Should surplus production models be fishery description tools rather than biological models?

Francis Laloë

Centre ORSTOM, Halieutique et Ecosystèmes Aquatiques, B.P. 5045, 34032 Montpellier Cedex 1, France.

Received May 31, 1994; accepted November 28, 1994.

Abstract

Using examples, we discuss some aspects of surplus production models. Although the precision of some parameter estimators may appear to be good, the strong asymmetry of confidence intervals and the large impact of the choice of a given formula on those estimators go against this feeling. Models are often formulated with inference to the biological background, but giving a biological meaning to (the estimates of) the parameters may be very dangerous. Fishing effort standardization does not lead necessarily to useful results for management. The fleet dynamics, per se, may not allow equilibrium states. In the context of general frameworks, where the evaluation of the resource is not the unique objective, surplus production models may be however very flexible tools for fishery analysis, with low parameter requirements.

Keywords: Population dynamics, fleet dynamics, simulation, adjustment, fisheries management, surplus production models, catch-effort models.

INTRODUCTION

Surplus production models are an important approach to the study of harvested population dynamics. Such models are based on quite simple equations, where both population state and fishing activity are each described by a single variable. At a given time \( t \), under fishing activity \( f_t \) and population state \( B_t \), the change in \( B_t \) is assumed to depend on population state and fishing activity. Hence, surplus production models are commonly defined by equations such as:

\[
\frac{dB_t}{dt} = g(f_t, B_t)
\]
Typical model formulations are, for instance, Pella and Tomlinson's (1969) model (equation 1), Graham Schaefer's model \((m = 2\) in equation 1, Graham, 1935; Schaefer, 1954, 1957) and the "exponential model" (equation 2, Garrod, 1969; Fox, 1970):

\[
\frac{dB_t}{dt} = r B_t (1 - B_t^{m-1}/B^m) - q f_t B_t
\]

(1)

\[
\frac{dB_t}{dt} = r B_t (1 - \log(B_t)/\log(B^m)) - q f_t B_t
\]

(2)

where \(r\), \(B^m\) and \(q\) are parameters.

Supposing a function \(g\) allowing stable equilibrium solution, \(B_t\) becomes constant when fishing activity is constant. The study of the equilibrium state equation, \(0 = g(f, B)\), is of interest, especially if \(f_t\) may be constrained to a fixed value. In such conditions, we can obtain relations of the form \(B = h(f)\). In the general case the state \(B\) is called "exploited biomass". If CPUE data, assumed to be proportional to \(B\) (or at least a monotonic function of \(B\)) are available, they can be used with fishing activity data to estimate the model parameters and equilibrium relationships between fishing activity and yield.

Research on surplus production models are mostly devoted to (1) model formulation, (2) parameter estimation, (3) extension to multispecies and/or multi-fleet fisheries and (4) introduction of "environmental information". Herein, we present a contribution to surplus production modelling based, with the help of examples, on the following questions:

1. What are the qualities of the parameter estimates?
2. May we use model fitting to choose between alternative formulations and biological interpretations?
3. What is fishing effort "\(f\)" in a surplus production model and might equilibrium occur?
4. Are such models able to reflect many sources of variation, and, as such, do they provide an adequate and powerful description of fisheries?

Even if this discussion deals with production modelling with fisheries data, most of it is much more general. As, for example, Lebreton et al. (1992) for modelling survival in marked populations, we refer to the considerations given by McCullagh and Nelder (1983, p. 6) for data analysis and model selection:

"Modelling in sciences remains, partly at least, an art. Some principles do exist, however, to guide the modeller. A first, though at first sight, not a very helpful principle, is that all models are wrong; some, though, are more useful than others and we should seek those. At the same time we must recognize that eternal truth is not within our grasp. A second principle (which applies also to artists!) is not to fall in love with one model to the exclusion of alternatives. Data will often point with almost equal emphasis at several possible models and it is important that the statistician recognize and accept this. A third principle recommends thorough checks on the fit of a model to the data, for example by using residuals and other statistics derived from the fit to look for outlying observations and so on. Such diagnostic procedures are not yet fully formalized, and perhaps never will be. Some imagination and introspection is required here in order to determine the aspects of the model that are most important and most suspect".

What are the qualities of the parameter estimates?

Tools for estimating parameters were provided early, together with the models (Graham, 1935; Schaefer, 1954 and 1957; Pella and Tomlinson, 1969; Garrod, 1969 and Fox, 1970). Some further pieces of work were devoted to this point with sometimes results on the precision of the parameter estimates (among them Gulland, 1969; Fox, 1975; Schnute, 1977; Rivard and Bledsoe, 1978; Uhler, 1980; Ludwig and Walters, 1989; Schnute, 1989; Polacheck et al., 1993 with catch effort time series data; Munro, 1979; Marten, 1979; Caddy and Garcia, 1983; Csirke and Caddy, 1983, with data on spatial catch and effort, or catch and mortality series).

Parameters are commonly estimated from yearly catch and effort data, \((P_i, f_i), i = 1 \ldots k\), where \(k\) is the number of years with data. A one-year time step is assumed to reduce problems arising from seasonality. During each step of time \(i\), \(f_i\) is considered as a constant value \(f_i^*\).

Many sources of variation or sources of errors affect the estimation process.

- The determinist form of the equation of the model is not true. Variations of \(B\) are not a function of \(B\) and \(f\) only; many other known or unknown sources of variation exist. In surplus production models, \(g(B_t, f_t)\) should be seen only as a conditional expectation with given values of \(B_t\) and \(f_t\); estimated values of catch and CPUE should also be seen only as conditional expectations estimated from given catch effort data.

- The catch and effort data are only estimates of unknown values.

- The form of the equation may be inadequate and/or may change with time.

Different methods have been proposed for parameter estimation. The "observation error" method (Pella and Tomlinson, 1969) is now frequently seen as the best one (Hilborn and Walters, 1992). This method consists in integrating the model equation to assess the evolution of \(B\) and estimate catch and CPUE values. One can then select the values of parameters which optimize a likelihood or a "sum of squares" criterion. The criterion depends on an assumption on the form of the error in the catch data.

Aquat. Living Resour., Vol. 8, n° 1 - 1995
The yellowfin tuna fishery in Central Eastern Pacific (1934-1967)

Rivard and Bledsoe (1978) used data from Pella and Tomlinson (1969, see table 6) on yellowfin tuna fisheries in Central Eastern Pacific gleaned over 34 years (1934-1967). With an observation error procedure, they obtained the estimates given in Table 1a. The estimates of the standard error of the estimators were obtained by linear approximations at the point estimates, where the following sum of squares was minimum:

$$\sum_i \left[ \frac{(P_i - \hat{P}_i)}{\hat{P}_i} \right]^2 \tag{3}$$

where $P_i$ and $\hat{P}_i$ are the observed and fitted yields. $Bu$ and $Bo$, the estimates of the "virgin biomass" ($Bu$ in equations 1 and 2) and the "initial biomass", respectively, are smaller than the estimate of the Maximum Sustainable Yield (MSY). This result appears unrealistic. Moreover, forcing $Bu$ and $Bo$ to higher values such as $4 \times 10^5$, increases the sum of squares only from 0.73 to 0.82 and leads to very small changes in MSY and $f_{MSY}$ estimates (cf. Table 1a). Thus, we may confirm that $Bu$ and $Bo$ estimates are extremely poor. This is also the case for $q$ (catchability) which strongly depends on biomass values. However, the estimation of MSY, "target parameter", seems at first good since the standard error of the estimator, 9000, is about 5% of the estimated value (192000). Because the model is not linear, the confidence intervals or areas associated with one or several parameters may be not symmetric around the point estimates. This asymmetry comes from a distribution of the parameter estimators, which is neither normal, nor symmetric, even if the distribution of the errors are normal (see for example Draper and Smith, 1981, p. 504). With $Bu$ and $Bo$ values equal to $4 \times 10^5$, we can compute the contour of the area, defined by the projection on the "MSY - $f_{MSY}$" plane of the "MSY - $f_{MSY} - m$" volume, of parameter values leading to a residual sum of squares lower than 1.05 (i.e. 0.82 [(1 + (3/30) 2.92)], where 2.92 is the 95% quantile value of a $F$ distribution with 3 and 30 degrees of freedom). We also imposed $m$ to be greater than or equal to 0.25. If the residuals were independent (this is not the case here, as noted by Rivard and Bledsoe, 1978), with identical 0-mean gaussian distribution, such a region would be a confidence region at a level of approximately 95% (see Bard, 1974). Nevertheless, if we consider the region presented in figure 1a as a "confidence region shape", it appears that this region may be very asymmetric.

The criterion given in equation (3) is based on an assumption of proportionality between the variance of observed catches and the square of their expectations. As the fitted values are not linear functions of the parameters of the model, the estimators of those parameters may be non-consistent (with an infinite number of observations, they would not give the true value of the parameters). If we minimize the following sum of squares:

$$\sum_i (P_i - \hat{P}_i)^2 \tag{4}$$

used by Pella and Tomlinson (1969), the estimators are consistents even if variances of catches are not equal to a constant value (but the variance of those estimators are then not minimum). The estimated values of MSY, $f_{MSY}$ and $m$ are given in Table 1b. We also give in Table 1b the estimated values of MSY and $f_{MSY}$ with $m=0.25$ or $m=2$. The confidence region for MSY, $f_{MSY}$ may be computed as in the previous case and is presented in figure 1a.

Another solution is to maximize the likelihood. Supposing that the observation errors are independent, 0-mean gaussian distributions with variance proportional to the square of the real catch values, the criterion to be minimized may be:

$$\sum_i \left[ \ln (\hat{\beta}_i) + \frac{(P_i - \hat{P}_i)^2}{(\hat{\beta}_i)^2} \right], \tag{5}$$

the estimated values obtained with this method are given in Table 1c. The confidence region for MSY and $f_{MSY}$ (fig. 1a) may be obtained as in the previous cases. It is the set of parameter values leading to a value of equation 5 lower than $717.8 = 709.5 + 8.3$,
where 8.3 is the 95% quantile of a $\chi^2$ distribution with 3 degrees of freedom and 709.5 is the minimum value found with equation 5.

The estimated values and the confidence regions are quite close to the first ones. All the adjustments are also made with $B_0$ and $B_v$ values equal to $4 \times 10^3$ and $m$ greater or equal to 0.25.

The confidence regions given in figure 1a are based on Pella-Tomlinson’s formula. The confidence region may highly depend on the assumption which may be made on the value of the parameter $m$. In order to illustrate this dependence, we give in figure 1b the confidence sub-regions obtained from the three procedures with $m=2$ and with $m=0.25$. It appears that an estimation procedure used with an a priori fixed value of $m$ is likely to be biased, unless one is sure of the value of $m$.

We would not conclude here that the solution is to use the Pella-Tomlinson formula, since this formula could be itself considered as a special case of a more general class of models. The example of the Yellowfin tuna Pacific fishery is interesting because, since the 1970s, yields obtained increased to values out of the confidence regions presented in figure 1a. For this fishery, Die et al. (1990) showed, with updated data, that, taking into account the increase in fished area over time, the MSY also increased over time. The same result was obtained with the East Atlantic yellowfin tuna fishery (Laloë, 1989). We could conclude that the work of Pella and Tomlinson and later users of those data (Fox 1971, Rivard and Bledsoe, 1978) could have been better with spatial information but such a conclusion would be too easy; with the information available at that time, it would not have been expected to do better than they did. Moreover, we would not affirm that those updated models describe adequately the yellowfin tuna dynamics.

In conclusion, estimation problems seem to be dramatic. We may have the feeling of a “good” $MSY$ estimate, but in fact, a very strong asymmetry in confidence intervals may upset this good impression. Furthermore, we cannot assess the quality of an estimation procedure, unless we are sure of the nature of the model formula and of the distribution of the errors (see Schnute, 1989 for the impact of the nature of error distributions on estimators).

The ability to choose between different formulations is thus important from both a biological and an “estimation” point of view.

**May we use model fitting to choose between alternative biological interpretations?**

Lotka (1924) introduced the equation $dX/dt = aX + bX^2$ as the simplest Taylor’s expansion satisfying the conditions of having two roots, one being nil and the other positive. However, production models are, most of the time, formulated from biological considerations. The Graham-Schaefer model used the simplest possible relationships between biomass, production and fishing activity. Pella and Tomlinson (1969) considered that the generalization is useful because biomass production has no reason to be highest when biomass is one half of the virgin biomass. The exponential model or Pella and Tomlinson’s formula with $m < 2$ are commonly chosen because equilibrium relations are more satisfactory if there is no (strong) stock recruitment relationships in which case the decrease of catches when fishing mortality becomes high is lower than can be expected with a parabolic curve (see for example Shepherd, 1992).

Schnute (1985) presented a general theory for the analysis of catch and effort data with a 7 parameter general model, from which classical models may
Surplus production models

Figure 1. — a: Possible shapes of the confidence areas (95%) on \( MSY \) (10^3 pounds) and \( f_{MSY} \) (10^4 days) parameters, from data given by Pella and Tomlinson (1969) on East Pacific yellowfin fishery. The three areas with dashed line, solid line and dashed-dotted line correspond to the methods defined by equation 3, 4 and 5 in the text. b: Sub regions obtained with \( m=2 \) (Schaefer's model) or \( m=0.25 \).

be obtained as particular cases. The interest is the theoretical ability to select between these models as special cases of the most general one: “This paper (Schnute, 1985) defines such a class (of models), unique to fisheries, complete with mathematical proofs and biological explanations of all important equations”. When using this general theory, the final model is obtained from a process which associates biological theory and goodness-of-fit results. Different models can give a very close fit. It seems then

logical, as in a classical model building procedure, to select the simplest. Unfortunately such a procedure is sometimes meaningless when competing models have the same number of parameters, with a very different biological interpretation. As noted by Schnute (1985), a mathematically rigorous procedure for a model identification procedure may be inaccessible; the external biological knowledge (assumptions on the nature of relationships and the values of some parameters) must play a valuable role in the modelization process, especially regarding the formulation of an appropriate class of models. The work of Feller (1940) gives an illustration of this point. He showed that very different formulations may give very good results when describing population growth. He said: “Thus in no special case any biological conclusion must be based solely on an agreement between the observed data and the logistic form”.

With production models used with catch effort data we have to combine a formulation dealing with biomass production with a formulation dealing with the impact of fishing activity. Then, a question is: if Graham-Schaefer’s model is not able to describe a catch effort data set, is it possible to describe this data set satisfactorily with a modification of the formulation of production or of the formulation of catch?

To illustrate this point we consider the following situation. Suppose a stock, whose dynamics satisfies the equation:

\[
\frac{dB_t}{dt} = r B_t \left(1 - \frac{B_t}{B_0}\right) - q f_t (B_t - \alpha B_t)
\]

Let \( B_0=2400 \), \( \alpha=0.1 \), and \( r \) and \( q \) be such that \( MSY \) and \( f_{MSY} \) are equal to 500 and 188, \( \alpha B_0 \) represents a fixed uncatchable quantity of biomass. Some characteristics of this model are described by Laloë (1988). Assuming an initial biomass value \( B_0=2100 \), we computed the yield vector corresponding to an arbitrary vector of fishing effort (table 2a, the procedure is described in annex A). The vector of fishing effort was chosen with values far below and beyond “\( f_{MSY} \)”, reflecting an exploitation with a phase of increasing effort followed by a phase of decreasing effort. Then, we used those catch effort data to estimate the parameters of a generalized surplus production model. The results are very good, since more than 99% of the variance of relation catches is explained (tables 2a and 2b). This goodness of fit evaluation is obtained with formula:

\[
100 \left[ 1 - \frac{\sum_i \left( \frac{\hat{B}_i - \bar{B}}{\bar{P}} \right)^2}{\sum_i \left( \frac{\hat{B}_i - \bar{P}}{\bar{P}} \right)^2} \right]
\]

effort data and equilibrium relations are presented in figure 2. It is interesting to note (table 2b) that
Table 2a. – Catch effort data simulated from a Graham Schaeffer model with an uncatchable quantity of biomass (see table 2b), and catch estimated with a Pella and Tomlinson model.

<table>
<thead>
<tr>
<th>Simulated Effort</th>
<th>Simulated catch</th>
<th>Fitted catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>485.8</td>
<td>482.7</td>
</tr>
<tr>
<td>120</td>
<td>524.7</td>
<td>528.0</td>
</tr>
<tr>
<td>150</td>
<td>590.0</td>
<td>593.4</td>
</tr>
<tr>
<td>450</td>
<td>1184.8</td>
<td>1186.0</td>
</tr>
<tr>
<td>450</td>
<td>667.3</td>
<td>671.3</td>
</tr>
<tr>
<td>350</td>
<td>526.8</td>
<td>531.4</td>
</tr>
<tr>
<td>350</td>
<td>298.1</td>
<td>294.7</td>
</tr>
<tr>
<td>180</td>
<td>213.3</td>
<td>211.9</td>
</tr>
<tr>
<td>150</td>
<td>258.7</td>
<td>260.8</td>
</tr>
<tr>
<td>100</td>
<td>236.3</td>
<td>238.8</td>
</tr>
<tr>
<td>100</td>
<td>299.4</td>
<td>300.7</td>
</tr>
<tr>
<td>150</td>
<td>487.1</td>
<td>486.2</td>
</tr>
<tr>
<td>150</td>
<td>564.1</td>
<td>560.8</td>
</tr>
<tr>
<td>150</td>
<td>462.6</td>
<td>458.5</td>
</tr>
<tr>
<td>100</td>
<td>333.5</td>
<td>330.5</td>
</tr>
</tbody>
</table>

Table 2b. – Parameters of the model used for generate catch effort data (first line), and parameters of the Pella and Tomlinson model fitting those data (second line). Standard errors of the estimators are on the third line.

<table>
<thead>
<tr>
<th>Bo</th>
<th>Bv</th>
<th>MSY</th>
<th>fMSY</th>
<th>α</th>
<th>m</th>
</tr>
</thead>
<tbody>
<tr>
<td>2100</td>
<td>2400</td>
<td>500</td>
<td>188</td>
<td>0.1</td>
<td>1.05</td>
</tr>
<tr>
<td>1810</td>
<td>2401</td>
<td>498</td>
<td>197</td>
<td>0.8</td>
<td>1.05</td>
</tr>
<tr>
<td>30</td>
<td>67</td>
<td>2.9</td>
<td>2.8</td>
<td>0.05</td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. – Adjustment with a Pella and Tomlinson model of data from a Graham Schaefer model with a quantity of inaccessible biomass. Catch effort data and equilibrium relationships of the initial model (continuous line) and of the adjusted model (dashed line).

This result illustrates that Feller's (1940) and Mac Cullagh and Nelder's (1983) comments apply with production modelling. This is not surprising. In our case, an important point is that production models present an interaction between, on the one hand, biomass production of a renewable resource and, on the other hand, the impact of fishing activity on that resource. Graham-Schaefer's model leads to a decreasing linear CPUE-effort equilibrium relationships, and the parameter \( m \) in the Pella and Tomlinson's adds a high flexibility in the shape of that relation; but such a flexibility may be introduced from Graham-Schaefer's with a modification of the description of the impact of the effort (equation 6). Under those conditions, the Pella and Tomlinson model can probably not be improved if it is only used with catch and effort data, but we must note that its ability to reflect data does not allow the validation of assumptions about the nature of the impact of fishery activity or the nature of biomass production. The same remark would, evidently, also hold with the use of the other model formulation (equation 6).

If we use catch effort (and CPUE) data, we may only evaluate the adequacy of the model from the similarity between observed and fitted catch-effort-CPUE values. One cannot talk about biomass without making an assumption on the form of the relation between biomass and CPUE, and if we cannot determine which of the different formulae given in equations 1 and 6 is to be preferred, interpretation of production models as “biomass dynamics models” may be misleading.

Models based on simple equations without complete biological interpretation may therefore be useful. As an example, Roff (1983) presented a “simple autoregressive model”, from a CPUE stability idea,

\[
Y_t = a + b f_t \frac{Y_{t-1}}{f_{t-1}}
\]

He showed that in practice, Deriso's model (Deriso, 1980) is no more accurate than this simple model and how predictions obtained from available data with sophisticated equations may in fact simply say that “next year, CPUE will be near to that observed this year” (fig. 6 in Roff, 1983).

We believe that “new” formulations can only be of interest if they might accept additional information on the fishery activity or on some environmental aspects. Fréon (1984, 1988), Cury and Roy (1987) introduced a relation between virgin biomass and/or catchability and environmental conditions. In one case, Deriso (1980) introduced a relation between recruitment and temperature. Laloë (1988, 1989) used models from equation (6) with relation between uncatchable biomass and environmental or exploitation (fished area) parameters. The impact of a variable fished area on catchability (\( q \) in equations 1, 2, and 6) was also introduced in a production model by Die et al. (1990).

We may highlight the problems presented above on estimation and on model selection with data on New Zealand Rock Lobster from Breen (1991) used by Polacheck et al. (1993).
Surplus production models

Table 3a. – MSY and fMSY estimates for New Zealand Rock Lobster fishery. The first three lines present results from Polacheck et al., 1993.

<table>
<thead>
<tr>
<th>Method</th>
<th>B0, Bu</th>
<th>m or α</th>
<th>MSY</th>
<th>fMSY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eff. aver. (k = 3)</td>
<td>m = 2 (fixed)</td>
<td>5278</td>
<td>2995</td>
<td></td>
</tr>
<tr>
<td>Process error</td>
<td>Bu = 52,600</td>
<td>m = 2 (fixed)</td>
<td>5898</td>
<td>3629</td>
</tr>
<tr>
<td>Observ. error</td>
<td>129,000</td>
<td>m = 2 (fixed)</td>
<td>2133</td>
<td>1338</td>
</tr>
<tr>
<td>Obs. error</td>
<td>120,000</td>
<td>m = 0.21</td>
<td>2705</td>
<td>5517</td>
</tr>
<tr>
<td>Obs. error</td>
<td>130,000</td>
<td>α = 0.31</td>
<td>2921</td>
<td>2927</td>
</tr>
</tbody>
</table>

The New Zealand rock lobster fishery

The data set we use here contains 46 years of catch, effort and CPUE (from 1945 to 1990). Polacheck et al. (1993) estimate the MSY and of fMSY values with the Schaefer model with “observation error”, “process error” and “effort averaging” procedures. The observation error procedure gives estimates of the two parameters that are much lower than those given by the other two methods (table 2, p. 2602, Polacheck et al., 1993). The results given by the observation error method, considered as the best one by the authors, indicate that the biomass at the end of the 46-year period is about 16% of the initial biomass and that “the catches are estimated to have been comprised almost entirely of standing stock. Surplus production is estimated to have been almost nothing over the period considered” (Polacheck et al., 1993, p. 2602).

We estimated MSY, fMSY and m values from the Pella and Tomlinson’s (hereafter called “PT”) formula, with an observation error procedure. The estimated MSY and fMSY are higher than those obtained with Schaefer’s model (table 3a). We also estimated MSY, fMSY and α from Schaefer’s model with an uncatchable αBu quantity of biomass (hereafter called “UB”) model. We used for those estimations the least-square criterion used by Polacheck et al. (1993):

\[ \sum_{i=1945}^{1990} (\ln (P_i/f_i) - \ln (\hat{P}_i/f_i))^2 \]

The results of adjustment made by Polacheck et al. (1993) and the results of our adjustments are given in table 3a.

The sum of squares obtained with the PT and UB models are similar (1.60 and 1.67) and lower than the sum of squares obtained with Schaefer’s model (1.99). The first two models are also quite identical in terms of fitted CPUE as can be seen on figure 3a where the time series of observed and fitted CPUE are given.

The observed catch and effort data, with the equilibrium catch effort relationships from the models described above are given (fig. 3b). The reader may observe that the interpretations which may be made with the PT and the UB models are similar, with at least an equilibrium situation after quite a long period of stable effort (see the star on fig. 3b). Schaefer’s model leads to a relationship whose interpretation may appear not so easy.

We may now see what results are given by the different models in terms of biomass dynamics. We give in figure 3c the evolution of the biomass with the three models. The PT and UB models are now different, since the biomass cannot be lower than
Figure 3c. – Biomass evolution with the three models (see fig. 3a).

Figure 3d. – Biomass production with the three models (see fig. 3a).

With the UB model. We give in figure 3d the evolution of biomass production; the trends from PL and UB models are quite similar. With the PL model the parameter \( m \) is quite low (0.21), allowing high biomass production at low biomass levels. In the UB model case, the production is highest when the biomass is \( B_{i+2} \), as with the Schaefer model, and a high production level is ensured by the uncatchable biomass. In the case of the Schaefer model, the production appears to be very low in recent years and the fishery is likely to collapse rapidly.

We may hence confirm from those results that any discussion on estimation procedures must not be based on Schaefer’s equation only and that no unique clear biomass dynamics description can be made.

Polacheck et al. (1993) conclude very firmly that the effort averaging method must be rejected. We are not sure that the examples they give support this conclusion. The major criticism against this method deals with the bias of estimators. We suspect this objection to be somewhat trivial.

The effort averaging method (Guillaud, 1961; Fox, 1975) consists in replacing each effort \( f_i \) by a weighted average effort as (Fox, 1975):

\[
\bar{f}_i = \frac{k f_i + (k - 1) f_{i-1} + \ldots + f_{i-k+1}}{k + (k - 1) + \ldots + 1}
\]  

and then in considering only the equilibrium relationships between CPUE and averaged efforts in order to estimate the \( MSY, f_{MSY} \) and \( m \) parameters of the model. The use of past efforts in the averaging procedure is made in order to take into account the impact of past fishing activity on the biomass and the choice of the number of years \( k \) is based on the number of age classes being fished.

With this method, the transition to equilibrium does not correspond to the classic equations of surplus production models as some consequences of this last sentence may illustrate:

- fishing activity before year \( i - k + 1 \) is assumed to have no impact at all on biomass \( B_j (j > i) \),
- all fishing activity vectors between years \( i - k + 1 \) and \( i \) which lead to the same weighted average are assumed to have the same impact on the biomass at year \( i \); hence, if after a year \( i, f_{j} (j > i) \) is fixed equal to \( \bar{f}_i \), the exploitation will be supposed to be in equilibrium state,
- a dimension of the space of the parameters is lost; with Schaefer’s model only two parameters can be estimated (giving the equilibrium CPUE-Effort and Catch-Effort relationships).

The effort averaging method corresponds in fact to a transfer function model of CPUE with an \( a \ priori \) given form of the function of effort based on biological knowledge or hypothesis leading to equation 7.

As a consequence of this, estimators of parameters depend on the value of \( k \). If we can choose \( k \) among \( n \) values, \( (n - 1) \) among them (probably all) will lead to biased estimators of parameters. It is \( a \ priori \) evident for some of them, as in the case of New Zealand rock lobster data, where the choice \( (k=3) \) made by Polacheck et al. (1993) is not adequate if we consider the longevity of the species.

It is essential with this example to consider a higher value for \( k \) and also to consider the Pella and Tomlinson’s model. If we consider that the period 1956-1975 may correspond to a complete transition to equilibrium, we may choose \( k = 20 \). The effort averaging method leads then to estimation of \( MSY, f_{MSY} \) much lower than those obtained with \( k = 3 \). If we consider the hypothesis, suggested by the adjustment made by Polacheck et al. (1993), that the catches almost entirely comprised standing stock, \( k \) should be at least equal to 46. We may possibly look for the
Surplus production models

Table 3 b. – Estimates from the effort averaging method with various k values.

<table>
<thead>
<tr>
<th>k</th>
<th>m</th>
<th>MSY ($10^3$)</th>
<th>f MSY ($10^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>2 (fixed)</td>
<td>5.28</td>
<td>30.0</td>
</tr>
<tr>
<td>3</td>
<td>1.44</td>
<td>4.82</td>
<td>28.5</td>
</tr>
<tr>
<td>10</td>
<td>2 (fixed)</td>
<td>4.79</td>
<td>28.0</td>
</tr>
<tr>
<td>10</td>
<td>1.50</td>
<td>4.43</td>
<td>27.8</td>
</tr>
<tr>
<td>20</td>
<td>2 (fixed)</td>
<td>4.15</td>
<td>27.3</td>
</tr>
<tr>
<td>20</td>
<td>1.45</td>
<td>3.77</td>
<td>24.0</td>
</tr>
<tr>
<td>30</td>
<td>2 (fixed)</td>
<td>3.62</td>
<td>22.3</td>
</tr>
<tr>
<td>30</td>
<td>1.50</td>
<td>3.20</td>
<td>21.0</td>
</tr>
<tr>
<td>46</td>
<td>2 (fixed)</td>
<td>2.92</td>
<td>18.5</td>
</tr>
<tr>
<td>46</td>
<td>1.21</td>
<td>2.46</td>
<td>18.0</td>
</tr>
<tr>
<td>72</td>
<td>2 (fixed)</td>
<td>2.14</td>
<td>13.7</td>
</tr>
<tr>
<td>72</td>
<td>1.22</td>
<td>1.70</td>
<td>12.5</td>
</tr>
</tbody>
</table>

The value of k leading to an estimate of MSY as near as possible to the value obtained with the observation error method with Schaefer’s model; we then obtain k=72 (MSY =2,136, f MSY =1,385) and an average effort value equal to 2,766 in the last year.

We give in table 3b the results of the adjustments made with the effort averaging method with different values of k (3, 10, 20, 30, 46 and 72) with m estimated or beforehand fixed at two. The equilibrium catch effort relationships with k=20 are also presented on figure 3 b. All those averaged efforts were obtained assuming zero values for efforts before 1945, which is equivalent to a hypothesis of equality between Bo and Bv.

Those results confirm that the estimates of MSY and f MSY highly depend on the value of k. With k =20 we may observe that the equilibrium relationship is quite near the “equilibrium point” described above (the star in fig. 3 b). However, the conclusions which may be tried in terms of prediction for the future of this fishery lie somewhere between those obtained from the various adjustments made with the observation error procedure.

We shall not say here which of the various adjustments is to be considered the best. This could only be made with reference to the knowledge (and/or clear assumptions) on the exploitation and on the resource. If we may firmly conclude that we share the conclusion of Polacheck et al. (1993) that assessment must not be based on effort averaging or process error estimators only, we may also add that this assertion must be applied to any other estimation method.

Surplus production models cannot be used as proof for biological theory; they can only be built as a support of such a theory. However, they also may accurately describe some aspects of the interaction between a resource and an exploitation and, as such they may be useful for describing “fisheries”. In that sense, they may be built as support for “fisheries theory”, where the resource is not the unique variable to be explained.

Production models may be considered as tools used to produce a synthesis of information. This information is usually a catch effort data set, and the synthesis is a low number (2 or 3) parameters. We may consider the catch effort data set itself as a synthesis of a much more important data set on fishing activity which may also be modelled. This leads to a discussion of “f”, the fishing effort, in a model formula.

What is fishing effort “f” in a surplus production model and might equilibrium occur?

The term “q f B” in equation 1 and 2 looks straightforward. Such a term leads us to use effort data proportional to mortality and corresponding to a CPUE that would be proportional to the exploited biomass.

As noted by Laurec and Le Guen (1981), an effective effort may not be strictly proportional to, but “as near a possible to a fishing mortality”. We saw in the preceding section that PL and UB models may be equivalent in terms of catch effort data description. It means that a model assuming a linear relationship between effort and mortality (the PL model) may adequately describe, at least in some cases, data associated with a non-linear relationship (the UB model). This shows that the knowledge of the relationship between fishing effort and its effect on the biomass is not a necessary condition. If this knowledge was necessary, we believe that surplus production models would now be forgotten. Nevertheless if a given relationship may be assumed, it may be important to incorporate it in a model formula. MacCall (1976) proposed a relation between the catchability q and the biomass in a model of the Californian Pacific sardine puse seine fishery where

\[ q = a B^k \] and \[ q f B = a f B^{1+k} \]

Gulland (1977) analyzed those situations in terms of stock stability. Such an expression may be useful when using a nominal effort, were nominal effort is expressed in terms of fishing days of one standard vessel, without trying to decompose the intra-day activity (Ulltang, 1980).

In those cases, the modelization deals with one stock and q, related to the nominal effort, is supposed to be a function of the biomass. If we consider fishing units which may choose between different alternatives, each of them generating different q values, the situation becomes more complicated due to a much larger distortion between effective and nominal efforts.
We illustrate that point with the following example. Suppose we study the exploitation of a stock \( a \) of which the dynamics satisfies the Graham Schaefer’s equation:

\[
\frac{dB_a}{dt} = r_a B_a \left( 1 - \frac{B_a}{B_{va}} \right) - q_a f, B_a
\]

where \( B_{va} = 2400 \), \( q_a = 0.002778 \) and \( r_a = 0.83 \) (\( MSY = 500 \) and \( f_{MSY} = 150 \)).

Suppose that the effort is proportional to the number of fishing units using a tactic “1” which allows catch on stock \( a \) only. Suppose that each fishing unit may choose a second tactic “2” which only allows catches on a second stock \( b \), whose dynamics satisfies equation

\[
\frac{dB_b}{dt} = r_b B_b \left( 1 - \frac{B_b}{B_{vb}} \right) - q_b f_b (B_b - \alpha B_{vb})
\]

where \( B_{vb} = 2400 \), \( \alpha = 0.2 \), \( r_b = 0.83 \) and \( q_b = 0.002163 \) (\( MSY = 500 \) and \( f_{MSY} = 313 \)).

If there are \( N \) fishing units, effective efforts on stocks \( a \) and \( b \) are \( N_1 \) and \( N_2 \), with \( N_1 + N_2 = N \). Under equilibrium, we may seek, for a given \( N \), which values of \( N_1 \) and \( N_2 \) lead to equal CPUE for the two species. All units adopt tactic 1 (\( N_1 = N \)) if CPUE with this tactic is higher than CPUE with tactic 2 on the virgin stock \( b \) (\( N \in [0, 108] \)) in our example; if \( N \) is greater than 108, there is a solution with \( N_1 \) and \( N_2 \) greater than 0. We have:

\[ q_a B_a = q_b (B_b - \alpha B_{vb}) \]

and

\[
B_a = B_{va} - B_{va} q_a (N - N_2)/r_a \\
B_b = B_{vb} (1 - q_b N_2 + \sqrt{\Delta})/2r_b
\]

with

\[ \Delta = (r_b - q_b N_2)^2 + 4 r_b \alpha q_b N_2 \]

We obtain:

\[
q_a (B_{va} - B_{va} q_a (N - N_2)/r_a) - q_b B_{vb} (r_b - q_b N_2)/2r_b + q_b \alpha B_{vb} = q_b B_{vb} (\sqrt{\Delta})/2r_b
\]

If we take the square of each term in this equation, we obtain an equation of degree 2 in \( N_2 \), which has only one acceptable solution. We may now calculate equilibrium yields on stock \( a \) as a function of \( N \) (a nominal effort), or \( N_1 \) (an effective effort) (fig. 4).

We could now discuss the qualities of each relation between catch and \( N \) or \( N_1 \). On the one hand, \( N_1 \) has a biological sense since it satisfies the \( q f B \) expression, but if a conclusion of a study is “\( N_1 \) could be twice the present value” we do not know what change in \( N \) would lead to this result. On the other hand, \( N \) does not make biological sense only, but if we could obtain an equilibrium relation between yield and \( N \), we could better discuss the impact of changes in unit number.

This example shows that a surplus production model is not only a biological (population dynamics) model; it is a fishery model. In the context of research programmes, where questions may focus on a particular stock or on a particular type of fishing units, it is not unusual to have available information on \( N_1 \) only or on \( N \) only. For example, if the central question is the dynamics of stock \( a \), all the accessible data on fishing trips with tactic 2 may be not seen or lost in effort standardization operations. In that case, information on \( N \) will be absent, or lost. We see in this very simple example how insufficient may be those partial sets of information, and therefore the questions leading only to collection or produce them.

The example presented above is also very unrealistic. In practice, it is much more difficult to define clearly effective and nominal efforts (Laloë, in press) and if some change appears in the species “prices”, in the costs of using the different tactics, or in environmental impacts, the equilibrium relationship changes. This leads to a discussion about equilibrium.

If we go on with the same example, with the two stocks \( a \) and \( b \) and one fleet, whose units are to choose between the two tactics 1 and 2, we may see what occurs if we allow changes of tactics decided by fishermen based on previous CPUE information.
At time \( t \), knowing the CPUE for the two stocks at time \( t-1 \), we suppose that the proportion of fishing units choosing tactic 1 is:

\[
\begin{align*}
    p_{1t} &= p_{1t-1} + \lambda \frac{(R_{1t} - R_t)}{R_t} \\
\end{align*}
\]  

(8)

where \( R_{1t} \) is an expected income from the use of tactic 1, say \( R_{1t} = P_a \text{CPUE}_{a_{t-1}} - C_1 \), where \( P_a \) and \( C_1 \) are the price per unit of weight for stock \( a \), and the cost of using tactic 1; \( R_t \) is the mean of the two expected incomes \( R_{1t} \) and \( R_{2t} \), and \( \lambda \) is a "flexibility parameter" the value of which must be set in relation with the unit of time used. In our example, \( \lambda = 1.5 \) means that the proportion of units choosing tactic 1 increases with value 0.5 if \( R_1 = 2 R_2 \); with a monthly step of time, this corresponds to a fairly flexible fishery. As equation 8 does not ensure that \( p_{1t} \) values will be inside the \([0, 1]\) interval, we impose constraints such that \( p_{1t} \) and \( p_{2t} \in [0, 1] \) and \( p_{1t} + p_{2t} = 1 \).

With starting values, say \( p_{10} = p_{20} = 0.5 \), \( B_{a0} = 1200 \) and \( B_{b0} = 2000 \), we may see the changes in monthly catches on stock \( a \) and the sum of the two catches. We made a simulation with \( N = 450 \), for ten years. Costs \( C_1 \) and \( C_2 \) equal zero, and prices \( P_a \) and \( P_b \) equal 1 for the first five years. At the beginning of the sixth year, we multiplied the price of stock \( b \) by 2 (\( P_b = 2 \)). Time-courses of efforts \( N_1 \) and \( N_2 \) and CPUE from each stock are presented in figures 5a and 6a. Equilibrium appears to be an inaccessible state, and we see the impact of price change. In fact, the evolution of descriptors of such a fishery highly depends on starting values which were chosen for this example in order to obtain analogous initial values for \( \text{CPUE}_a \) and \( \text{CPUE}_b \).

In this example, we consider a discrete time equation for the changes in fishing effective effort. Fishing units update their decisions only once per month. The lengths of the time step used for the discrete time equation may be strongly linked with the behaviour of the system. If we suppose that fishing units may update those decisions on a daily basis the situation may be reflected with a one-day step increment with equation:

\[
\begin{align*}
    p_{1t} &= p_{1t-1} + \frac{\lambda}{30} \frac{(R_{1t} - R_t)}{R_t} \\
\end{align*}
\]

The evolution is then different (fig. 5b and 6b) with lower (damped) amplitudes in variations, showing the potential importance of the frequency of fishermen tactical changes.

Allen and MacGlade (1986) gave examples of the impact of fishermen's strategies. With the example presented here, it appears that high fluctuations could be observed even in a very simple "one fishery-two species" model, and without any fluctuations or changes in some "biological" parameters.

In conclusion, fishing effort "\( f \)" is a synthesis of information on fishing activity which should not be uniquely devoted to a maximization of information on mortality. It has to be clearly defined in each case study with reference to available information and the aim of the study.

Are such models able to reflect many sources of variation, and, as such, do they provide an adequate and powerful description of fisheries?

The use of production models, with catch-effort data seems to be very difficult for biological purposes. We believe, however, that such models can be very useful to give representations of many sources of variation and interaction.

Aquat. Living Resour., Vol. 8, n° 1 - 1995
Figure 6. — Evolution of CPUE from tactics 1 (continuous line) and 2 (dashed line), (see text). a: with effort updated every month. b: with effort updated every day.

As an example, when the environment of the resource appears to be important, it is possible to search for a formulation of the model equation with an impact of environmental variates on some of the parameters. For that purpose, Fréon et al. (1990) propose an expert system "CLIMPROD" allowing choice of which formulation, among 30 possibles, appears to best represent the case in study, according to information external to the data set (species biology, stock history, etc.)

More generally, for "conventional use", fishing activity is seen as an "independent variate" in a regression-like procedure. For this, fishing effort (a synthesis of information on fishing activity) has to be an (increasing) monotonic function of mortality. It has also to be a function of the fishing activity, as it can be "managed". An illustration of this point is the shortcut which often leads to call "effort multiplier" a "fishing mortality multiplier" in Yield per Recruit graphs. This shortcut can be misleading because it implies the existence of a linear relationship between two representations of fishing activity which implies, at least in terms of expectation, that at any given "value" of the first representation there is a corresponding unique "value" of the second and vice-versa.

Surplus production models may be linked with models of fishing activity in a general framework where nominal and effective efforts are separately presented. This may be done with multispecies and/or multifleet fisheries and examples were given by Allen and MacGlade (1986) and Hilborn and Walters (1987). This can also be made with analytical models, when data are available (Charreau and Biseau, 1989; Laurec et al., 1991) but in most of these examples the models are based upon production models. This demonstrates the versatility of production models in relating biomass production to explicit formulations of the dynamics of nominal and effective efforts (see Hilborn and Walters, 1992).

As an example, we used such an approach to give a general framework for the Senegalese artisanal fishery (Laloë and Samba, 1990, 1991). In that case, the purpose was to provide a simulation tool that can take into account the following features.

1. Fishery units may choose between different tactics: the activity of a unit (nominal effort) may lead to different mortality distributions among stocks (effective efforts); this problem was identified by Garrod (1973). Fishery units have strategies identified by sets of available tactics and a decision rule. The choice of a tactic (related to an effective effort) at a given time is made by fishermen (whose activity corresponds to a nominal effort) from the knowledge of recent incomes (that take into account prices, costs, opportunity costs, etc.), and from the knowledge of global annual periodicity in stock accessibilities.

2. Stock dynamics are modelled with very simple Schaefer's like models with quantities of inaccessible biomass. Those models are used in non-equilibrium situations, that is, without assumptions such as \( \frac{dB}{dt} = 0 \). Such formulations are chosen because the values of the parameters may be chosen to reflect some features that appear a priori important. Hence inaccessible quantities of biomass depend on the stock, the season (migration patterns etc.) and tactic (operating ranges, etc.).

3. Change in the parameters (prices, costs, catchabilities, accessibilities, strategies, biological parameters etc.) of the model may be introduced in order to take into account observed or assumed changes in the general environment of species and fishermen.
Surplus production models

With such a representation, it is possible to mimic the main changes observed during the last fifteen years, and to obtain output values similar to those observed from the real world. It is also possible to show that, in this case, fleet dynamics are needed to reflect the global changes in exploitation pattern among stocks and to show the importance of this aspect for the prediction of fishing units success.

An important question then is the use of production models in some predictive sense.

With the classical use of stock production models, many authors noted that, as with every model, results cannot be extrapolated out of the domain of observed effort values or that many problems are associated with \(MSY\) or \(f_{MSY}\) as management objectives (see Laurec and Le Guen, 1981; Larkin, 1977 and Sissenwine, 1978). Production models are often considered as "postdiction" tools (see Fonteneau, 1981). We think that those difficulties remain present in any use of production models.

An important point is the stability of the model, i.e. the stability of the parameters or even the stability of the formulation itself. With populations of Yellowfin tuna in Atlantic (Laloë, 1989) and Pacific (Die et al., 1990), models including changes in fished area give better fit than models that do not include these changes. However, different formulations can be used, and these pieces of work were done after an interpretation of the evolution of \(MSY\) estimates (see Fonteneau, 1988). In another work (Laloë, 1988), the evolution of \(Sardinella aurita\) catches in Ivory Coast and Ghana was modelled "well" with a formulation including the effect of coastal river flow, but this formulation was made after an ecological interpretation (Binet, 1982); moreover two formulations with very different \(MSY\) estimates gave the same goodness of fit! Eventually, catches in the 1980s invalidate both of these formulations. New fit could be attempted, but at the price of taking into account new interpretations in adapted formulations and, now, interpretations of this fishery evolution are mostly attempted with upwellings without reference to river flows (see Roy, 1992; Pezennec et al., 1993).

More generally adjustments of data cannot be used to prove an assumption (i.e. an example cannot be a proof of an assertion), but can be used to invalidate an assumption (i.e. a counter example may invalidate an assertion).

If we consider prediction as an attempt to answer a question such as: "what will be a CPUE at a given future time if the fishing activity (fishing effort?) remains stable?" or, in more statistically and realistic terms: "what will be the distribution from which the observed CPUE will be a realization?", production models are likely to be in many cases poor prediction tools. Some events may lead to changes in the model, as it is formulated in the present time, because they are unpredictable or because their link with the translation of fishing activity in terms of fishing mortality or with the biomass production are not (well) known. For each case, predictability must be analyzed from the knowledge on global stability of the system (including the knowledge of stability of the fishing activity in terms of effective and nominal efforts). We must accept the evidence that we cannot give any definitive answer on predictability, especially regarding what may be predicted and how many years ahead prediction may be appropriate.

When sources of variation are identified and appear to be "important", we may try to introduce them in a framework. If a framework is "adequate" with what we know from the real world (which is not the real world), we may use it to explore consequences of changes which can be taken into account in this framework. That approach is in agreement with this sentence of Gulland (1982):

"Instead of making assessments of the effects of changing biological parameters (fishing mortality, size at first capture, etc.) and then considering what specific measures would have the necessary effects, the first stage might be to identify, in general terms, possible measures, and then make the assessment".

In that sense, production models, as part of such frameworks, may be used as prediction tools; for instance if they lead to illustrate that there is no "decision centre" which may fix a fishing mortality level and that a necessary condition for fishing units (future) viability appears to be its ability to choose between different tactics (i.e. different catchability vectors). In such a situation, the minor conclusion is not that stability of mortality for each component of a resource is an inaccessible (and possibly dangerous) management objective. Hence any response to the classical question "what will be the CPUE or the catches if effective efforts remain stable" is not sufficient in order to fully use the available information. Another question must be then, also, whether the adaptability of fishing units will be sufficient to ensure their viability, for a given context of (possibly unpredictable) variability in fish and fishermen environments.

However, as we tried to show it, such a prediction must be made with great prudence and modesty.

CONCLUSION

Surplus production models are often seen as "poor cousins" of age structured ones (Hilborn and Walters, 1992). However, those authors (who call those models "biomass dynamics models") say that many of the problems, as for example poor contrasts between effort and stock abundance, are shared by both surplus production and age structured models; Moreover, they note that biomass dynamics models may "provide better estimates of management parameters than age structured approaches even when important parameters such as growth and vulnerability are known".

Aquat. Living Resour., Vol. 8, n° 1 - 1995
We think that this quality is due to the high versatility of surplus production models with a rather low parameter requirement. Highly linked with this quality their "flaw" is that a good adjustment cannot be solely used as a demonstration of the validity of the natural biological interpretation of the parameters present in a formulation.

The use of surplus production models occurs in an intermediate phase of synthesis: the data (effort, CPUE, catch, environmental indices) are themselves a synthesis of information, and the parameter estimates are a further synthesis of those data. The first step of this synthesis is highly linked with a representation, with a more or less explicit set of assumptions, allowing only the consideration of "fishing activity" in terms of fishing mortality. This leads us to ignore many available or easily accessible information on fishing activity which is not directly used to estimate a fishing effort, whose quality is to be "as near as possible to a fishing mortality". This largely restricts the use of models in order to answer only biological questions.

In other words, the possible progress in the use of surplus models is more likely to concern the quality of questions that can/should be addressed rather than respond to usual questions. As part of "fisheries dynamics models", surplus production models should be used in frameworks in order to give representations of fisheries, taking into account "expert knowledge" as well as a greater set of information.

I believe that their use will continue for fisheries analysis, especially as exploration and simulation tools.

Acknowledgments

I thank Drs. P. Fréon, F. Gauthiez, X. Lazzaro, J. D. Lebreton, D. Roff and anonymous referees for their very helpful remarks on the manuscript.

REFERENCES


Surplus production models


ANNEX A

For the simulated fishery with the model

$$\frac{dB_t}{dt} = r B_t \left( 1 - \frac{B_t}{B_v} \right) - q f_t (B_t - \alpha B_v)$$

the catches are obtained from the integration of the equation (see for example Jolivet, 1983).

With biomass at time $t_0$ equal to $B_{t_0}$ and with a constant value $f_{t_0}$ between $t_0$ and $t_0+1$, $B_t (t \in [t_0, t_0 + 1])$ may be computed from:

$$\log |B_t - s_1| - \log |B_t - s_2| = -\frac{t}{B_v} (s_1 - s_2) t + c$$

with

$$c = \log |B_{t_0} - s_1| - \log |B_{t_0} - s_2|$$

were $s_1$ and $s_2$ are the roots of equation:

$$0 = -\frac{r B^2}{B_v} + B (r q f_{t_0}) + q f_{t_0} \alpha B_v$$

(if $\alpha \in [0, 1]$, $s_1$ and $s_2$ are real with $s_1 > 0$ and $s_2 \leq 0$).

Mean biomass during time interval $[t_0, t_0 + 1]$ is computed from

$$\overline{B_{t_0}} = \sum_{j=0}^{5} B_{t_0+j}/6$$

and catch from

$$P_{t_0} = q f_{t_0} (\overline{B_{t_0}} - \alpha B_v)$$

Initial biomass is given for the first step and computed from the integration of the equation for the others.