Int. Symp. Long Term Changes Mar. Fish Pop., Vigo 1986

INTRODUCTION OF ENVIRONMENTAL VARIABLES INTO GLOBAL PRODUCTION MODELS

Pierre FREON
(ORSTOM, BP 81, 97201 Fort de France Cedex, Martinique, France)

Abstract

It is well-known that the traditional use of global production models is not suitable for certain stocks, because fishing effort variations explain only a small part of the total variability of annual catches. Often the residual variability originates from the influence of climatic phenomena, which disturb either the abundance or the catchability of a stock from one year to the next.

Therefore, in this paper, one (sometimes two) additional environmental variable has been inserted into the traditional models in order to improve their accuracy. These variables appear in the formulae, either at the level of the stock abundance, or at the level of the catchability coefficient, or at both levels. The models described here were first developed from Schaefer's linear production model, then from Fox's exponential model. The generalized production model (Pella and Tomlinson) has also been used as a starting point in one case.

The limitations of this kind of model have been considered, especially those related first to the decrease in number of degrees of freedom compared with traditional models, and secondly in getting good fits due only to chance if the models and the variables are selected after an exhaustive and fully empirical procedure of research, among many formulae and data sets.

When a stock is not under equilibrium (transitional state), the most favourable cases, using this type of model, are obtained with short-lived species, or when the critical period of the environmental influence is relatively short. Furthermore the inter-annual fluctuations of the environment should show a mean duration (sufficiently short in relation to the data set length, but sufficiently long in relation to the critical period duration and to the duration of the exploited stage).

Under these conditions, the models can provide a fairly good interpretation of fishery history, particularly when a stock

collapses unexpectedly without any appreciable increase in the nominal fishing effort. These models can also provide a useful tool for the efficient management of a fishery in those instances where climatic phenomena can be forecast, or when their influence is restricted to the year preceding exploitation.

Resumen

Es bien conocido que el uso tradicional de los modelos de producción no es adecuado para ciertas poblaciones, porque las variaciones del esfuerzo de pesca explican sólo una pequeña parte de la variación total de las capturas anuales. Con frecuencia la variación residual se origina a causa de la influencia de fenómenos climáticos, que perturban ya sea la abundancia o la capturabilidad de la población de un año a otro.

Por tanto, se han incluído en los modelos tradicionales una (a veces dos) variables ambientales adicionales para mejorar la exactitud. Esta variable aparece en las fórmulas, ya sea al nivel de abundancia de la población, ya sea al nivel de coeficiente de capturabilidad, o a ambos niveles. Estos modelos han sido en principio desarrollados a partir del modelo de producción lineal de Shaeffer, luego del modelo exponencial de Fox. El modelo de producción general (Pella y Tomlinson) se usó sólo como punto de partida en un caso.

Se han considerado los límites de esta clase de modelos, especialmente los relacionados en primer lugar con la disminución del número de grados de libertad, y luego con el mejoramiento del ajuste entre los valores estimados y observados debido sólo al azar.

Cuando la población no está en equilibrio (estado de transición), los casos más favorables se obtienen con especies de vida corta, o cuando el período crítico de la influencia ambiental es relativamente corto. Además sus fluctuaciones inter-anuales deben mostrar un período medio de tiempo (suficientemente corto de acuerdo con la longitud de datos aportados, suficientemente largo de acuerdo con la longitud del período crítico y la longitud de la etapa de explotación).

En estas condiciones, los modelos permiten una buena interpretación de la historia de la pesquería, particularmente de los colapsos de poblaciones, que tienen lugar imprevistamente sin un aumento apreciable en el esfuerzo nominal de pesca. A veces este método sirve para una gerencia eficiente de la pesquería, pero solo si es posible predecir los fenómenos climáticos, o si se usa solamente en el año previo al de la explotación.

I. Introduction

The usual global production models for stock assessment use only one input variable: the fishing effort. From the initial linear model conventionally called "Shaefer's model" (Graham, 1935; Schaefer, 1954), two other global models have been widely used: the exponential model (Garrod, 1969; Fox, 1970) and the generalized production model (Pella and Tomlinson, 1969). They have been revised and adapted in order to improve the fit of observed data to the models, specially for non-equilibrium conditions of the fishery or for time lags in the stock response (Schaefer, 1957; Gulland, 1969; Fox, 1975; Walter, 1973, 1975; Schnute, 1977; Fletcher, 1978; Rivard and Bledsoe 1978; Uhler, 1979). In these models variability not linked to the fishery is considered as a random noise. Some recent stochastic models use a random variable (Doubleday, 1976).

Although relationships between environment variations and stock abundance or availability have been described (see for examples Saville, 1980; Le Guen et Chevalier 1983, Sharp and Csirke, 1983; Csirke and Sharp, 1983), I did not find any deterministic model using both the fishing effort f and a climatic variable V, representative of the environment. Such an approach was suggested by Dickie (1973) but, as far as I know, only Griffin *et al.*, (1976) used an empirical relationship between shrimp yield Y on the one hand, and fishing effort and river out-flow on the other:

$$Y = aV^{b} \ (1 - c^{f})$$

where a, b and c are constant parameters. This relationship is an increasing asymptotic function and so far is relevant only in a few special cases. However, we will see that theoretical bases for such models are available in various publications on terrestrial or aquatic ecology. A number of authors have introduced hydroclimatic variables into the structural production models (Nelson *et al.*, 1977; Loucks and Sutcliffe, 1978; Parrish and MacCall, 1978), but these all require detailed data on the life history as do some of the more complex simulation models (Laevastu and Larkins, 1981).

The aim of this paper is to give the theoretical basis for production models using a climatic variable. The influence of environmental factors has been considered first at two levels: on stock abundance and on stock catchability. For each case the linear and exponential models (and sometimes the generalized model) are considered. Then the case of an influence on both abundance and catchability is considered.

II. HOW THE ENVIRONMENTAL VARIABLE ACTS UPON A STOCK

II. 1. Definitions

Let be an environmental or climatic variable, any environmental factor likely to represent an index of a natural phenomenon which would modify the fisheries catches. Common examples are temperature, salinity, wind speed, turbidity, strength or direction of currents, river out-flow, etc.

The common notation, mainly borrowed from Ricker (1975), will be used in this paper:

- B : Instantaneous stock biomass
- Bi : mean annual biomass
- B_∞: environmentally limited maximum biomass of "carrying capacity" (K of terrestrial ecological models)
- k : Constant of the rate of population increase (r of terrestrial ecological models)
- t : time, conventionally in years
- F : fishing mortality
- q : catchability coefficient
- f_i :annual fishing effort during year i, standardized to be proportional to F : $F_i = q_i \; f_i$
- Y_i :annual yield
- $\hat{Y}_i$:predicted annual yield
- U_i :annual mean catch per unit of effort (or c.p.u.e.)
- B_∞, f_∞, Y_∞ and U_∞ :correspond respectively to B, f, Y, and U under equilibrium conditions
- Y_{max} :maximal sustainable yield
- U_{max} :optimal c.p.u.e. corresponding to Y_{max}
- f_{max} :optimal effort corresponding to Y_{max}
- E :residual
- e :base of natural logarithms

II. 2. Mathematical bases

Lineal model

Surplus-yield models are based on a regulatory function of the rate of population increase, corresponding to logistic growth:

$$\frac{dB}{dt}\frac{1}{B} = \frac{k\,(B_\infty - B)}{B_\infty} = k\,(1 - \frac{B}{B_\infty}) \qquad (1)$$

Various authors, working on terrestrial ecology, studied the effects of an habitat modification (in time or space) on the relationship. A synthesis can be found in MacCall (1984). Habitat modification can theoretically be introduced into equation (1) in three different ways: effect on B_∞ only (fig. 1a), effect on k only (fig. 1b) or effect on both B_∞ and k .

Having analysed all these cases, Mac Call (1984) concludes that the last one is the most convenient, specially using the solution of a constant slope for equation (1) (fig. 1c):

$$\frac{dB}{dt}\frac{1}{B} = k - hB \qquad (2)$$

where k keeps the same meaning and h is the slope of the relative rate of population increase. It is obvious that: $h = k/B_\infty$ = constant, and so far h corresponds to k_1 from Schaefer (1954), who considered it already as a constant.

Considering that the variations of exploited biomass result from environmental condition and from fishery catches qfB leads to the usual equation of Schaefer's model:

$$\frac{dB}{dt} = kB - hB^2 - qfB = hB\,(B_\infty - B) - qfB \qquad (3)$$

According to that formulation, environmental factors may interact at only two levels: on q if catchability is changing, or on the pair of variables k-B_∞ (the ratio of these two variables being constant), if natural variations of abundance are considered. In the latter case, in order to make the presentation easier, I chose only the formulae where B_∞ and h appear, and allowed B_∞ to change according to the environment. It must be kept in mind however that any variation of B_∞ corresponds to a symmetrical variation in k (the inverse choice would lead to similar formulae). Let g(V) be the function representing the fluctuations of B_∞ according to the environment, and y(V) representing the fluctuations of q .

Schaefer's model assumes that, under equilibrium conditions, the rate of population increase is zero, which can be obtained from (3) if:

$$B_\infty = B_\infty - qf/h = g(V) - y(V)\ f/h \qquad (4)$$

such that:

$$U_e = qB_\infty = qB_\infty - q^2\ f/h = y(V)\ g(V) - y^2(V)\ f/h \qquad (5)$$

$$Y_e = fU_e = qB_\infty f - q^2 f^2/h = y(V)\ g(V)\ f - y^2(V)\ f^2/h \qquad (6)$$

f_{max} will be the value of f obtained by cancelling out the derivative of equation (6):

$$f_{max} = B_\infty h/2q = g(V)\ h\ /\ 2\ y(V) \qquad (7)$$

therefore:

$$U_{max} = qB_\infty\ /2 = y(V)\ g(V)/2 \qquad (8)$$

and:

$$Y_{max} = B_\infty\ h/4 = g^2\ (V)\ h/4 \qquad (9)$$

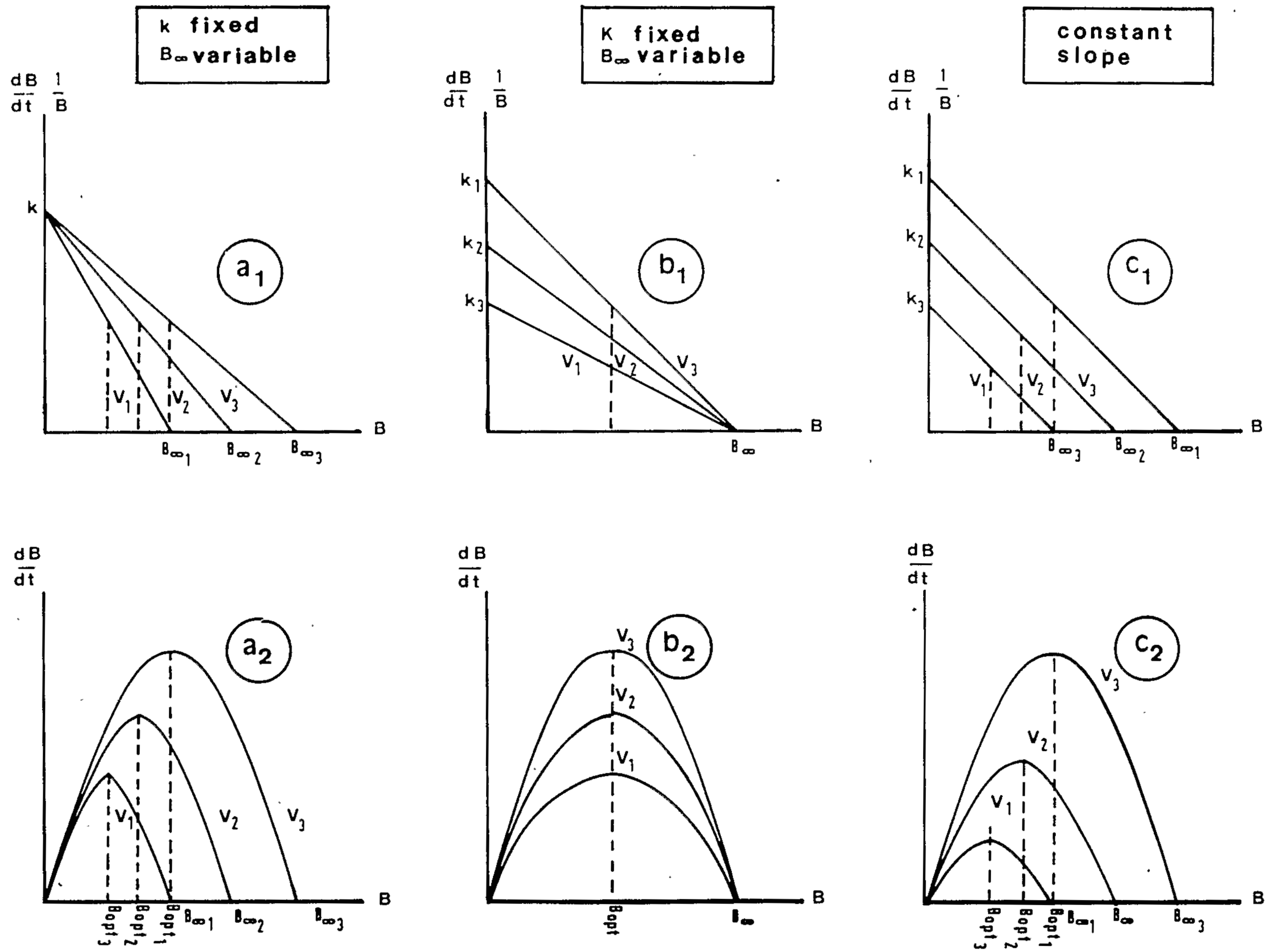


Fig. 1. Graphical comparison of three kinds of environmental effects on the relationship between the rate of growth of the biomass (relative rate in fig. a_1, a_2, a_3 and absolute rate in fig. b_1, b_2, b_3) and the size of this biomass, according to 3 values (V_1, V_2 and V_3) of an environmental variable (adapted from MacCall, 1984).

Exponential model

The exponential model described by Garrod (1969) and Fox (1970) supposes that:

$$\frac{dB}{dt}\frac{1}{B} = k\ (\log_e B_\infty \ - \log_e B\ ) \qquad (10)$$

In this formulation, not strictly equivalent to equation (1), in order to get a constant slope as before, k must be a constant and $B_\infty = g(V)$. In order to obtain a formulation similar to the linear models (and related to the generalized model) equation (1) must be written:

$$\frac{dB}{dt}\frac{1}{B} = k\ \left(\frac{\log_e B_\infty - \log_e B}{\log_e B_\infty}\right) = k - h\ \log_e B = h(\log_e B_\infty - \log_e B) \qquad (11)$$

where is a constant such as: $h = k/\log_e B_\infty$.

Following Fox's (1970) demonstration we obtain under equilibrium conditions (fig. 3b):

$$U_e = qB_\infty e^{-qf/h} = y(V)\ \ g(V)\ \ e^{-y(v)f/h} \qquad (12)$$

$$f_{max} = h/q = h/y(V) \qquad (13)$$

$$U_{max} = qB_\infty\ /e = y(V)\ g(V)/e \qquad (14)$$

$$Y_{max} = B_\infty\ h/e = g(V)\ h/e \qquad (15)$$

It must be stressed that owing to logarithm properties such models generate a single value for f_{opt}, independent of the variable V as far as abundance is only concerned, in opposition to previous linear models. In addition, the theoretical stock collapse is obtained when f reaches infinity, for any V value. In fact, these models behave as if in equation (1) k was a constant and B_∞ a variable. In order to overcome these difficulties, other formulations have been developed (see chap. III.2).

Generalized model

The basic equation of the generalized model (Pella and Tomlinson, 1969) can be written (Ricker, 1975):

$$B_\infty = (B_\infty^{m-1} + qf)^{1/(m-1)} \qquad (16)$$

where : $B_\infty^{m-1} = k/h$

Following the method used for linear models we get:

$$U_e = ((g(V)\ y(V))^{m-1} + y(V)^m\ f/h))^{1/(m-1)} \qquad (17)$$

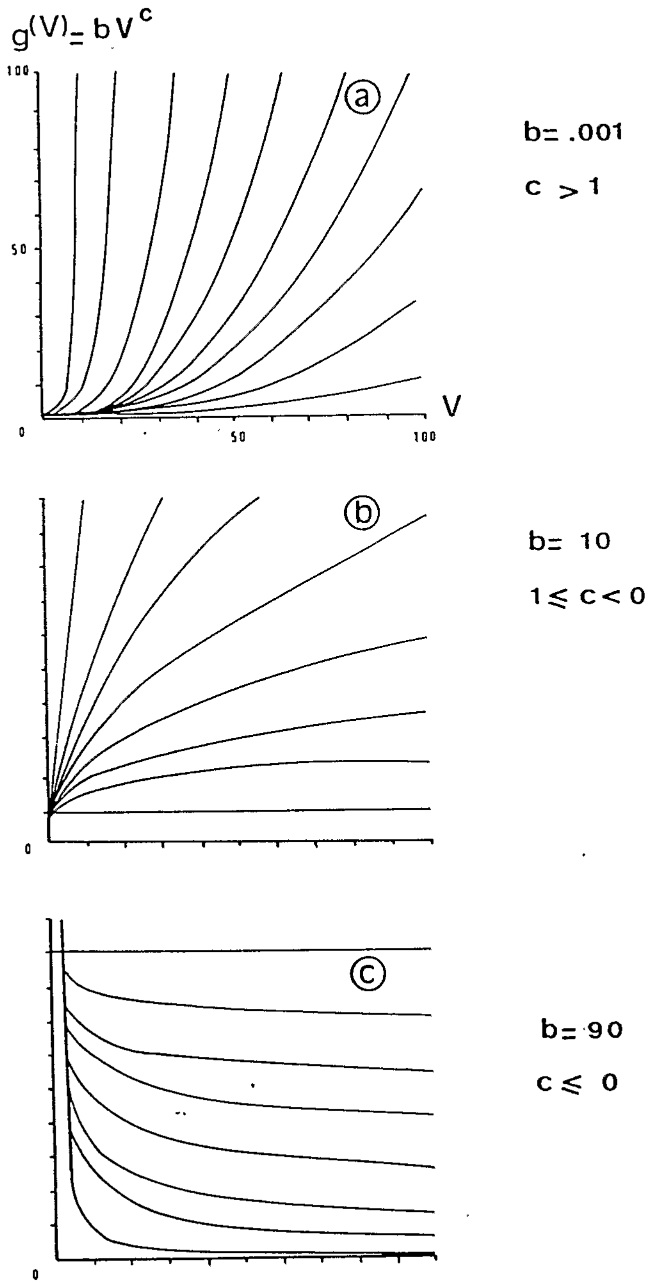


Fig. 2. Examples of graphical behaviour of the function g (V) = bV^C when V and g (V) are positive.

Fig. a : b = .001 and C > 1
Fig. b : b = 10 and 1 ≦ C < 0
Fig. c : b = 90 and C ≦ 0

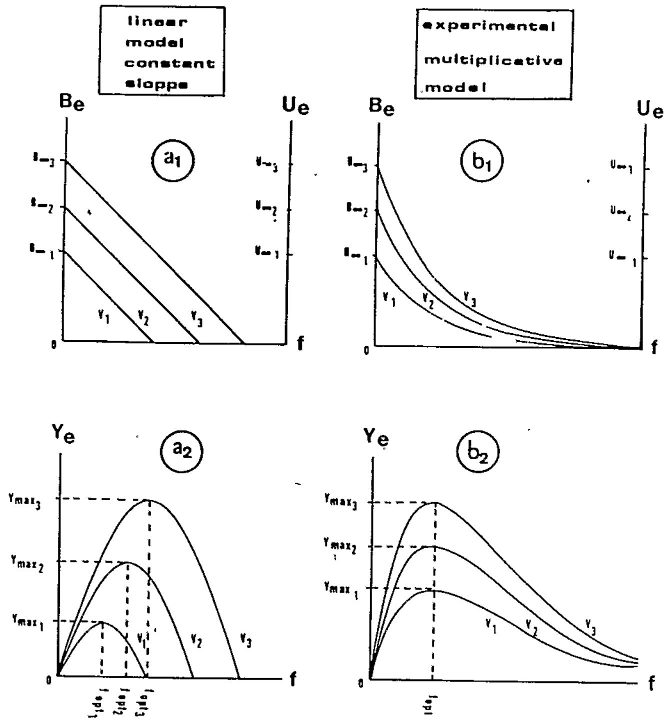


Fig. 3. Linear production model (fig. a_1 and a_2) and exponential multiplicative model (fig. b_1 and b_2) where an environmental variable V influence the abundance ($B_\infty = g$ (V)) according to three different values (V_1, V_2, V_3).

Functions g(V) and y(V)

The real mathematical functions g(V) or y(V), linking a climatic variable with respectively B_∞ or q, are generally unknown. So far a very flexible function has been used such as:

$$g(V) \text{ or } y(V) = a + b\, V^c \qquad (18)$$

which will be used only as a general tool leading to the four particular cases where:

$a = 0$; $b \neq 0$ and $c = 1$	or: bV	(18.I)
$a = 0$; $b = 1$; $c \neq 0$ and $c \neq 1$	or: V^c	(18.II)
$a \neq 0$; $b = 0$ and $c = 1$	or: $a + bV$	(18.III)
$a = 0$; $b \neq 0$ and $c \neq 1$	or: bV^c	(18.IV)

The last function (18.IV) is still very flexible: if we are just interested in situations where g(V) or (V) are positive and monotonic functions, it covers a large number of situations (fig.2). MacCall (in: Fox, 1974) used it to describe the relationship between q and B_∞.

In the case where $g(V)$ is non-monotonic but is a shaped function, other equations must be used, as for example the parabolic one:

$$g(V) \text{ or } y(V) = aV - bV^2 \tag{19}$$

or the Ricker's stock-recruitment relationship:

$$g(V) \text{ or } y(V) = aVe^{-bv}$$

Such more complicated cases will be studied only for some models.

The value of parameters a , b and c (or the value of global parameters p_1 obtained after restructuring) will be estimated by fitting the model to the data. Models with more than four parameters will not be analysed.

As underlined by Bakun and Parrish (1980) the selection of the environmental variable to be introduced into the model must, as far as possible, be deterministic and not only empirical.

III. INFLUENCE OF ENVIRONMENT ON THE STOCK ABUNDANCE

III. 1. Linear model

Let us consider a stock under equilibrium conditions, not only with regard to its fishery, but also with regard to the environment. By supposing that the catchability coefficient q is constant and by using equation 18.IV as $g(V)$ function, the equation (5) becomes:

$$U_e = bqV^c - q^2 f/h$$

by regrouping constant parameters:

$$U_e = p_1 V^{p2} - p_3 f \tag{20}$$

where p_1 , p_2 and p_3 are fixed parameters for a particular stock and fishery. From equations (7), (8) and (9) values of f_{max}, U_{max} and Y_{max} can be obtained. Using the same method, solutions can be found for different values of $g(V)$ even when non monotonic (tabl. 1).

These models are three-dimensional and f_{max} , Y_{max} and U_{max} no longer have a single solution but are functions of V (fig. 3a).

III. 2. Exponential model

Using the same process as previously, from equation (12) to (15) we get various exponential models (tabl. 1) but here f_{max} , is always independent of $g(V)$. Even though the use of such a multiplicative model has been attempted for the Senegalese sardine fishery (Fréon, 1983) an additive exponential model was retained (fig. 4a):

$$U = a\, e^{a'f} + bV + c$$

wich can be written :

$$U_e = U_\infty + a - ae^{-a'} \tag{21}$$

if $U_e = bV + c - a$ (in order to get $U_e = U_\infty$ when $f = 0$)

There are no mathematical solutions for f_{max} , Y_{max} and U_{max} but they can easily be estimated using iterative or graphical methods. Here, Y_{max} is always a function of V .

Considering the same kind of model with $U_\infty = bV^c - a$, we get

$$U_e = p_1\, V^{p2} + p_3\, e^{-p_4 f} \tag{22}$$

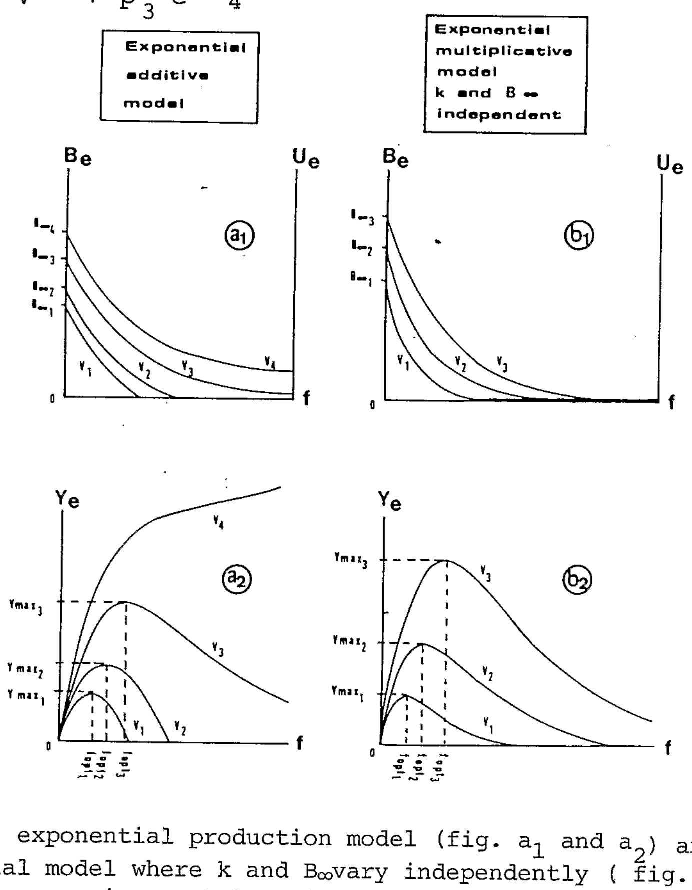


Fig. 4. Additive exponential production model (fig. a_1 and a_2) and multiplicative exponential model where k and B∞vary independently (fig. b_1 and b_2) including an environmental variable V influencing the abundance (B∞ and K) = g(V) according to three or four different values (V_1, V_2, V_3, V_4).

However, such additive models may give forecasted catches approaching infinity when fishing effort is increasing under favorable environmental conditions. This disadvantage can be eliminated if the parameter a' is fixed within reasonable limits. This problem is comparable to the arbitrary choice of m in the generalized model (Pella and Tomlinson, 1969).

In order to give to the multiplicative exponential model similar characteristics to those of the linear model when V is changing, another solution is to link this variable to k and to B_∞ independently in equation (10). Considering the simple situation where:

$$B_\infty = g(V) = bV \quad \text{and} \quad k = g'(V) = b'V^c$$

we get : $U_e = q\, bV \; e^{-q\, f\, V^{-c}/b'}$

which can be written : $Ue = p_1\, V^{p2} e^{-f p_4 V^{p3}}$ (23)

then :

$$f_{max} = 1/p_4 \; V^{p3}$$
$$U_{max} = p_1 V^{p2} / e$$
$$Y_{max} = p_1 \; V^{p2-p3} / p_4 e$$

With this formulation, the model will be similar to the linear model (20) only if p_2 and p_3 are different from zero and have the same sign (fig. 4b). If the fit does not give such results, a fitting under contraints must be used, or other models must be investigated, such as models (21) and (22) or models where V influences the catchability.

III. 3. Generalized model

In order to limit the number of parameters to four, the only situation investigated here is the case where $B_\infty = bV^c$. Following the example of the linear model we get:

$$U_e = \left((bV^c \; q)^{m-1} + \frac{q\,m}{h} f\right)^{1/(m-1)}$$

By keeping the same notation for m, this can be written:

$$U_e = \left((p_1 \; V^{p2}) + p_3 f\right)^{1/(m-1)} \qquad (24)$$

If m = 2, this equation is identical to the corresponding linear model. Values of f_{max}, Y_{max} and U_{max} are given in table 1.

IV. INFLUENCE OF ENVIRONMENT ON CATCHABILITY

IV. 1. Introduction

The catchability coefficient q may be linked to the environmental conditions through either of its two components: accessibility or vulnerability. For instance, water mass movements can be related to fish migrations, and therefore linked to accessibility, specially in the case of short-range fleets. The water turbidity can increase the vulnerability when using some gears (gill-nets, trawls) or, on the contrary, decrease it (light fishing).

The case where q is changing according to stock abundance has already been investigated by Fox (1974). Let it be remembered also that in some cases q may decrease when f increases, because of local competition among the fishing units.

IV. 2. Linear model

Supposing B_∞ is constant and replacing q by expression (18.IV) in equation (5) of Schaefer's model, we get under equilibrium conditions (fig. 5a):

$$U_e = bV^c \; B_\infty - b^2 \; V^{2c} \; f/h$$

Or, by regrouping constant factors:

$$U_e = p_1 V^{p2} - p_3 V^{2p2} f \tag{25}$$

Expression of U_{max}, f_{max} and Y_{max} are easily obtained from equations (7) to (9). In the same way, other expressions of y(V) can be used (see table 2). In all cases, it is obvious that Y is independent from V (fig. 5a).

IV. 3. Exponential model

By following the same method as previously, exponential models can be developed (table 2, Fig.5b). For $y(V) = bV^c$ we get:

$$U_e = p_1 \; V^{p2} e^{-p3 \; V^{p2} f} \tag{26}$$

It may be noted that Y_{max} is still independent of V .

The generalized model will not be developed here, owing to the excessive number of parameters it would have.

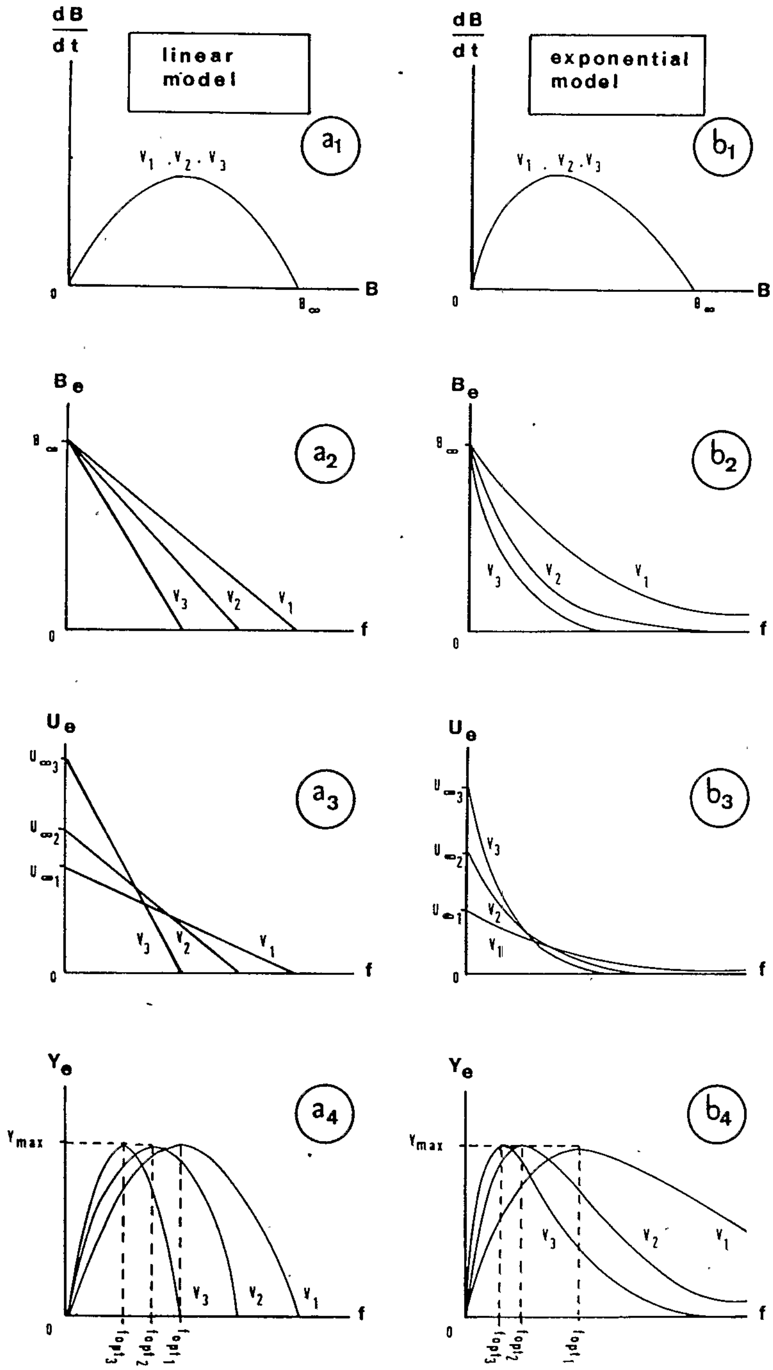


Fig. 5. Linear production model (fig. $a_1 \ldots a_4$) and exponential production model (fig. $b_1 \ldots b_4$) where an environmental variable V influences the catchability according to three different values (V_1, V_2, V_3).

LINEAR	$B_\infty = g(V)$	$Y_e = qg(V)f - q^2f^2/h$	$f_{opt} = g(V)h/2q$	$Y_{max} = g^2(V)\ h/4$	$U_{opt} = qg(V)/2$
	bV^c	$p_1V^{p_2}f - p_3f^2$	$p_1V^{p_2}/\ 2p_3$	$p_1^2V^{2p_2}/4p_3$	$p_1V^{p_2}/\ 2$
	$a + bV$	$p_1f + p_2Vf - p_3f^2$	$(p_1 + p_2V)\ /2p_3$	$(p_1 + p_2V)^2\ /\ 4p_3$	$(p_1 + p_2V)\ /2$
	bV	$p_1Vf\ - p_2f^2$	$p_1V\ /\ 2p_2$	$p_1V^2\ /\ 4p_2$	$p_1V\ /\ 2$
	$aV - bV^2$	$p_1Vf - p_2V^2f - p_3f^2$	$(p_1V + p_2V^2)\ /\ 2p_3$	$(p_1V + p_2V^2)^2\ /\ 4p_3$	$(p_1V + p_2V^2)\ /2$
MULTIPLICATIVE EXPONENTIAL	$B_\infty = g(V)$	$Ye = qg(V)e^{-qf/h}f$	$f_{opt} = h/q$	$Y_{max} = g(V)h/e$	$U_{opt} = qg(V)/e$
	bV^c	$p_1V^{p_2}e^{-p_3f}f$	$1/p_3$	$p_1V^{p_2}/p_3e$	$p_1V^{p_2}/e$
	$a + bV$	$(p_1+p_2V)\ e^{-p_3f}f$	$1/p_3$	$p_1 + p_2V/p_3e$	$p_1 + p_2V/e$
	bV	$p_1V\ e^{-p_2f}f$	$1/p_2$	p_1V/p_2e	p_1V/e

Table 1. Linear models and multiplicative exponential models where the environmental variable V influences only the stock abundance.

LINEAR	$q = y(V)$	$Y_e = y(V)B_\infty f - y^2(V)f^2/h$	$f_{opt} = B_\infty h/2y(V)$	$Y_{max} = B_\infty^2h/4$	$U_{opt} = y(V)B_\infty/2$
	$a + bV$	$p_1p_2f + p_2p_3Vf - (p_1+p_3V)^2f^2/p_4$	$p_2p_4\ /\ 2\ (p_1 + p_3\ V)$	$p_2^2p_4/\ 4$	$(p_1p_2 + p_2p_3V)\ /\ 2$
	bV^c ou V^c	$p_1V^{p_2}f - p_3V^{2p_2}f^2$	$p_1\ /\ 2p_3V^{p_2}$	$p_1^2\ /\ 4p_3$	$p_1V^{p_2}\ /\ 2$
	bV	$p_1Vf - p_2V^2f^2$	$p_1\ /\ 2p_2V$	$p_1^2\ /\ 4p_2$	$p_1V\ /\ 2$
EXPONENTIAL	$q = y(V)$	$Y_e = y(V)B_\infty\ e^{-y(V)f/h}f$	$f_{opt} = h/y(V)$	$Y_{max} = B_\infty h/e$	$U_{opt} = y(V)\ B_\infty/e$
	bV^c (identical to V^c after restructuration)	$p_1V^{p_2}\ e^{-p_3V^{p_2}f}$	$1/(p_3V^{p_2})$	$p_1\ /\ (p_3e)$	$p_1V^{p_2}/e$
	$a - bV$	$(p_1+p_2\ V)\ e^{-(p_3\ +\ p_4Vf)}f$	$1/(p_3 + p_4\ V)$	$(p_1+p_2V)/(p_3+p_4V)e$	$(p_1+p_2V)/e$
	bV	$p_1V\ e^{-p_2Vf}f$	$1/p_2V$	$p_1/(p_2e)$	$p_1V\ /e$

Table 2. Linear models and exponential models where the environmental variable V influences only the catchability.

V. INFLUENCE OF ENVIRONNEMENT ON BOTH ABUNDANCE AND CATCHABILITY

V. 1. Introduction

In some cases, it is obvious that environment influences both stock abundance and catchability. In such cases, q and B_∞ will be replaced by functions of V.. I have examined only the simple case where both g(v) and y(v) are described by the function (18 IV), in order to limit the number of parameters. This is acceptable because this function is very flexible, but in theory, nothing allows us to suppose that g(v) and y(v) would be identical. Moreover, in some cases it is likely that abundance and catchability are related to two different environmental variables, V and V'(see latter the example of Ivory Coast).

V. 2. Linear model

Supposing that $B_\infty = g(V) = bV^c$

and $q = y(V) = b'V^{c'}$

and following the usual method we get (fig. 6) :

$$U_e = bb'V^{c+c'} - b'^2 V^{2c'} f/h$$

which can be written :

$$U_e = p_1 V^{p2+p3} - p_4 V^{2p3} f \qquad (27)$$

Characteristic values of this model and of derived models are shown in table 3. It should be noticed that when $p_3 = 0$ this model is identical to model (20) where B alone is a function of V (table 1), and when $p_2 = 0$ the model is identical to model (25) where q alone is a function of V .

If, for instance, g(V) is a parabolic function (19), we would get:

$$U_e = (p_1 V^{1+p2} - p_3 V^{2+p2}) - p_4 V^{2p2} f \qquad (28)$$

V. 3. Exponential model

If, in Fox's (1970) formulation of the exponential model we consider that : $B = g(V) = bV^c$ and $q = y(V) = b'V^{c'}$, then we get:

$$U_e = bb' V^{c+c} e^{-b' V^{c'} f/k}$$

which can be written identically to equation (23), when constant factors are regrouped. This model is very flexible (fig.7). When g(V) and y(V) have opposite signs, the figures are similar to those obtained when influences only the abundance. When $p_2 = p_3$ the model is similar to those obtained when V influences only the catchability.

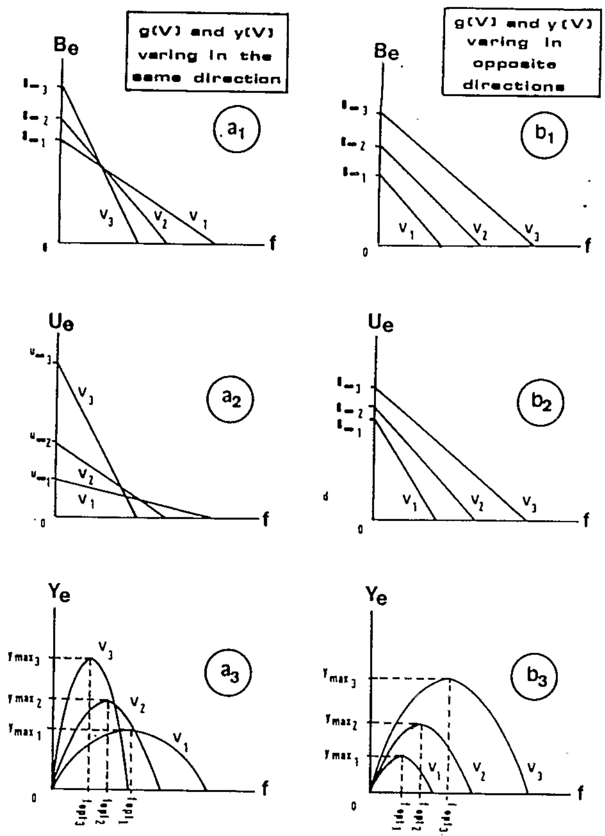


Fig. 6. Linear production model for three values (V_1, V_2, V_3) of an environmental variable V influencing both the stock abundance ($B_\infty = g(V)$) and the catchability ($q = y(V)$), when g(V) vary in the same direction (fig. a_1, a_2, and a_3) or in opposite directions (fig. b_1, b_2 and b_3).

LINEAR	$B_\infty = g(V)$ $q = y(V)$	$Y_e = y(V)\ g(V)f - y^2(V)f^2/h$	$f_{opt} = g(V)h/2y(V)$	$Y_{max} = g^2(V)\ h^2/4$	$U_{opt} = g(V)\ y(V)/2$
	bV^c	$p_1V^{p_2+p_3} f - p_4 V^{2p_3} f^2$	$p_1V^{p_2+p_3} / 2p_4 V^{2p_3}$	$p_1^2 V^{2p_2} / 4p_4$	$p_1V^{p_2+p_3} / 2$
EXPONENTIAL	bV^c	$Y_e = y(V)\ g(V)\ e^{-y(V)\ f/k} f$	$f_{opt} = k/y(V)$	$Y_{max} = k\ g(V)/e$	$U_{opt} = y(V)\ g(V)/e$
		$p_1V^{p_2} e^{-p_4 f V^{p_3}} f$	$1/p_4 V^{p_3}$	$p_1 V^{p_2 - p_3}/p_4 e$	$p_1 V^{p_2}/e$

Table. 3. Linear models and multiplicative exponential models where the environmental variable V influence the stock abundance and the catchability.

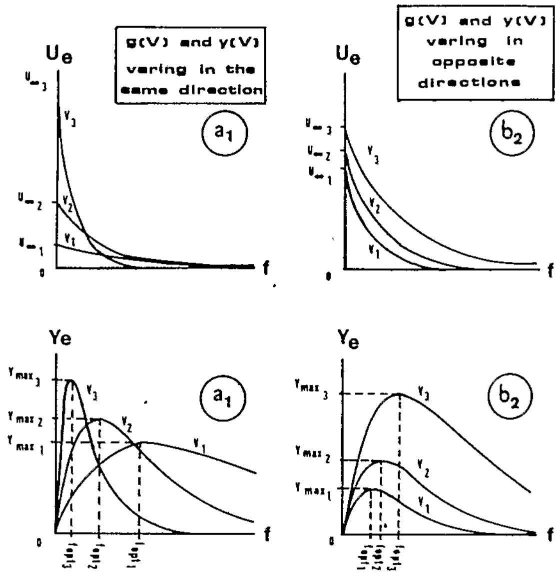


Fig. 7. Exponential production model for three values (V_1, V_2, V_3) of an environmental variable V influencing both the stock abundance ($B_\infty = g(V)$) and the catchability ($q = y(V)$), when g(V) and y(V) vary in the same direction (fig. a_1 and a_2) or in opposite directions (fig. b_1 and b_2).

Finally, the exponential model (23) , as well as the linear model (27), allows three possibilities of action for the variable *V*:

- only on abundance (B_∞ and), if p and p have opposite signs and are different from zero,

- only on catchability if $p_2 = p_3$

- on both abundance and catchability when p_2 and p_3 alone are different from zero.

Therefore, it is evident that, considering only annual data of catch and effort, it is not possible to separate the first and the last of these three possibilities, specially if g(V) and y(V) have opposite signs in this last case. Then, the choice of the appropriate model must be based on hypothesis or, better, on other data analyses (for instance, studies on recruitment or on catchability variation using a monthly stratification).

VI. USING THE MODELS WITH TRANSITIONAL STATE DATA

VI. 1. Introduction

The preceding equations are based upon a stock in equilibrium state at various stable levels of fishing effort and environmental conditions. In order to fit one of the models to the observed data, one of three traditional approaches (Fox, 1974) can be adopted, modified to take account of the case when the environment results in a stock in transitional state :

- by selecting within the data set some period of equilibrium state,

- by adjusting the data of fishing effort and environment so as to estimate an equilibrium state. Gulland's (1969) method involves the relationship between the annual c.p.u.e. in year i (U_i), and the fishing effort averaged over some number of previous years. Then Fox (1974) proposed a weighted average. The same approach can be used for the environment variable (transition prediction approach),

- or by using integral calculations to predict the population changes and yield (equilibrium aproximation approach). This approach has been developed by Schaefer (1957), Pella and Tomlinson (1969) and by Rivard and Bledsoe (1978).

The first method is the easiest one, but it is rarely appropriate because in most cases the fishing effort and environment are not stable during a period equivalent to the number of year classes in the catches. However, for short-lived species (shrimps, small pelagic fish) specially in tropical areas, this approach can be used. In some extreme cases, data from each individual year can be used to fit the model (Fréon, 1983a and 1983b).

The second approach is also easy to use, but one still faces the traditional problem of the artefact caused by the non-independence of the data series concerning fishing effort and c.p.u.e. (Roff and Fairbairn, 1980). Even though this approach is not convenient when g(V) and/or y(V) are not monotonic functions, I propose to adapt it to the environmental production models for pragmatic reasons. The third approach is indeed complicated when an environmental variable has been introduced into the models, specially when this involves the catchability coefficient. Restructuring of the models, such as the one proposed by Fletcher (1978) and used by Rivard and Bledsoe (1978) are difficult to apply here without increasing the number of parameters, because our models have already been restructured.

It has been recognized that the transition prediction approach can lead to some bias or errors concerning the parameter estimations, as emphasized by Walter (1975), Schnute (1977) and Uhler (1980). However, this last author shows that the best statistical estimations of the parameters do not necessarily

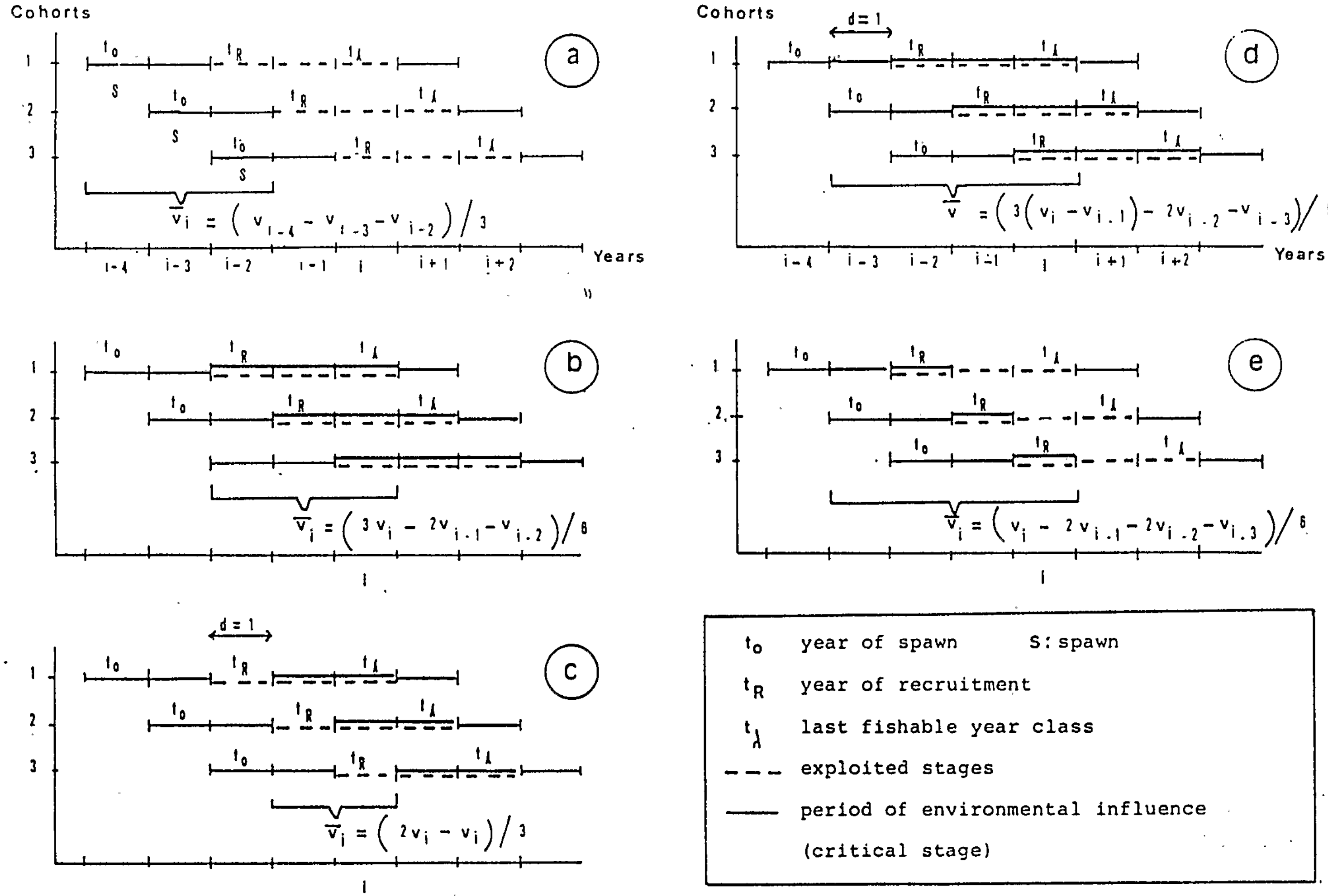


Fig. 8. Graphical solutions of the estimated weighted average $\overline{V}_i$ involving the number of years during which the environment influences the c.p.u.e. (U_i) of year $\underline{i}$, according to different temporal locations (fig. a, b ... e) of the critical stage (see text).

provide the best estimations of Y_{max} and f_{max} , which remain the main objectives of the global production models.

VI. 2. Transitional states when environment influences the stock abundance

Concerning the environmental variable, the use of the transition prediction approach assumes that the life stage during which environment acts upon the stock is already known. Schematically four periods, or critical stages have been identified :

1 - Before spawning, by influencing the fecundity of the parent stock;

2 - During the early life stages, by influencing fecundation and/or natural mortality of eggs and larvae;

3 - During the period of high growth rate (corresponding generally to the pre-recruitment stage) when the environment influences the individual growth and/or the natural mortality;

4 - During the post-recruitment, if natural mortality and/or the condition-factor (and secondarily the growth rate) are concerned at this stage.

These four cases are not mutually exclusive, of course, and in some cases it is difficult to identify at which stage the environmental influence is greatest.

By considering that a possible effect on the stock-recruitment relationship is already taken into account by the usual formulation of the global production models, it can be assumed that, concerning the first case, the environmental factors will act on the stock mainly during the months prior to spawning. The c.p.u.e. of the total fishable population, assuming equal catchability of each year class , is:

$$U_i = U_{i,j} + U_{i,j-1} + U_{1,j-2} + \dots\dots\dots + U_{i,j-n+1}$$

where $U_{i,j}$ is the c.p.u.e. of the incoming year class j in year i, for n year classes in the fishable population. So far, U_i will be related to the average V_i of seasonal environmental factor during the years corresponding to the sexual maturation of the different parental stocks of each fishable cohort. When the sexual maturation and the spawn occur during the same year i , this can be written as (fig. 8a) :

$$\overline{V_i} = \frac{V_{i-t} + V_{i-t+1} + \dots\dots\dots\dots + V_i}{t_\lambda - t_r + 1}$$

where t is the mean age at recruitment and t the mean age of the oldest fishable year class. When the information is available, it is possible to weight the V values according to relative abundance of the year classes.

The same approach can be developed for the second case, using environmental data from the spawning period.

The two last cases need different formulations because an environmental factor can affect the abundance of a cohort during several years, which leads to the use of weighted averages. Following an approach similar to Fox's (1975) concerning the fishing effort, let us see first the simple case where the environment has an effect throughout the post-recruitment period. Then the c.p.u.e. of the incoming year class j in year i , U_{ij} , is related to the value of V_i during the same year; that of the previous year class, $U_{i,j-1}$, is related to the values of V_i and to V_{i-1} ; and so forth (fig. 8b). This can be written as :

$$U_{i,j} \sim g(V_i + V_{i-1} + \ldots\ldots. V_{i-t_r})$$

and

$$U_i \sim g(nV_i + (n-1)V_{i-1} + (n-2)V_{i-2} + \ldots. + V_{i-n+1})$$

The expression of $\bar{V}_i$ will be given by :

$$\bar{V}_i = \frac{n(V_i + (n-1)V_{i-1} + \ldots\ldots. V_{i-n+1}}{n + (n-1) + \ldots\ldots + 1}$$

This formula is easy to modify for the cases when the environment effect starts d years after the recruitment, replacing n by $n-d$ in this case (fig. 8c).

If the environment effect starts d years before the recruitment (fig. 8d), we get :

$$\bar{V} = \frac{n(V_i + V_{i-1} + \ldots. + V_{i-d}) + (n-1)V_{i-d-1} + \ldots\ldots + V_{i-n+1}}{n(d+t) + (n-1) + (n-2) + \ldots. + 1}$$

For other cases, when for example the environment effect on a cohort is not continuous, a graphical solution can be used in order to obtain the proper formulation of $\bar{V}_i$ (fig. 8e).

The calculations of mean fishing effort $\bar{f}_i$ can be carried out independently of those of $\bar{V}_i$ using Fox's (1975) weighted averages for example.

VI. 3. Trnasitional state when the environment influences the catchability

When the environment influences the catchability (or the abundance and the catchability) the models must be reformulated, replacing in a first step *qf* by a mean fishing mortality coefficient $\bar{F}$ taking into account the various fishing efforts f_i and catchability coefficients q_i estimated for the different years. Using Fox's (1975) weighted average, we get :

$$\bar{F}_i = \frac{nq_1 f_i + (n-1)\, q_{i-1}\, f_{i-1} + \dots + q_{i-n+1}\, f_{i-n+1}}{n + (n-1) + (n-2) + \dots + 1}$$

In a second step, the remaining values of q in the models (corresponding to the relationship $U_i = q_i\, B_i$) receive the index *i*. Finally, all the *q* can be subtituted by corresponding y(V) function, where *V* receives the same index as *q* (see the Ivory Coast case for example). It must be recorded that the objective is not to determine the *q* value, but only to take into account its variability in the model.

VI. 4. Conclusion on transitional states.

The shorter the life span, (or at least the fishable life span), the better will be the transition prediction approach. In such cases it is easier to determine and to quantify the environmental effect on the catchability or on the abundance. In the latter case, the most favorable situations are provided by rapid action of the environment on a life stage, or by slow fluctuations of the environment (auto-correlated data series). With the aim of simplifying the presentation, let us consider as cyclic the inter-annual environment fluctuations, with a "period" *T* (bearing in mind that, in most of cases, the reality is no more than an alternation between positive and negative climatic anomalies, not necessarily of the same duration).

If the fishery data series has a negligible duration compared to *T* (geological scale for example), it will be impossible to quantify an eventual environmental influence. Nevertheless this influence can exist, as suggested by the results of Soutar and Isaac (1974). Stochastic production models using a periodical function can be used in such a case (Steele and Henderson, 1974).

If the extent of the fishery data series is shorter than *T* but greater then T/4, a model could be attempted if, by chance, the whole data series is located on one single side (increasing or decreasing) of the function. But in this limited case, any extrapolation of the result would be hazardous.

If the duration of the critical stage Φ is greater than or equal to *T* , it will be very difficult to identify environmental effects because they will be smoothed for each cohort.

The most favourable conditions for using these models occur when Φ is shorter than T, and specially when shorter than T/2, and when the fishable life span n is also shorter than T/2. In such cases, the mixture of various cohorts in the annual catches will produce a minimal smoothing of the global yields.

Replacing these considerations in the context of the usual species classification according to their demographic strategy (Cole, 1954; Mac Artur and Wilson, 1967), it is obvious that the r group of species is easier to study than the K group as far as environmental models are concerned. Using the recent and more detailed classification of Kawasaki (1983) for teleosts, *IA* and *IB* groups can justify the use of such models. Nevertheless, only the *IB* group can support predictive models if a long enough delay separates the environmental action from its effects on catches, or if climatic teleconnections have been identified. The *II* group of long life span species can not support such models, except when the climatic changes are of long duration and present smooth variations, and if long term data series are available. In most of the cases the best approach for this group is the introduction of a climatic factor in structural production models (Parrish and Mac Call, 1978).

VII. IMPLICATIONS FOR FISHERIES MANAGEMENT

VII. 1. Influence of the environment on the abundance

We have seen that, in some cases, the environmental effect on stock abundance is more than a "white noise" and therefore it is possible to modulate the fishing effort according to abundance predictions.

In situations where forecasting of abundance is reliable (delay of climatic influence or teleconnections) the difficulty of the management will result from its duality of objectives : on the one hand optimization of the yield by increasing the effort when the abundance increases, on the other hand protection of the stocks against a collapse by reducing quickly the fishing effort when environmental factors are unfavorable. As a matter of fact, this collapse can happen rapidly without any increase of effort by maintaining an "optimal" effort which does not correspond any more to the actual climatic situation (fig. 9a). The collapse will occur more rapidly when there are few exploited cohorts acting as a buffer and when the critical life stage lasts less than a year (Fréon, 1983a and 1983b). This permanent adjustment of the fishing effort is not easy to apply because there is a delay between profits and investments (Fréon and Weber, 1981). An analysis of this problem is available in a working group report edited by Csirke and Sharp (1983). The fishery management can be based on variable yearly quotas or on variable maximum efforts.

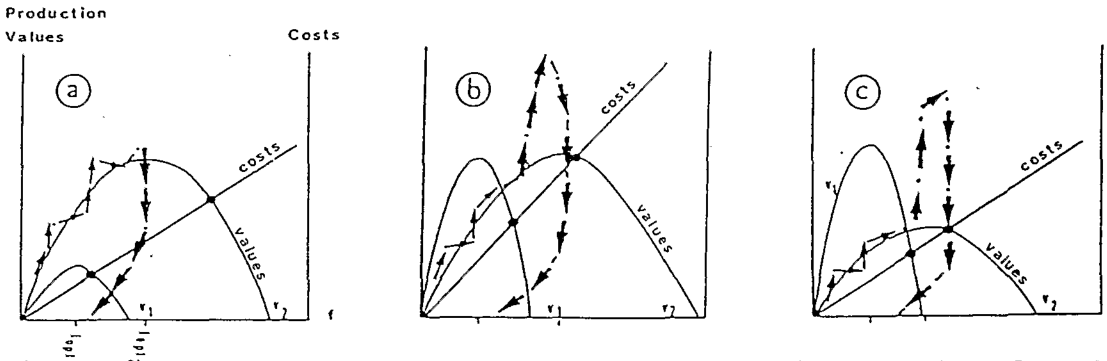


Fig. 9. Bio-economical production models and theoretical examples of stock collapses when the environment influences the stock abundance (fig. a), the catchability (fig. b) or both these two factors in the same direction (fig. c), according to values V_1 and V_2) of the environmental variable V

Theoretical curves (V_1 an V_2)
observed values under v_2
observed values under V_1 (sudden transition)
Threshold of profitability

VII. 2. Influence of the environment on the catchability

Here the main risk of collapse occurs when shifting from unfavorable climatic conditions to favorable ones. The first situation will lead after a few years to an increase of the fishing effort providing catches approach close to Y_{max} (Fig.9b). When later catchability increases suddenly, the yields will increase too, and the non equilibrium state of the fishery will result in its collapse. In such a case the proper management decision is to fix a single quota, generally easier to determine and to control than variable effort limitations.

VII. 3. Influence of environment on both abundance and catchability

Depending on whether the environment influences B_∞ and q in the same direction or in opposite directions, the resulting figures will be completly different (fig. 6b and 6a where $p_2 > p_3$ in equation 27). Only two extreme cases will be analysed here, but numerous intermediate situations exist, with the particular case where there is a single f_{max} (when $p_2 = p_3$).

In the first case where g(V) and y(V) have the same sign of variation, a sudden occurrence of unfavorable environment relative to abundance is not dangerous because the catchability would then be low. On the other hand, when the environmental conditions are both favorable to the abundance and to the catchability and if there is no regulation mechanism provided by a market saturation or by prices self-adjustment, the effort will have a tendency to exceed f_{max}. A strong limitation is then necessary.

In the second case, when a high abundance is associated with a low catchability, the main risk of collapse occurs when bad climatic conditions follow good ones (fig. 6b). This situation is comparable to which has been described previously in the case of an influence of environment on the abundance only (fig. 9a).

VIII. METHOD AND CRITERIA OF FITTING

Most of these models do not allow the use of a multilinear regression, even after linear transformation of the variables. Non-linear regression as, for example, those based on Marquardt's (1963) algorithm or on the Gauss-Newton's modified method (Dixon an Brown, 1979; Genstat, 1980) can be used. They are iterative and use the least-square criterion. Fitting can be done by using formulae of c.p.u.e. (U_i) or catches (Y_i). This last solution theoretically avoids the bias on the regression coefficient due to the non-independence of f_i and U_i, provided that f_i and Y_i have been estimated independetly.

Modifications of the procedure can be made by weighting the residuals. Fox (1971) analysed this problem and retained the solution considering ε_i as an error proportional to the estimated catches $\hat{Y}_i$ such that :

$$Y_i = \hat{Y}_i + \hat{Y}_i \varepsilon_i$$

leading to a minimization of the function :

$$S = \Sigma^n_{i=1} ((Y_i - \hat{Y}_i) / Y_i)^2$$

All the algorithms need estimated starting values of the various parameters for initializing the iterative process. In order to avoid convergences toward local minima or toward irrational solutions from a biological point of view, those starting values must be estimated carefully. This can be done by using the initial model formulation where B_∞ or U_∞ appear. Their values can be estimated by doubling the maximum catch (or c.p.u.e.) observed in the data series. Exponents of g(V) and y(V) function can be initialized as 1.

A non-parametric estimation of the fit can be obtained using jackknife or cross-validation methods (Ducan, 1978, Efron and Gong, 1983). These methods show the stability of the model when one year of observation is removed from the data series. It is interesting to observe that, in some cases, all the parameter values change while the fitting remains more or less the same inside the range of observed data, but the curves are divergent outside this range. This indicates the risk of using such models outside the range of observed data on fishing effort and environmental factors. On some occasions it seems preferable to fix a "reasonable" value to one of the parameters, as already mentioned by Pella and Tomlinson (1969) in their generalized model.

IX. CHOICE OF THE APPROPRIATE MODEL

Owing to the generally low number of yearly observations and to the relatively high number of parameters to estimate, the models present few degrees of freedom. Consequently, the choice of the appropriate model, among the numerous ones presented here, must not be based reasonably on the criterion of the best fit.

Two categories of objective criteria can be identified. First, it must be decided if environment influences the stock abundance or the catchability. The choice of the models where both phenomena are considered must be supported by observations instead of being an opportunist choice. The second step is then to decide whether a linear or an exponential (or even generalized) model must be used. If the stock has never been over exploited when considering any "maximal fishing efforts", the three kinds of models provide similar fits. However, the curves are divergent over those maximal efforts, and it is preferable to give a representative tendency, even if reasonably any model must not be used for predicting situations outside the range of observed data.

In some cases, additional information may help the choice between a pessimistic linear model and an exponential one which allows a slow decline towards stock collapse: e.g. a small number of exploitable year-classes, subdivision into sub-stocks, natural reserves where fishing is impossible, gear selectivity, etc.) When the stock has already been over-exploited, the usual data on effort and c.p.u.e. provide directly decisive information.

X. MODEL LIMITATIONS

The introduction of an environmental variable into the global production models brings about an increase in the number of parameters in the final formulation, and consequently three main difficulties :

- Although fitting is easier, the confidence limits of the parameters are often high and the models may be unstable.

- It is sometimes difficult to estimate the real contribution of each variable (f and V) in the models, owing to their interaction and/or colinearity.

- By increasing the number of explanatory variables one increases also the probability of getting randomly good correlations, independently of any real biological phenomenon (Ricker, 1975, P. 227-279).

These difficulties, common for any multi-regression, can be overcome by an objective choice of the variables (supported by biological observation as far as possible) and by a careful use of the models for predictions.

In addition, those models still have the usual limitations of the traditional global production models, linked to the basic assumptions :

- single stock considered,
- no time lags in the population responses to exploitation,
- c.p.u.e. representative of abundance (at least local abundance),
- constant catchability coefficient of the different year classes,
- stability of the total catchability coefficient relative to non climatic factors (specially stability of the vulnerability).

These models may seem to contradict some recent findings concerning the reactions of competing species to environmental changes. Skud (1982) showed that when two competing species are reacting independently and identically to the same climatic factor, the dominant species will have a positive response to a favorable environment, while the dominated species will have an apparently negative response. This indicates that the abundance of the dominating species controls completely the abundance of the dominated one. If this observation is general, this would mean that our models, applied to one or the other species individually, would be relevant only if there is no inversion of the dominance.

In some cases, a solution to this problem is to consider the two species as a single one, if they live in the same ecological niche. Then the model deals with the productivity of a link of the trophic chain. Another advantage of this approach is that it can be used to overcome the problem of a target-species change, when the two species are caught by the same fleet.

XI. EXAMPLES OF APPICATION

Three examples concerning clupeoid stocks of West Africa have been studied. They all deal with short-lived species living in upwelling areas and supporting purse-seine fisheries. The main assumptions have been checked. However, owing to the low number of yearly observations and to the data quality, the confidence limits of the parameters are just indicative, as are the values of the regression coefficients r.

XI. 1. The sardinella stock of the "Petite Côte" in Senegal

Under some hypotheses, the sub-stocks of *Sardinella aurita* and *Sardinella maderensis* of the "Petite Côte" (Senegal) can be considered as a single stock. Its abundance is regulated by the coastal upwelling strength. A cross-correlation between the monthly anomalies of wind stress and the anomalies of c.p.u.e.

corrected by the inter-annual trend (linked to the increase of the fishing effort) shows an effect of the cold season upwelling on the production of each species with a clear lag of 3 to 7 months and a probable lag of around one year (fig. 10a, b, c). Owing to the high auto-correlation coefficient of both data series, the figures are difficult to analyse more precisely. An additive exponential model of production (equation 19) has been used for this stock (Fréon, 1983 and 1984). The catches are comprised of 8 to 18 month-old fishes. Therefore the catch of year *i* has been related to the fishing effort of year i and to the weighted average of wind speed V such that :

$$\bar{V}_i = (2\ V_i + V_{i-1}) / 3$$

The stock has never been strongly overfished and the fit is rather good for the whole period of observation, between 1966 and 1983 (table 4 and 5 ; fig.11). The model explains around 94% of the catch variability and it is relatively stable, as shown by cross-validation analyses (Fréon, 1986).

Table 4: Fishery statistics of the *Sardinella* spp. sub-stock of the Senegalese Petite Côte (artisanal and industrial fisheries) from 1966 to 1983, and weighted average of the upwelling index during two years. (Sources : CRODT Dakar - Thiaroye, Senegal).

Years	Catches	Efforts	C.P.U.E.	Upwelling Index (Aver. 2years)
66	29 290	1 443	20.3	4.93
67	26 370	1 490	17.7	4.74
68	28 550	1 808	15.8	4.53
69	33 240	2 324	14.3	4.40
70	28 250	2 498	11.3	4.32
71	30 670	2 324	13.2	4.70
72	53 720	2 570	20.9	5.63
73	59 940	3 678	16.3	5.53
74	69 250	4 356	15.9	5.76
75	61 290	4 903	12.5	5.66
76	80 940	5 506	14.7	5.79
77	77 600	5 243	14.8	5.72
78	76 400	6 016	12.7	5.21
79	69 470	6 493	10.7	4.68
80	70 240	6 003	11.7	4.98
81	78 870	7 809	10.1	5.09
82	66 800	8 675	7.7	4.86
83	71 970	13 840	5.2	4.60

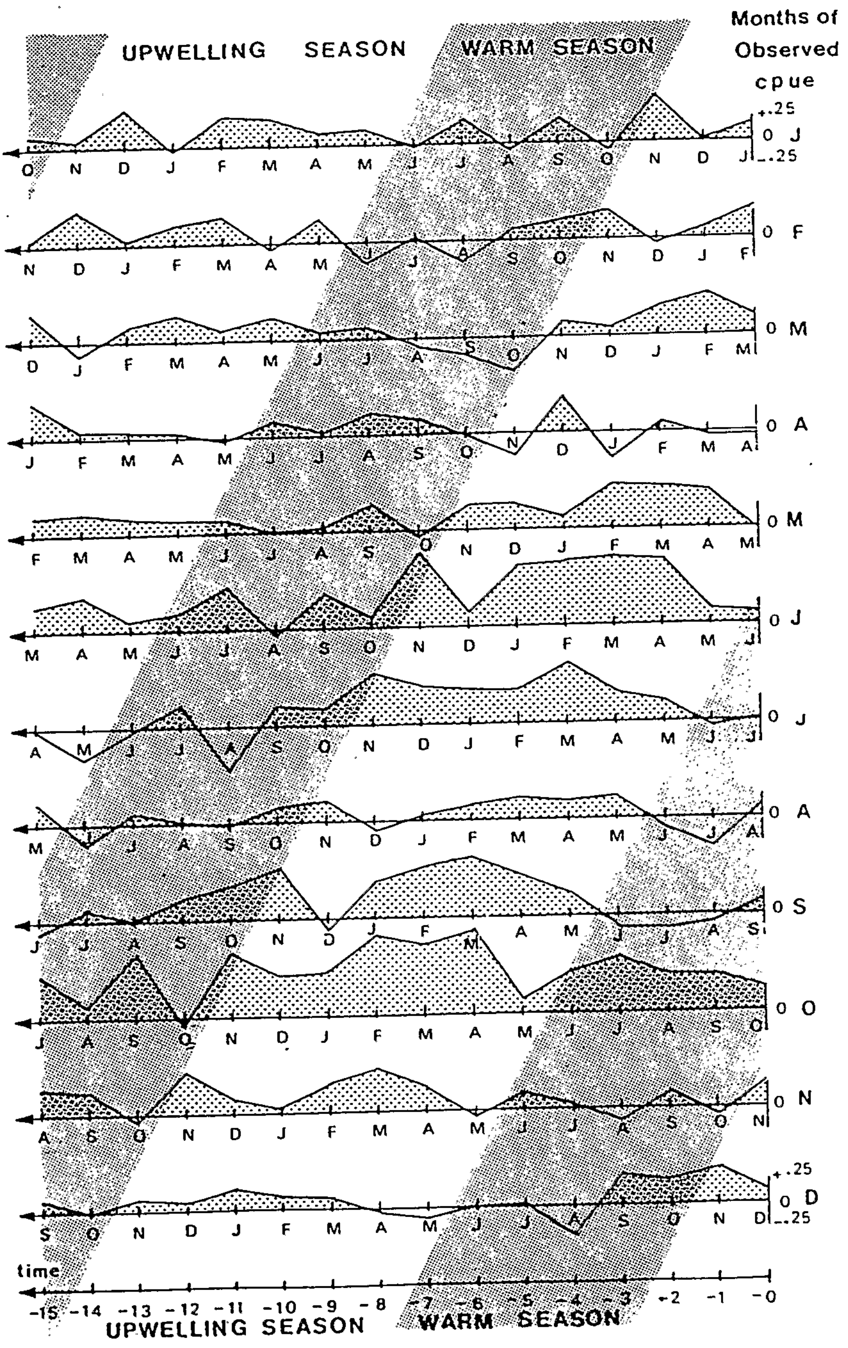


Fig. 10a. Cross-correlations results between the monthly anomalies of the wind speed in Dakar-Yoff station and the monthly anomalies of the young *Sardinella aurita* c.p.u.e. in the "Petite Côte" fishery after correction by the interannual trend.

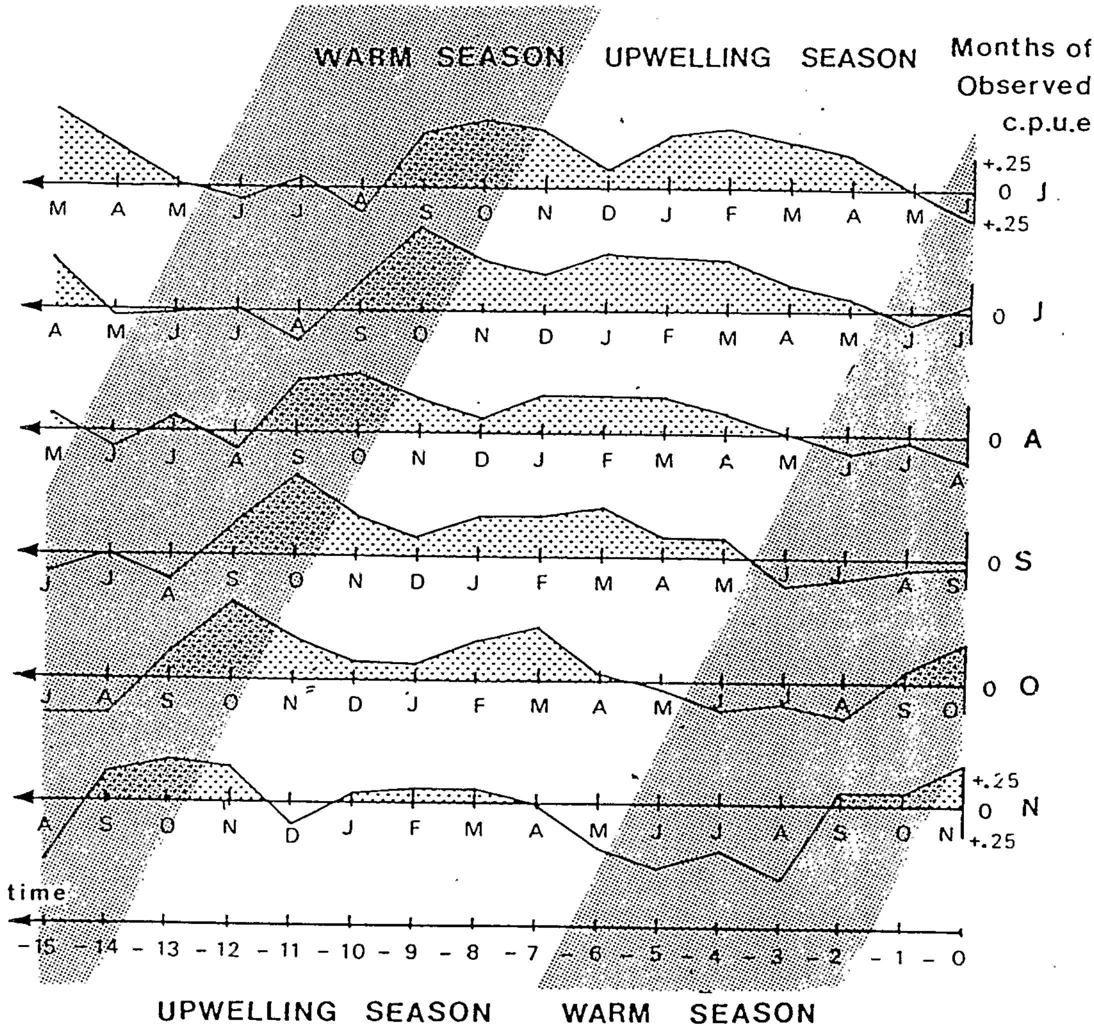


Fig. 10b. Cross-correlations results between the monthly anomalies of the wind speed in Dakar-Yoff station and the monthly anomalies of the young *Sardinella maderensis* c.p.u.e. in the "Petite Côte" fishery.

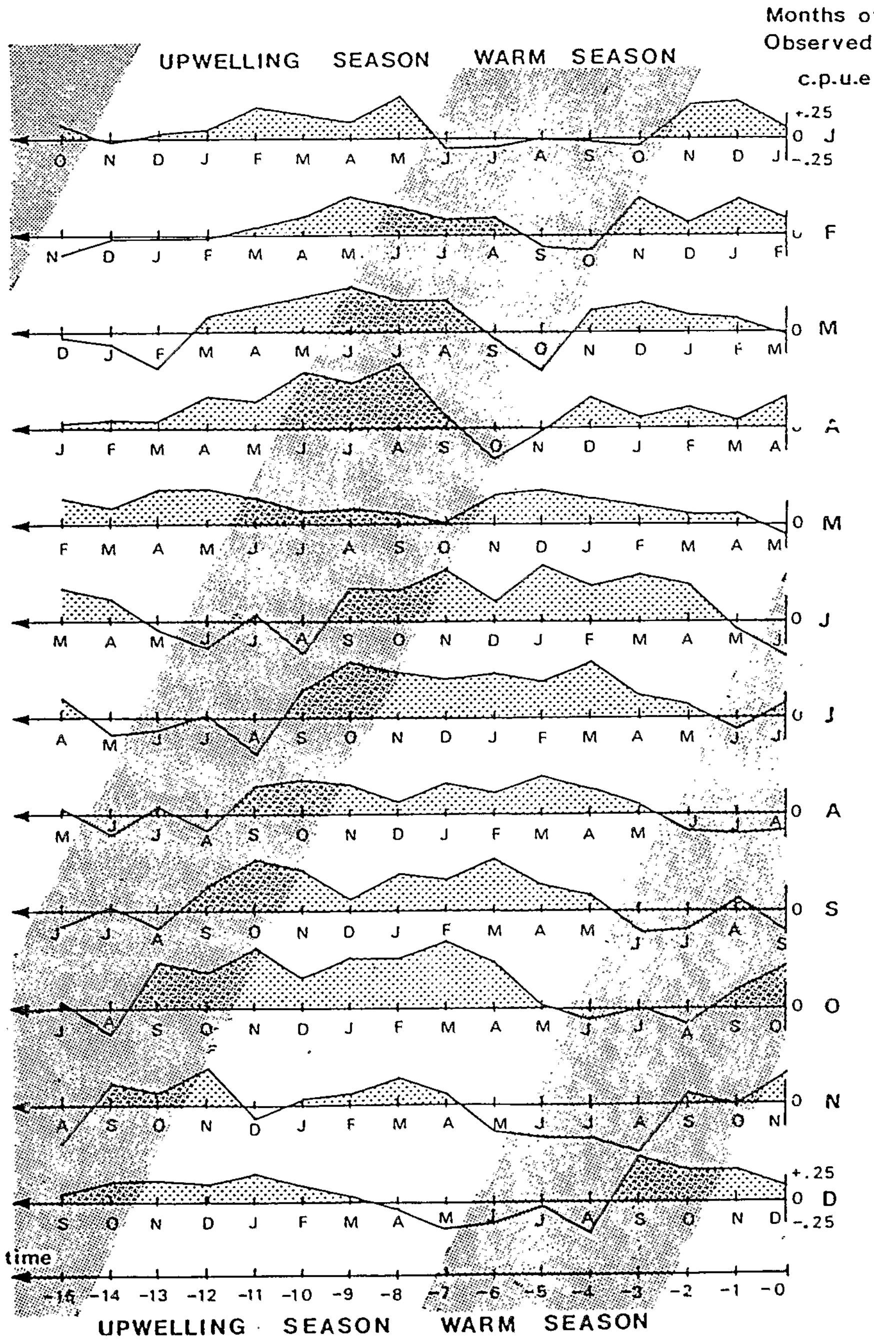


Fig. 10c. Cross-correlations results between the monthly anomalies of the wind speed in Dakar-Yoff station and the monthly anomalies of the young *Sardinella spp.* c.p.u.e. in the "Petite Côte" fishery after correction by the interannual trend.

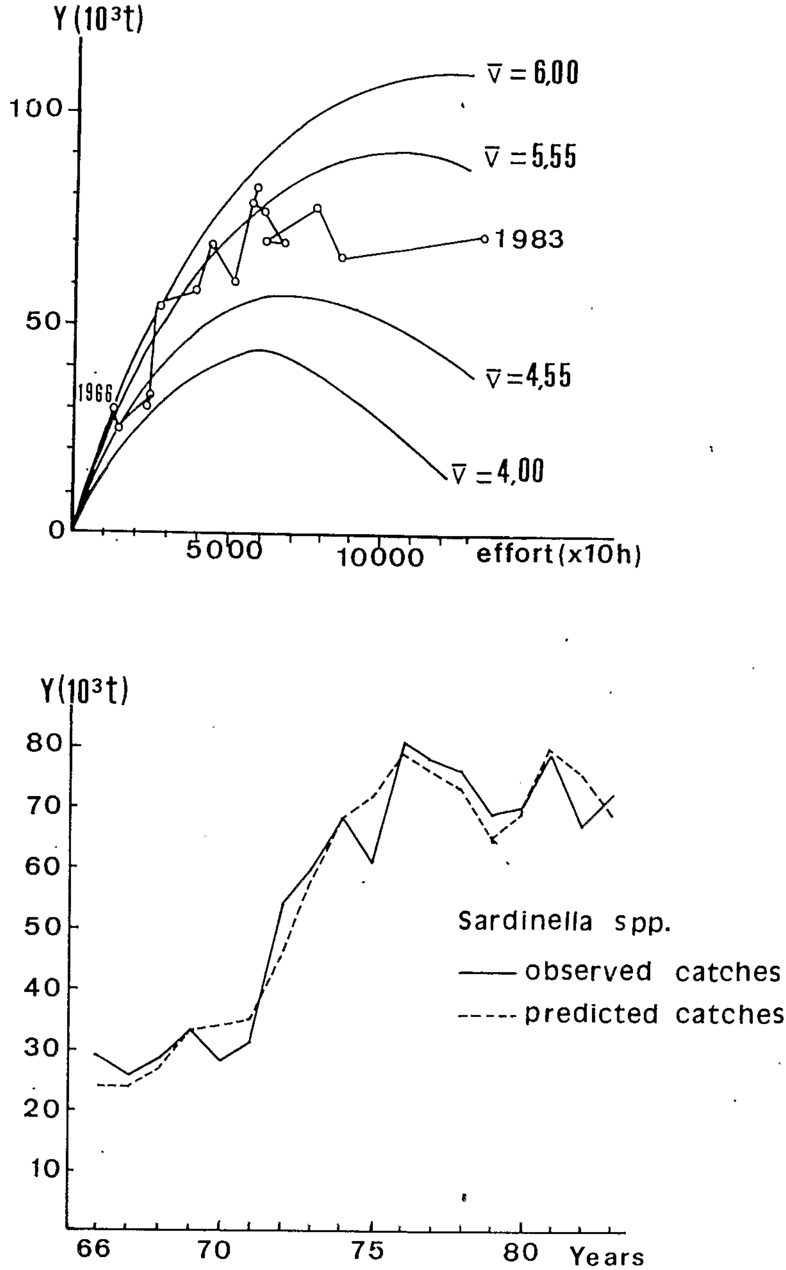


Fig. 11. Observed and predicted total catches (C) according to an additive exponential model (equation 21) where the upwelling index influences the *Sardinella spp.* stock abundance in the "Petite Côte" fishery, from 1966 to 1983.

COUNTRIES	SENEGAL		MOROCCO		IVORY COAST AND GHANA (11 years)			
Models	$Y_i = f(p_1 e^{-p_2 f} + p_3 \bar{V}_i + p_4)$		$U_i = p_1 V_i^{p_2} e^{-(p_3 s \bar{f}' + \frac{3}{6} p_3 V_i^{p_2} \cdot f_i + \frac{2}{6} p_3 V_{i-1}^{p_2} f_{i-1} + \frac{1}{6} p_3 V_{i-2}^{p_2} f_{i-2})}$		$U_i = p_1 \bar{V}_i^{p_2} V_i^{p_3} - \frac{2}{3} p_4 V_i^{2p_3} f_i - \frac{1}{3} p_4 V_i^{p_3} V_{i-1}^{p_3} f_{i-1}$		$Y_i = f(p_1 \bar{V}_i^{p_2} V_i'^{p_3} - \frac{2}{3} p_4 V_i'^{2p_3} f_i - \frac{1}{3} p_4 V_i'^{p_3} V_{i-1}'^{p_3} f_{i-1})$	
Parameters	Estimation	σ	Estimation	σ	Estimation	σ	Estimation	σ
p_1	17.84	1.69	57.41	15.63	0.235	0.222	0.158	0.708
p_2	1.0E-4	-	0.996	0.21	1.107	0.431	1.866	0.933
p_3	3.049	0,66	2.56 E-5	1.7 E-5	0.097	0.302	0.343	0.332
p_4	-13.51	2.86			3.21 E-4	5.93 E-4	0.016	0.063
r^2	94 % (86 %)		72 % (27 %)		82 % (22 %)		78 % (22 %)	

* Fixed value (biological optimum)

Table. 5. Results of the non-linear regressions corresponding to different examples of application (in brackets, the regression coefficient of the same model without environmental variables).

XI. 2. The sardine stock of Sahara area

The stock of *Sardina pilchardus* observed between Safi and El Ayoun was seasonaly subdivided into two sub-stocks supporting two independent fisheries until 1980 (table 6). Sub-stock *A* was exploited by the Moroccan fishery in the northern part of the area (Agadir, Essaouira and Safi). Sub-stock was exploited by the Spanish fishery of the Canary Islands in the south, where the whole stock is regrouped during the winter (Copace, 1978, 1980a; Bravo de Laguna *et al.*, 1980; Belveze, 1984). This changed considerably from 1981 onwards and our analysis is limited to the previous period.

According to Belveze (1984) the seasonal migrations of sardines from area *A* to area *B* depend on the upwelling strength. He suggested using the square-root of the square of wind speed multiplied by its variance as the best upwelling index.

The standardization of the effort between the two fleets has been done roughly, taking into account the changes in catchability of the two fleets from year to year and the slight difference in age of the cohorts caught inside the two areas (more details on this standardization are available in Fréon (1986)).

The exponential model where the environment influences the catchability in area only has been chosen because the stock seems relatively resistant to a collapse (subdivided stock). Then, we get under equilibrium conditions:

$$B_e = B \; e^{-\left(\frac{q'}{k} sf' + \frac{q}{k} f\right)}$$

where q' is the catchability coefficient of the Spanish fleet in area B (assumed constant) and f' the corresponding fishing effort; q and f have the same meaning for the Moroccan fleet in area A, s is an average coefficient of standardization of the two fleets computed for the whole period such that: $f = sf'$. The others parameters keep their usual meaning. By considering that $q = q'bV^c$, bV^c becomes a correction factor taking into account the influence of the upwelling index V on the Morocann fleet catchability. The average value of bV^c must be equal to 1 during the fitting process because $q = q'$ after the standardization of the efforts between the two fleets. Then we get :

$$U_e = qB_\infty = B_\infty q' \, bV \; e^{-\left(\frac{q'}{k} sf' + \frac{q' \, bV^c}{k} f\right)}$$

regrouping the constant parameters it becomes :

$$U = p1 \; V^{p2} \; e^{-(P3 \; sf' + P3 \; bV^{p2} f)}$$

Considering that the Moroccan catches are based mainly on three year classes and that the Spanish catches are on average three years older, we get under non equilibrium conditions:

$$U_i = p_i \; V_i^{p2} \; e^{-(P3 \; s\bar{f}' + \frac{3}{6} P3bV_i^{P2} f_i + \frac{2}{6} P3bV_{i-2}^{P2} f_{i-1} + \frac{1}{6} P3bV_{i-2}^{P2} f_{i-2}}$$

This model explains 72% of the total variability of the c.p.u.e. (table 5, fig.12). The parameter p_2 concerning the fishing effort is not significatively different from zero using the 95% confidence limits (but only at 90%). The reason is the low range of variation of the fishing mortality during the period of observation (the increase in the nominal effort was associated with low catchability coefficients). As a result, the values of f_{max} and secondarly Y_{max} are not very precise. Nevertheless, the analysis shows that the stock seems robust and not over exploited (until 1980 at least) contrary to the initial impression given by a quick look at the decline of the c.p.u.e. series. These conclusions are consistent with the detailed analysis made by Belveze (1984) from structural models.

XI.3. The Sardinella stock off Ivory Coast and Ghana

This stock is exploited by different artisanal and industrial fleets belonging to both countries, and different abundance indexes are available (table 7). The more reliable indices are given by the industrial purse-seiner fleets and their fishing effort has been standardized (Fréon, 1986).

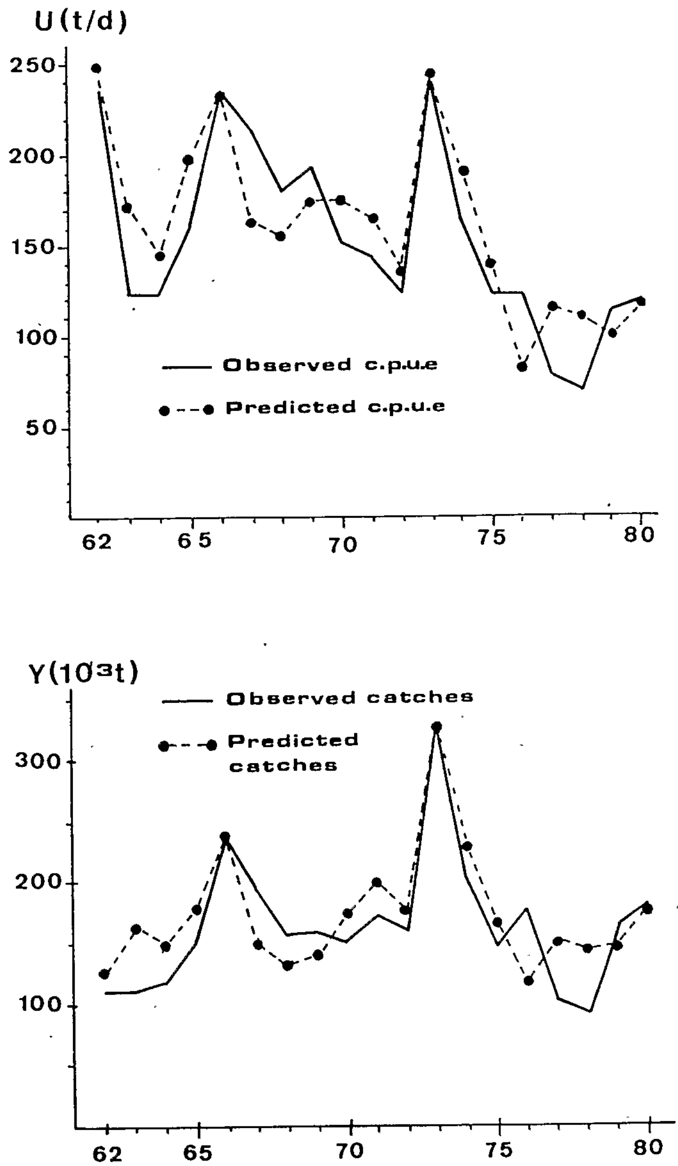


Fig. 12. Observed and predicted c.p.u.e. (U) and catches (Y) according to an exponential model where the upwelling index influences the *Sardina pilchardus* catchability in the area A between 1962 and 1980.

Table 6: Fishery statistics on the north-saharian stock of *Sardina pilchardus* and upwelling index from 1962 to 1980 (in brackets estimations). Sources: Copace 1980; Bravo de Laguna *et al.*, 1980; Belveze, 1984.

Years	Fishing Efforts		Catches		
	Morocco (A)	Spain (B)	Morocco (A)	Spain (B)	Total
62	508	(100)	120 000	(2 000)	122 000
63	963	(100)	119 000	(2 000)	121 000
64	1 045	(300)	128 000	(6 000)	134 000
65	922	900	148 500	14 600	163 100
66	1 023	1 090	237 700	20 900	258 600
67	921	1 590	196 600	28 600	225 200
68	870	1 700	155 400	32 300	187 700
69	812	1 940	157 200	36 000	193 200
70	996	3 480	150 200	50 500	200 700
71	1 204	3 270	172 700	55 500	228 200
72	1 292	2 470	159 200	46 900	206 100
73	1 350	3 430	326 300	67 600	393 900
74	1 250	3 620	204 200	86 200	290 400
75	1 199	7 340	146 600	135 700	282 300
76	1 430	5 860	176 200	128 900	305 100
77	1 306	5 850	101 900	133 500	235 400
78	1 325	7 550	91 100	140 500	231 600
79	1 457	4 210	163 400	90 900	254 300
80	1 516	4 250	181 200	85 000	266 200

Years	C.P.U.E. Morocco (A)	Upwelling index
62	236	4.13
63	123	2.83
64	122	2.39
65	161	3.30
66	232	4.02
67	213	2.83
68	179	2.74
69	194	3.14
70	151	3.18
71	144	3.15
72	123	2.66
73	242	4.59
74	163	3.51
75	122	2.73
76	123	1.79
77	78	2.59
78	69	2.40
79	112	2.29
80	120	2.50

Previous studies showed a large instability of the c.p.u.e. which was related to the upwelling index calculated from temperature anomalies. There is a dual effect of this upwelling which influences both the stock abundance and the catchability (Orstom, 1976 ; Copace, 1980b, 1982). At the same time, Binet (1982) also found a negative correlation between the catches and the main river streams. He supposed that the increase in turbidity and the decrease in surface salinity decreased availability.

In order to investigate this example, one of the models in which environment influences both the stock abundance and the catchability has been chosen. Owing to the stock fragility (a collapse was observed in 1973), the linear model has been retained. Taking into account on the one hand the age of the exploited year classes and on the other hand the belief that the upwelling influences the production over the total life span of the fish, the transitional equation over two years (*i* and *i* -1) for the fishing effort and the upwelling index is :

$$U_i = q_i \; B_\infty - (\frac{2}{3} q^2 i \; f_i + \frac{1}{3} q_i q_{i-1} \; f_{i-1}) / h$$

considering that : $B_\infty = b \; (\frac{2 \; V_i + V_{i-1}}{3}) = b\overline{V}_i{}^c$

and : $q_i = b' \; V_i^{c'}$; $q_{i-1} = b' \; V^{c'}_{i-1}$

we get : $U_i = bb' \; V_i^c \; \overline{V}_i^{c'} - \frac{2}{3} (\frac{b'^2}{h} \; V_i^{2c'} \; f_i \frac{1}{3} \frac{b'^2}{h} V_i^{c'} \; V_{i-1}^{c'} \; f_{n-1}$

or, after regrouping constants parameters :

$$U_i = p_i \; \overline{V}_i^{P2} \; V_i^{P3} - \frac{2}{3} P_4 \; V_i^{2P3} f_i - \frac{1}{3} P_4 \; V_i^{P3} \; V_{i-i}^{P3} \; f_{i-1}$$

This model may be able to explain the over-fishing in 1972 and the collapse during the following year but, as with any production model, it is not able to predict the duration of the stock recovery, even if lags are introduced (Walter, 1973, 1975; Fletcher, 1978). In a first step, to improve the fit, only the two years with c.p.u.e. approaching zero have been removed (1974 and 1975). However the resulting model yields highly significant negative residuals for 1976 and 1977, which indicate that the stock recovery was still incomplete (fig. 13). Removing also these two years the model explains 82% of the c.p.u.e. variability. Nevertheless, the overfishing in 1972 is still not very well explained (high residual), and the parameters present a high standard deviation (table 5).

Following Binet's (1982) hypothesis, two explanatory environmental variables have been introduced into the model: *V* is the upwelling index which influences the stock abundance and *V'* is the river stream average influencing the catchability such that :

$$B_\infty = b \; \overline{V}_i^c \quad ; \quad q_i = b' \; V_i^{c'} \quad ; \; q_{i-1} = b' \; V'^{c'}_{i-1}$$

then : $U_i = p_i \; \overline{V}_i^{P2} \; V_i'^{\,P3} - \frac{2}{3} P_4 V_i'^{\,2P3} \; f_i - \frac{1}{3} P_4 \; V_i'^{\,P3} \; f_{i-1}$

Table 7. Fishery statistcis of the *Sardinella aurita* stock from Ivory Coast and Ghana (dat from Togo available only from 1976, but negligible before), upwelling index and rivers flow.

STANDARDIZED C.P.U.E.

	Canoë (Gh.)		Purse seiners			
	Poli/Ali	beach seines	Ivorian in C.I.	Ivorian in Gh.	Ghanean in Gh.	Weighted average
63	-	-	-	-	-	-
64	-	-	-	-	-	-
65	-	-	-	-	-	-
66	-	-	6.37	8.73	-	8.37
67	-	-	6.70	14.50	-	13.73
68	-	-	3.67	6.17	-	5.63
69	-	-	8.64	6.04	2.38	4.39
70	-	-	4.54	5.56	3.43	4.50
71	-	-	2.81	3.33	2.48	3.85*
72	19.71	2.38	17.06	7.45	7.97	7.96
73	0.84	1.41	0.81	0	0.42	0.43
74	0.50	0.47	1.40	Arrêt	0.35	0.39
75	0.33	0.24	0.06	de la	0.18	0.18
76	4.18	3.30	9.94	pêche	2.16	2.34
77	1.34	7.32	4.86	1.65	7.08	4.40
78	9.02	10.86	10.37	11.93	12.64	12.20
79	0.67	0.47	1.84	Arrêt	4.33	4.13
80	4.68	0.71	8.10	de la pêche	5.92	6.05

	CATCHES BY E.E.Z.			TOTAL	UPWELLING	RIVERS
	Ivory Coast	Ghana + Togo	Total	STANDARD EFFORT	INDEX C.I.+Gh 2	FLOW (Bandama Comoé)
63	-	-	8 000	-	24.3	1 056
64	-	-	40 000	-	32.5	758
65	-	-	8 200	-	19.8	840
66	1 800	13 500	15 300	1 820	19.2	627
67	2 100	41 600	43 700	3 180	38.9	424
68	1 200	7 400	8 600	1 530	8.0	1 091
69	2 300	26 900	29 200	6 660	26.0	499
70	1 700	28 700	30 400	6 750	19.7	548
71	1 100	35 000	36 100	9 370*	27.4	364

Table 7 cont.

	CATCHES BY E.E.Z.			TOTAL STANDARD EFFORT	UPWELLING INDEX $\frac{C.I.+Gh}{2}$	RIVERS FLOW (Bandama Comoé)
	Ivory Coast	Ghana + Togo	Total			
72	5 600	89 800	95 400	11 980	24.2	176
73	200	5 300	5 500	12 880	17.1	256
74	270	1 670	1 940	4 960	22.3	370
75	10	2 060	2 070	11 620	26.5	335
76	1 500	14 000	15 500	6 610	28.8	197
77	900	16 200	17 100	3 880	24.9	266
78	2 000	49 000	51 000	4 180	32.1	124
79	400	12 900	13 300	3 220	8.4	511
80	1 800	22 000	23 800	3 930	17.1	242

* Estimated data by interpolation of the fishing effort between 1970 and 1972 - data not available.

By using the same data set of 11 years as previously, this model explains 83% of the c.p.u.e. variability but none of the parameters are significatively different from zero, except p_2 (table 5 : fig. 14). This is probably due to the low number of degrees of freedom associated with the poor quality of the data set and also to an extreme non equilibrium state of the fishery for a few years. Even if the residuals are lower than previously, specially for the years 1972 and 1973, the Y_{max} values given by the model are probably imprecise.

In spite of these limited results, this example remains interesting and has a didactic interest. It confirms that the upwelling plays a primordial role for the stock but is not able, when used alone, to explain why in 1972 the c.p.u.e. did increase drastically even when the stock was intensively exploited. The models show also that river flow (or salinity) plays an important role, even if it is difficult to quantify it precisely owing to the quality and the quantity of the available data and because there is a colinearity of this variable with the upwelling index. Maybe there is an interaction of the two variables or a threshold mechanism. Anyway, the conclusion is that the natural instability of this stock is amplified by the intensive exploitation it supports. The minimum and easiest management decision at the moment is to fix a quota on the catches, around 40,000 t per year.

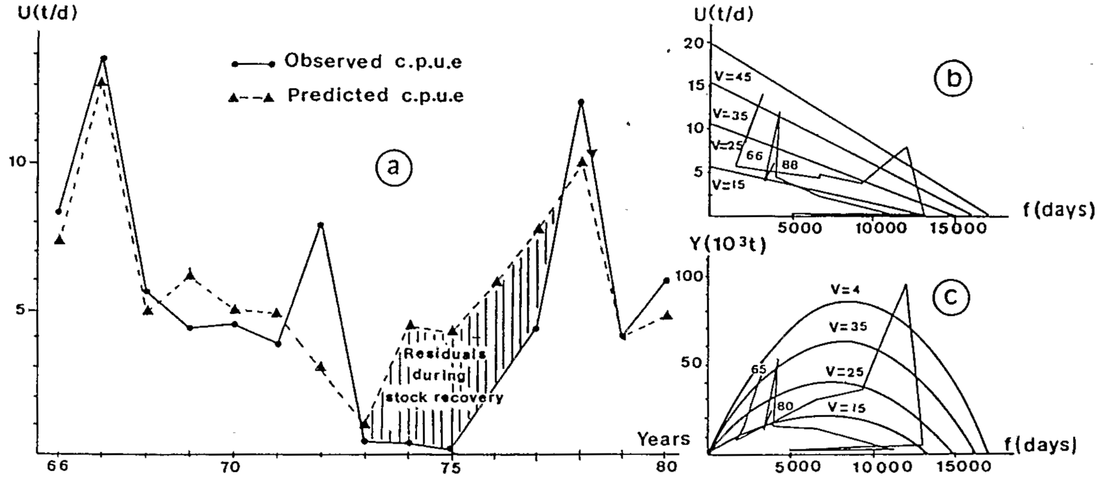


Fig. 13. Observed and predicted c.p.u.e. (U, Fig. a) according to a linear production model (fig. b and c) where the upwelling index V influences both the stock abundance and the catchability (fit made without the years 1974 and 1975) of the *Sardinella aurita* stock of Ivory Coast and Ghana, from 1966 to 1980.

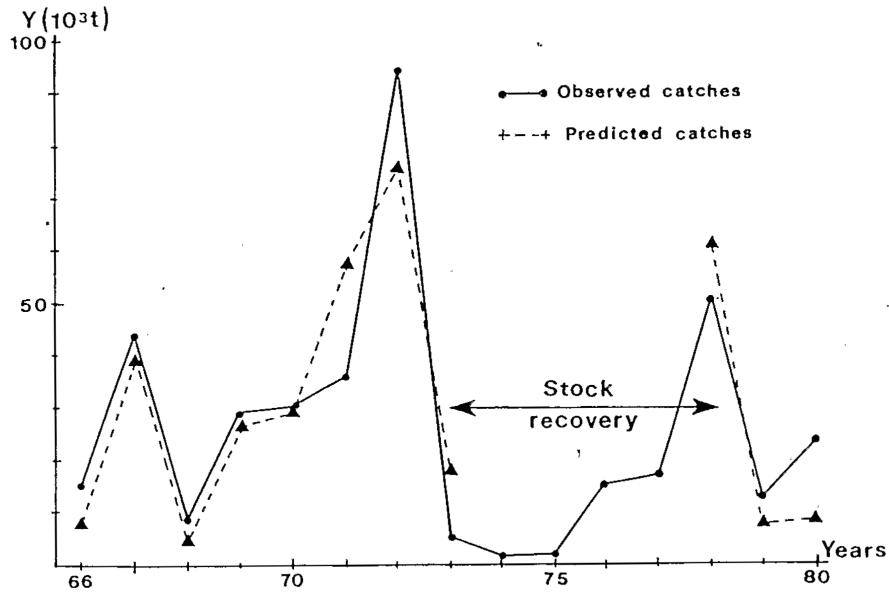


Fig. 14. Observed and predicted total catches according to the linear production model where the upwelling index influences the stock abundance and the river streams influence the catchability of the *Sardinella aurita* stock off Ivory Coast and Ghana between 1966 and 1980 (fit made without the period of stock recovery).

XI. 4. Conclusions on the modelling of fish production in upwelling areas

The usual mechanism of production in a coastal upwelling area involves successively the wind stress, the upwelled cold water mass, rich in nutrients, the phytoplankton production and the zooplankton production which are both the main food items of small pelagic fish (fig. 15). When looking at the variability of this system, it is evident that it increases on the space-scale axis during the evolution of the process, while it decreases on the time-scale axis (Fréon, 1986). For instance the wind speed and direction are rather constant over large sea-areas during a short period, but present rapid and large-scale variations when observed at a single point over a long period. By contrast, the total fish abundance of a stock is rather stable during a period of a few months, but presents large-scale fluctuations when observed in a small area.

As a matter of fact, in order to model the production in upwelling areas, the easiest way is to sample at the two extremes of the production chain, in order to be faced with sampling problems on only one of the two axes (space or time). Wind speed and direction can be measured at a few points (only one if the area is limited) at sea or at a representative coastal station, but on a very short time scale, or better by using an integrator system. When the upwelling is more related to internal waves than to the wind stress, as in Ivory Coast and Ghana, the sub-surface temperature can be used under the same conditions. At the opposite end of the production chain, the fish abundance can be sampled few times a year by experimental fishing survey or by acoustic survey when the fishery does not provide a reliable index of abundance covering the whole area of the stock distribution.

The modeling of the intermediate links of the production chain, specially the planckon production, is an ambitious and tempting objective. But it would need such a high level of sampling on both time and space scales that it seems very difficult to realize succesfully without an intensive and continuous sampling program, i.e. excessively expensive.

XII. CONCLUSION

The models outlined here allow one to take into account the effect of environment on the yields and therefore to overcome the difficulties caused by two underlying requirements of the traditional production models, namely : the data set must concern a period where the environmental factors influencing the stock abundance were stable (or fluctuated randomly over a long enough period of observation) and the catchability must also be independant of environment. This advantage allows an increase of the usable data series but requires more parameters to be estimated. The decision whether to use the traditional models or their modified versions proposed here will result from such considerations.

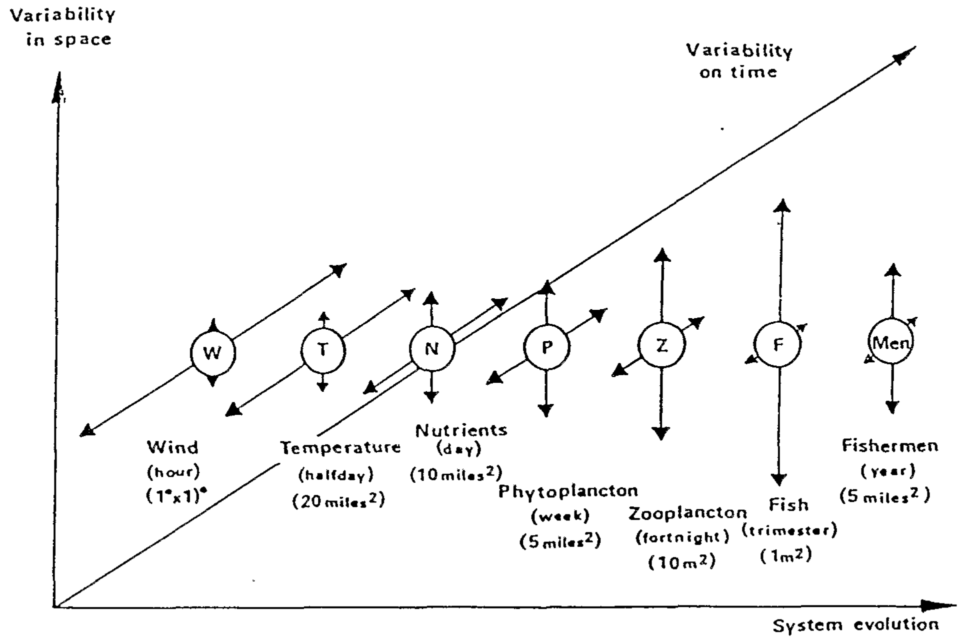


Fig. 15. Schematic description of the variability along a coastal upwelling system (score variables), using a non-linear scale of variablility (in brackets : duration or surface of relative stability of a chain link).

As these models are still global they present some limitations in their aptitude to explain the reality, and they also require the other usual basic assumptions. Despite such contraints, however these models are often a more acceptable solution than traditional models, specially in tropical areas where environmental factors have the predominant influence on production of short lived species. In such areas fish ageing is often difficult, expensive and requires intensive sampling owing to the high variability of the fish length within the cohorts associated with a special type of aggregation in the case of small pelagic species (Fréon, 1985). Under such circumstances the usual analytic methods are hardly usable. Although the environmental production models do not need quantitative biological data, it is preferable to possess a minimum knowledge of the species ecology for their proper use.

The utilization of these models for predictions is not devoid of risks. It requires a forecast of fishing effort and in some cases a forecast of one environmental factor (when there is not enough lag between this factor and its effect on the fishery). This latter forecast is often imprecise, as underlined by Walters (1985). Moreover, the confidence limits of the parameters are sometimes so high that prediction within the observed range of the variables would be hazardous, and of course it would be even worse to forecast using input values outside the observed range. "Interpolation is a science, extrapolation is an art" (Laurec, comm. pers).

Although a brilliant epitaph of the MSY was written 8 years ago (Larkin, 1978), this concept can still be used, but in a plural sense, with the present models. They provide different MSYs for each state of the environmental variable, or at least a different f_{max} when the catchability is modified. In other respects, these models can explain how large fluctuations of the catches (and sometimes collapses) may occur without any increase of the nominal effort, but owing to environmental changes. Such an eventuality has already been catered for in stochastic models (Laurec *et al.*, 1980) but only in a statistical way. A deterministic tool is proposed here for the use of fishery managers. It is still imprecise in the prediction of catches, but it allows one to understand -and sometimes to forecast- fishery tendencies. In this last case, the goal is not only to preserve the resource but also to optimize the surplus production provided by favourable environmental situations.

Acknowledgements

I am very grateful to Dr A. Laurec and Dr. E.L. Cadima for their comments and improvements to this paper. I would like to thank Dr M. Walsh for correcting the English.

References

Belveze, H., 1984. Biologie et dynamique des populations de sardine *Sardina pilchardus* Walbaum peuplant les côtes atlantiques marocaines et proposition pour un aménagement des pêcheries. Thèse Université Bretagne Occidentale, Brest, France : 532 p.

Binet, D., 1982. Influence des variations climatiques sur la pêcherie des *Sardinella aurita* ivoiroghanéennes : relation sécheresse surpêche. Océanologica Acta 5 (4) : 443-452.

Bravo de Laguna, J., Fernández, M.A.R. et Ariz, J., 1980. Determinación de una medida de esfuerzo pesquero de una flota de cerco española que faena en Africa Occidental, in : Rapport de la deuxième réunion du groupe de travail sur la sardine, *Sardina pilchardus* Walb. COPACE/PACE. Series/79/15 : annexe 5.

Cole, L.C., 1954. The population consequences of life history phenomenons. Quart. Rev. Biol., 29 : 103-137.

Copace, 1978. Report of the *ad hoc* working group on sardine (*Sardina pilchardus* Walb.). CECAF/ECAF Series 78/7 : 35 p.

Copace, 1980a. Rapport de la deuxième réunion du groupe de travail sur les sardines (*Sardina pilchardus* Walb.). COPACE/PACE Series 79/15 : 40 p.

Copace, 1980b. Rapport du groupe de travail *ad hoc* sur les sardinelles des côtes de Côte d'Ivoire-Ghana-Togo, COPACE/PACE Series 80/81, FAO, Rome : 73 p.

Copace, 1982. Report of the *ad hoc* working group on Sardinella off the coast of Ivory Coast/Ghana/Togo. CECAF/TECH/82/40: 57p.

Csirke, J. and Sharp, G.D. 1983. Reports of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO. Fish. Report, FIRM/R 291(1) : 102 p.

Dickie, L.M., 1973. Interaction between fishery managment and environmental protection. J. Fish. Res. Board. Can. 30 : 2496-2506.

Dixon, W.J. and Brown, M.B., 1979. BMDP-79 : biomedical computer programs. P. séries. University of California Press, Berkeley, CA. : 880 p.

Doubleday, W.G., 1976. Environmental fluctuations and fisheries managment. ICNAF selected papers, 1, 1976 : 141-150.

Duncan, G.T., 1978. An empirical study of jacknife-constructed. Confidence regions in nonlinear regression. Technometrics, 20(2) : 123-129.

Efron, B. and Gong, G., 1983. A leisurely look at the Bootstrap, the Jackknife and Cross-validation. The American Statistician, 37(1) : 36-48.

Fletcher, R.I., 1978. On the restructuring of the Pella Tomlinson system. Fish. Bull., 76(3) : 515-521.

Fréon, P., 1983. Production models as applied to sub-stocks depending on upwelling fluctuations, in : G.D. Sharp and J. Csirke (eds.). Procedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, FAO, FIRM/R 291(3) : 1047-1064.

Fréon, P., 1984. Des modèles de production appliqués à des fractions de stocks dépendantes des vents d'upwelling (pêche sardinière au Sénégal). Océanogr. Trop., 19(1) : 67-94.

Fréon, P., 1985. La variabilité des tailles individualles à l'intérieur des cohortes et des bancs de poissons; II :

application à la biologie des pêches. Océanol. Acta, 8 (1) : 87-99.

Fréon, P., 1986. Réponses et adaptations des stocks de clupéidés d'Afrique de l'Ouest à la variabilité du milieu et de l'exploitation : Analyse et réflexion à partir de d'exemple du Sénégal. Thèse de doctorat d'état. Université Aix-Marseille : 287 p.

Fréon, P. et Weber, J., 1985. Djifère au Sénégal : la pêche artisanale en mutation dans un contexte industriel. 1ère partie : le milieu, la senne tournante, son impact national. 2ème partie : conséquences d'une innovation technique sur l'organisation économique artisanale. Rev. Trav. Inst. Pêches marit., 47(3-4), 1983 : 261-304.

Fox, W.W., 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99 (1) : 80-88.

Fox, W.W., 1971. Randon variability and parameters estimation for the generalized production model. Fish. Bull. (U.S.), 69 (3) : 569-580.

Fox, W.W., 1974. An overview of production modeling. ICCAT workshop on tuna population dynamics, Nantes, France 1974, Rec. Doc. Scient. CICTA, 3 : 142-156.

Fox, W.W., 1975. Fitting the generalized stock production model by least squares and equilibrium approximation. Fish. Bull. (U.S.), 73 (1) : 23-36.

Garrod, D.J., 1969. Empirical assessments of catch effort relationship in the North Atlantic cod stocks. Res. Bull. ICNAF, 6: 26-34.

Genstat, 1980. Logiciels statistiques. Lawes Agricultural Trust. Rothanstep experimental station.

Graham, M., 1935. Modern theory of exploiting a fishery and application to North Sea trawling. J. Cons. Explor. Mer 10 : 264-274.

Gulland, J.A., 1969. Manuel of methods for fish stock assessment. Part I : Fish population analysis. FAO Man. Fish. Sci. 4 / 154 p.

Kawasaki, T., 1983. Why do some pelagic fish have wide fluctuation from the view point of evolutionary ecology, p. 1065-1080. In : G.D. Sharp and Csirke, J. (ed.). Procedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO Fish Rep. 291 (3) : 557-1224.

Laevastu, T. and Larkins, H.A., 1981. Marine fisheries ecosystems, its simulation and management. Fishing News Book Ltd, Farnham, Surrey, England : 162 p.

Larkin, P.A., 1978. An epitaph of the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106 (1) : 1-11.

Laurec, A., Fonteneau, A. et Champagnat, Ch., 1980. Etude de la stabilité des modèles autorégénérants : 423-438, in : A. Saville (ed.). The assessment and management of pelagic fish stocks. Aberdeen 3-7/7/1978. Rapp. P.-v. Réun. Cons.int. Explor. Mer, 177 : 517 p.

Le Guen, J.C. et Chevalier, R., 1983. Etude des pêcheries; réflexions sur l'environnement et la gestion multispécifique. Rev. Trav. Inst. Pêches marit., 46 (1) : 9-70.

Mac Arthur, A.H. and Wilson, E.O., 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.: 203 p.

Mac Call, A., 1984. Population models of habitat selection, with application to the northern anchovy. Nat. Mar. Fish. Serv. Southwest Fisheries Center. Adm. Rep. LJ-84-01 : 98 p.

Marquardt, D.W., 1963. An algorithm fo least-square estimation on non linear parameters. J. Soc. Ind. Appli. Math. 11: 431-441.

Nelson, W.R., Ingham, M.C. and Shaaf, W.E., 1977. Larval transport and year-class strength of atlantic menhaden, *Brevoortia tyranus* Fish Bull. (U.S.) 75 (1) : 23-41.

Orstom, 1976. Rapport du groupe de travail sur la sardinelle (*S. aurita*) des côtes ivoiro-ghanéennes. Fishery Research Unit Tema, Centre Rech. Océanogr. Abidjan, ORSTOM : 86 p.

Parrish, R.H. and Mac Call, A., 1978. Climatic variation and exploitation in the pacific mackerel fishery. Calif. 7 Dept. Fish. and Game, Fish Bull., 167 : 110 p.

Pella, J.J. and Tomlinson, P.K., 1969. A generalized stock production model. IATTC Bull., 13 (3) : 419-496.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish.Res. Board Can., 191 : 382 p.

Rivard, D. and Bleosoe, L.J. 1978. Parameter estimation for the Pella-Tomlinson stock production model under non equilibrium conditions. Fish. Bull. U.S., 76 (3) : 523-534.

Roff, D.A. and Fairbairn, D.J., 1980. An evaluation of Gulland's method for fitting the Schaefer model. Can. J. Fish. Aquat. Sci., 37 : 1229-1235.

Saville, A., 1980. The assessment and management of pelagic fish stocks. A symposium hold in Aberdeen 3-7/7/1978. Rap. P.-v. Réun. Cons. int. Explor. Mer, 177 : 517 p.

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. IATTC, 1 (2) : 27-56.

Schaefer, M.B., 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific ocean. Bull. IATTC, 1(2) : 245-285.

Schnute, J., 1977. Improved estimates from Schaefer production model : theoretical considerations. J. Fish. Res. Board Can., 34 : 583-603.

Sharp, G.D. and Csirke, J., 1983a. Proceedings of the expert consultation to examine changes in abundance and species composition of neretic fish resources. San José, Costa Rica, 18-29 april 1983. FAO Fish. Rep., 291 (2) and (3) : 553 p et 557-1224.

Skud, B., 1982. Dominance in fishes : the relation between environment and abundance. Science 216 (9) : 144-149.

Soutar, A. and Isaacs, J.D., 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. U.S., 72 (2) : 257-273.

Steele, J.H. and Henderson, E.W., 1984. Modeling long-term fluctuations in fish stocks. Science, 224 : 985-987.

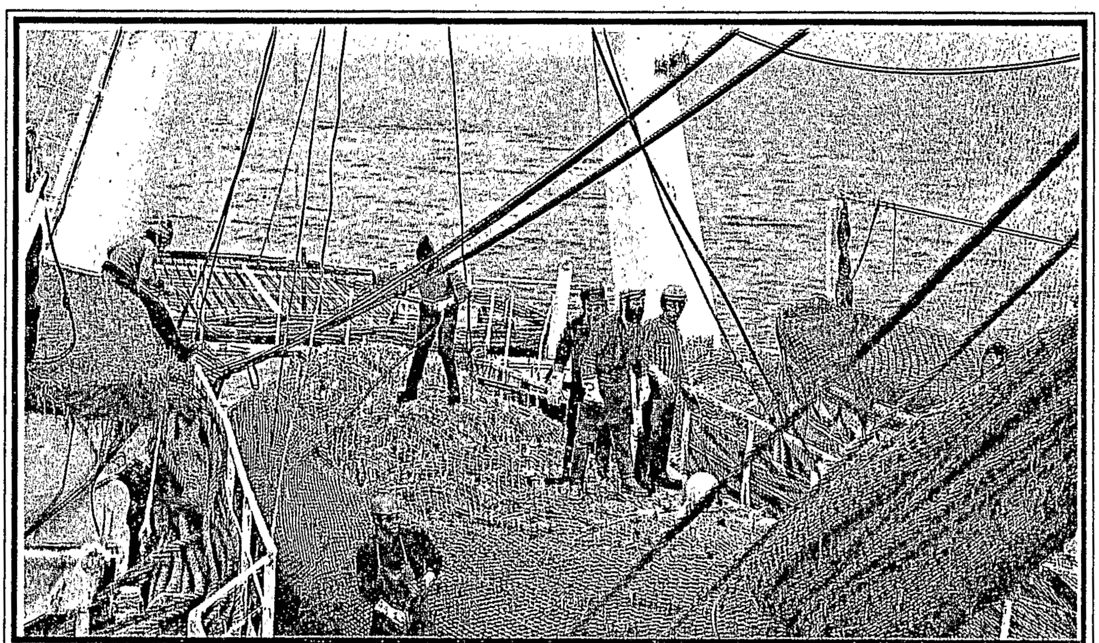
Uhler, R.S., 1980. Least squares regression estimates of the Shaefer production model : some Monte Carlo simulation results. Can. J. Fish. Aquat. Sci., 37 : 1284-1292.

Walter, G.G., 1975. Nonequilibrium regulation of fisheries. ICNAF Res. Doc., 75/IX/131.

Walters, C.J., 1985. Managing fisheries under uncertainty, in : Exploitation of Marine Communities, ed. R.M. May. Dantem Konferengen, Wallostst r 19, Berlin, 15p.

LONG TERM CHANGES IN MARINE FISH POPULATIONS

CAMBIOS DE LARGO TERMINO EN POBLACIONES DE PECES MARINOS



A Symposium held in: Un Simposio en:

Vigo. España, 18-21 Nov. 1986

Edited by: Editado por:

T. Wyatt and/y M. G. Larrañeta

Vigo, 1988