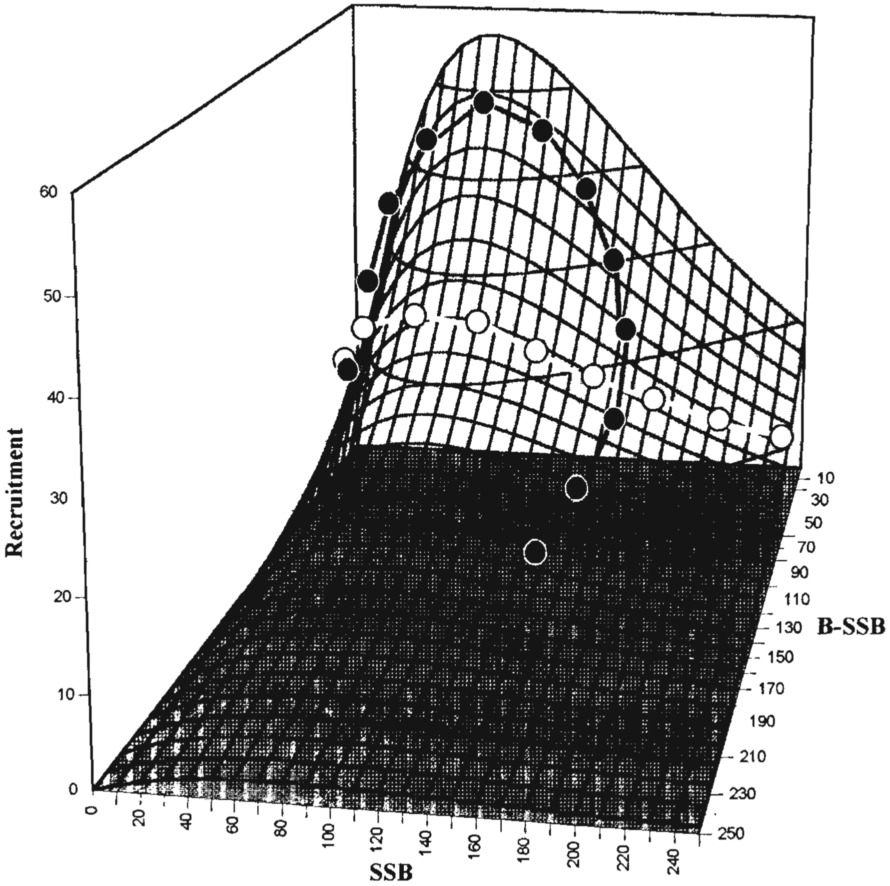

Figure 8. – Diagram of a theoretical 3D stock-recruitment relationship expressing $E(R)$ versus SSB and B-SSB (because we necessarily have $B \geq SSB$). The surface is calculated with the modified Ricker model $E(R) = a.SSBe^{-b.B} = f(B, SSB)$. The points represent two different trajectories due to two different fishing patterns.

If we do accept a relationship $E(R) = f(B, SSB)$, a 3D stock recruitment relationship will be logical. But if we can assume that the fishing pattern is constant (not necessarily the effort) or the recruitment sufficiently stable for the relationship between B and SSB to be constant, then a 2D graph $E(R) = f(SSB)$ will be sufficient.

Which applications are appropriate for the recruitment predictions?

If one adds « extrinsic » environmental fluctuations, at present hardly predictable, to « intrinsic » fluctuations of the recruitment, one can easily understand that quantitative predictions of the recruitment are, if not impossible, at least extremely problematic. Because of this impredictability, a qualitative investigation of recruitment evolution (*i.e.* an investigation of its expectation) would be facilitated by knowledge of the generalized stock-recruitment relationship. This relationship could permit the determination of recruitment overexploitation levels usable by fisheries administrators.

Quantitatively speaking, the recruitment evolution can be theoretically predicted knowing the main « extrinsic » determinants (environmental) whose effects alter the intrinsic stock-recruitment relationship. Both qualitative and quantitative applications of the GSRR are hence conceivable.

CONCLUSION

The stock-recruitment relationship is a necessary tool for both understanding and management of fish stocks. As Gulland wrote in 1983, it must be understood in terms of conditional expectation of recruitment because recruitment is a multivariate phenomenon.

From a practical point of view, the method we propose allows the fitting of a generalized stock recruitment relationship ($GSRR$) to production data. It gives satisfactory aspect curves close to models of Ricker (1954) and Beverton and Holt (1957). It also gives loop shaped curves which allow two possible levels of recruitment for the same level of stock spawning biomass but different fishing effort.

From a theoretical point of view, 3D curves ($E(R) = f(B; SSB)$) could be more realistic than 2D curves ($E(R) = f(SSB)$). Those 3D curves can be projected in 2D diagrams with the assumption of stable demographic structure (constant fishing pattern for instance).

ANNEX 1

Besides growth and mortality phenomena, production models take heuristically into account the increase of stock productivity when there is a reduction of biomass (*i.e.* a fishing pressure):

« – demographic structure modifications: when fishing makes old fish scarce, the increase of the proportion of young fish increases the total productivity because young fish have a higher productivity;

– *increase of R/SSB*, recruitment given by a spawning biomass unity;

– increase of the individual growth. This phenomenon is linked with the trophic competition. (...)

– decrease of the natural mortality » due to the predation by adult fish (Laurec and Le Guen, 1981).

Implicitly, the method we propose assumes that all the compensation phenomena are concentrated on the pre-recruited stages. This assumption is generally considered as not being an important constraint (Sissenwine and Shepherd, 1987). Indeed, one considers that the natural mortality is less variable after the younger ages (Cushing, 1975) and that the growth modification of adult fish (phenotypic plasticity) is negligible compared with the density dependent modifications of the number of prerecruited fish. « The key to both the density-dependent processes which regulate the size of fish populations, and the stochastic variations which perturb it, is to be found during the egg and larval stages of life history, when enormous mortalities occur » (Shepherd *et al.*, 1982). Following this point of view, Iles (1980) even suggests the recruitment age to be defined as the age after which the biological phenomena are independent from the fish density.

ANNEX 2

Biomass density-dependence even permits us, by carrying the reasoning to the extreme, to consider that a curve of biomass versus effort may admit a maximum for a non-null effort. Let us imagine, for instance, an ideal population of biomass B1, consisting of young fish, all fecund, and of old fish all infecund. Recruitment depends on two antagonistic components: it depends on the proportionality of the number of eggs spawned to the fecund biomass, and on the mortality of the pre-recruited stages which is an increasing function of the total biomass. In the equilibrium situation, the first component exactly compensates for the second one. Let us now consider an exploitation where all non-fecund old fish are fished out. The population then consists exclusively of fecund fish ($B = SSB$). The decrease of the level of the total biomass causes a decrease in the mortality density-dependent component which leads to an increase of recruitment, and hence to an increase of the level of the stock spawning biomass. This process goes on until the level of the fecund biomass reaches the level B1. Then, the density-dependence component regains its initial level, but it is not sufficient merely to compensate for the component proportional to the stock spawning biomass which has also increased in comparison with its initial value. The recruitment keeps on increasing until its two antagonistic components have reached again an equilibrium. The final level of the total biomass at equilibrium is greater than its initial value.

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REFERENCES

Anon. 1993. Report of the working group on the assessment of northern shelf demersal stocks. *Int. Counc. Explor. Sea.* 20.

Anon. 1994. Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. *Int. Counc. Explor. Sea.* 2.

Beverton R. J. H., S. J. Holt 1957. On the dynamics of exploited fish populations; *Fish. Invest. Lond. Ser.* 2, **19**, 533 p.

Clark C. W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. *J. Cons. Int. Explor. Mer* **36**, 7-14.

Cury P., C. Roy 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* **46**, 670-680.

Cury P. 1991. Les contraintes biologiques liées à une gestion des ressources instables. *In*: Pêcheries Ouest Africaines. Variabilité, instabilité et changement. P. Cury, C. Roy eds. 506-523.

Cushing D. H. 1973. The dependence of recruitment on parent stock. *J. Fish. Res. Board Can.* **30**, 1965-1976.

Cushing D. H. 1975. Marine ecology and fisheries. Cambridge University Press, 278 p.

Deriso R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* **37**, 268-282.

Fox W. W. J. 1975. Fitting the generalized stock-production model by least square and equilibrium approximation. *Fish. Bull. U. S.*, **73**, 23-37.

Fréon P. 1991. L'introduction d'une variable climatique dans les modèles globaux de production. *In*: Pêcheries ouest africaines. Variabilité, instabilité et changement. P. Cury, C. Roy eds. 395-424.

Garcia S. 1983. The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretation? *Océanogr. Trop.* **18**, 25-48.

Garrod D. J., B. W. Jones 1974. Stock and recruitment relationship in the NE Arctic cod stock and the implications for management of the stock. *J. Cons. Int. Explor. Mer* **36**, 35-41.

Gulland J. A. 1977. The stability of fish stocks. *J. Cons. Int. Explor. Mer* **37**, 199-204.

Gulland J. A. 1983. Fish stock assessment, a manual of basic methods. FAO/Wiley Series on Food and Agriculture, Vol. 1.

Hilborn R., C. J. Walters 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman and Hall, 570 p.

Iles T. D. 1980. Environmental pressure and intra -and inter-year class competition as determinants of year class size. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* **177**, 315-331.

Kimura D. K. 1988. Stock-recruitment curves as used in the stock-reduction analysis model. *J. Cons. Int. Explor. Mer.* **44**, 253-258.

Koslow J. A. 1992. Fecundity and the stock-recruitment relationship. *Can. J. Fish. Aquat. Sci.* **49**, 210-217.

Laloë F. 1988. Un modèle global avec quantité de biomasse inaccessible liée aux conditions environnementales. Application aux données de la pêche ivoiro-ghanéenne de *Sardinella aurita. Aquat. Living Resour.* **1**, 289-298.

Laloë F. 1995. Should surplus production models be fishery description tools rather than biological models? *Aquat. Living Resour.* **8**, 1-16.

Laurec A., J. C. Le Guen 1981. Dynamique des populations marines exploitées. Publ. CNEXO., Rapp. scient. techn. 45 p.

Lepage C., P. Cury 1995. Age-dependent fecundity and the dynamics of a density-dependent population model. *Math. Comput. Model.* **21**, 13-26.

Maury O., D. Gascuel 1996. Stock-recruitment relationship, minimum biological levels and stock collapse risk: a method of assessment based on production data. *Int. Counc. Explor. Sea, Statistics Comm. CM.D*, 5.

May R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science* **186**, 645-647.

Myers R. A., A. A. Rosenberg, P. M. Mace, N. J. Barrowman, V. R. Restrepo 1994. In search of thresholds for recruitment overfishing. *ICES J. Mar. Sci.*, **51**, 191-205.

Myers R. A., N. G. Cadigan 1993. Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* **50**, 1576-1590.

Myers R. A., N. G. Cadigan 1995. Was an increase in natural mortality responsible for the collapse of northern cod? *Can. J. Fish. Aquat. Sci.* **52**, 1274-1285.

Pauly D. 1979. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality, and stock recruitment relationships. *In*: Stock Assessment for tropical small-scale fisheries. Proc. workshop Sept. 1979 Univ. Rhode Island, Kingston. S. B. Saila, P. M. Roedel eds. Kingston, 154-172.

Pauly D. 1982. A method to estimate the stock-recruitment relationship of shrimps. *Trans. Am. Fish. Soc.* **111**, 13-20.

Pella J. J., P. K. Tomlinson 1969. A generalized stock production model. *Bull. IATTC* **13**, 419-496.

Ricker W. E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**, 152-216.

Shepherd J. G., D. H. Cushing 1982. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons. Int. Explor. Mer* **39**, 160-167.

Shepherd J. G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Cons. Int. Explor. Mer* **40**, 67-75.

Sissenwine M. P., J. G. Shepherd 1987. An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* **44**, 913-918.

Thompson W. F., F. H. Bell, 1934. Biological statistics of the Pacific halibut fishery, 2, Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. (Pacific Halibut) Comm., 8, 49 p.