Equilibrium Production Models that Incorporate Fished Area

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Abstract.—Users of stock production models assume that a time series of catch-per-effort data reflects changes in the size of a self-sustaining biological population. This assumption is often violated in analyses of fisheries that have undergone changes in the areal coverage of the fishing fleet because the fraction of the population that is available to fishing also changes. Furthermore, the problem is aggravated when there is biomass transfer (in the form of migration) between the exploited and unexploited segments of the population. We present a general production model that can be used to understand the dynamics of equilibrium population size and yield as functions of fishing mortality and exploitable population fraction. We then develop two simple subsets of this model in which biomass transfer is either nil or high between the unexploited and exploited fractions, and we discuss methods to estimate the models’ parameters given data on catch, effort, and area. The application of the models is illustrated with data on the fishery for yellowfin tuna Thunnus albacares in the eastern Pacific.

Stock production model analysis has been widely used in fisheries research because it provides estimates of maximum sustainable yield (MSY) and of the fishing effort necessary to achieve it ($f_{msy}$). Despite recent trends that favor the use of age-structured techniques for stock assessment, production models are likely to remain an important element of fishery analysis, particularly for data-limited situations in which catch-at-age data are not available. Furthermore, the concept of MSY, closely associated with production models, is simple, well understood, and accepted by the fishing industry and fishery managers alike (Barber 1988).

Numerous production models have been formulated in the past (e.g., Graham 1935; Schaefer 1954; Chapman 1967; Pella and Tomlinson 1969; Fox 1970), all of which share some common assumptions. One of the main implicit assumptions made in using production models is that the data reflect changes in the population size of a single biological unit (Pella and Tomlinson 1969; Fox 1974). This assumption is likely to be unfulfilled in many situations. One possibility is that the data have been gathered from two or more stocks that are exploited at different levels of fishing effort. Fox (1977) showed that it is possible to estimate the relevant exploitation parameters in such a situation for highly migratory species, given that the rates of mixing of individuals between the various stocks are known. In the case of distinct but sedentary stocks, a possible solution is to treat total catch per unit of effort as a function of the efforts and areas of the individual stocks (Munro 1977; Caddy 1986).

A similar cause for the failure of the assumption of a single biological unit may be encountered in expanding fisheries. Many fisheries develop by initially exploiting that part of the stock that is closest to the fishing ports and then expand to include more distant grounds as the catch per unit of effort is reduced inshore. During this process, the fishery may exploit areas with higher fish densities first and then move to less productive grounds, or vice versa. Thus, it would be desirable to develop models that account for trends in the areal extent of the fishery, as well as for trends in effort. The purpose of this paper is to describe a stock production model that accounts for historical changes in the exploited fraction of a stock, and to present a method to estimate the parameters of the model. Data from the fishery for yellowfin tuna Thunnus albacares in the eastern Pacific are used to illustrate the model’s applicability.

The Basic Model

As the starting formulation, we use Fox’s (1977) model for two stocks (denoted by the subscripts 1 and 2):
\[
\frac{dP_1}{dt} = (K_1P_{1t} + T_1P_{2t})\left(\frac{P_{1\infty} - P_{1t}}{P_{1\infty}}\right) \\
- T_1P_{1t}\left(\frac{P_{1\infty} - P_{2t}}{P_{2\infty}}\right) - F_{1t}P_{1t}, \tag{1a}
\]

and
\[
\frac{dP_2}{dt} = (K_2P_{2t} + T_1P_{1t})\left(\frac{P_{2\infty} - P_{2t}}{P_{2\infty}}\right) \\
- T_2P_{2t}\left(\frac{P_{1\infty} - P_{1t}}{P_{1\infty}}\right) - F_{2t}P_{2t}; \tag{1b}
\]

\[P_t = \text{population sizes (biomass) at time } t,\]
\[K = \text{intrinsic rates of population increase},\]
\[T = \text{rates of biomass transfer between the stocks},\]
\[P_{\infty} = \text{virgin population biomass or carrying capacity of the stocks},\]
\[F_t = \text{fishing mortality rates at time } t.\]

Equations (1a) and (1b) imply that biomass growth and biomass transfer are both logistic functions of population size.

In this paper we consider a single population (one stock) that is only partially exploited. The subscripts 1 and 2 from equations (1a) and (1b) will now denote the exploited and unexploited segments of the population, respectively (thus, \(F_2 = 0\)). We also assume that the rates of population growth are identical for the two segments of the stock \((K_1 = K_2 = K)\). Furthermore, we assume that biomass transfer takes place exclusively from the unexploited to the exploited segment \((T_{21} = 0, T_{12} = T)\). The basic set of equations now becomes:
\[
\frac{dP_1}{dt} = (KP_{1t} + TP_{2t})\left(\frac{rP_{\infty} - P_{1t}}{rP_{\infty}}\right) - F_{1t}P_{1t}, \tag{2a}
\]

and
\[
\frac{dP_2}{dt} = KP_{2t}\left(\frac{(1 - r)P_{\infty} - P_{2t}}{(1 - r)P_{\infty}}\right) \\
- TP_{2t}\left(\frac{rP_{\infty} - P_{1t}}{rP_{\infty}}\right); \tag{2b}
\]

\(r\), denotes the fraction of the virgin population biomass that is potentially affected by fishing at any given time. Note that when \(r = 1\) the entire virgin population biomass is affected by fishing, and equations (2a) and (2b) reduce to Schaefer's (1954) equilibrium stock production model.

In equilibrium \(\frac{dP_1}{dt} = \frac{dP_2}{dt} = 0\), the system of equations given by (2a) and (2b) results in the following relationships. From equation (2b),
\[
P_2 = \frac{(1 - r)\left[\frac{P_{\infty} - T}{K} - \frac{P_{1t}}{r}\right]}{P_{\infty}},
\]

and by substituting into equation (2a),
\[
AP_1^2 + BP_1 + C = 0, \tag{3}
\]

for which
\[
A = \frac{1}{rP_{\infty}}\left[\frac{rK}{T}\right],
\]

\[
B = \frac{2T(r - 1) + T(r - 1)}{rK} + K - F_1,
\]

and
\[
C = TP_{\infty}\left[\frac{1}{r} + \frac{T(r - 1)}{K}\right].
\]

In the most general sense, the use of equation (3) requires some knowledge of the transfer rate, \(T\). The model's behavior, as affected by \(T\) and \(r\), can be studied by plotting yield \((Y = F_{1t}P_{1t})\) against \(F_1\). To do so, we arbitrarily set \(K = 1.0\) and \(P_{\infty} = 100.0\). Then, given various sets of \(T\) and \(r\) values, we estimated \(P_{1t}\) and calculated equilibrium yield for \(F_1\) values ranging from 0 to 5.

Without biomass transfer \((T = 0)\), the fishing mortality that maximizes yield is independent of \(r\), as shown by the equilibrium yield–fishing mortality relationship in Figure 1a. In contrast, the maximum sustainable yield increases with increasing \(r\) (Figure 1b). This simple case \((T = 0)\) is henceforth referred to as the "no-mixing model" and is thoroughly developed in a subsequent section. When the transfer rate takes on intermediate values, the shape of the equilibrium yield–fishing mortality relationship is largely dependent on the value of \(r\) (Figure 1b; \(T = K/2)\). Thus, in this partial-mixing case, the values of maximum sustainable yield and of the fishing mortality that maximizes it \((F_{msy})\) vary with varying \(r\) (Figure 1b). In extreme contrast to the no-mixing model, very high values of \(T\) result in relationships in which \(F_{msy}\) varies with changing \(r\), but maximum sustainable yield does not (Figure 1c; \(T = K)\). This is another simple case \((T = K)\) that will be thoroughly developed in subsequent sections and is referred to as the "high-mixing model."

When \(T > K\), solutions of equation (3) are obtained only for a limited range of fishing mortality values (Figure 1d; \(T = 2K)\), implying that equilibrium is not possible at high levels of fishing mortality. This is a consequence of the assumption
that net biomass transfer takes place only from the unexploited to the exploited segments of the population.

Two Simple Models

Case I: No Mixing

In the absence of mixing between the exploited and unexploited segments of the population \( T = 0 \), equation (3) reduces to

\[
P_1 = rP_\infty - \frac{F_1 r P_\infty}{K}.
\]

This is equivalent to allowing the carrying capacity of the stock to increase linearly with increasing \( r \). The relationship between equilibrium yield and population size is

\[
Y = F_1 r P_\infty - \frac{F_1 r^2 P_\infty}{K};
\]

\[
F_{msy} = K \frac{r}{2},
\]

and

\[
MSY = \frac{KrP_\infty}{4}.
\]

Case II: High Mixing

In our model, \( T = K \) is the highest mixing rate that allows equilibrium to be achieved at any level of fishing mortality. Replacing \( T \) by \( K \) in equation (3) gives

\[
P_1 = rP_\infty - \frac{F_1 r^2 P_\infty}{K}.
\]

The relationship between equilibrium yield and population size is

\[
Y = F_1 r P_\infty - \frac{F_1 r^2 P_\infty}{K};
\]

\[
F_{msy} = K \frac{r}{2},
\]

and

\[
MSY = \frac{KP_\infty}{4}.
\]

Use of Fishing Area and Fishing Effort

Estimation of the parameter values in the two cases above requires information on the values of the (equilibrium) annual yield and the fishing mortality (or an index of it), as well as some
knowledge of \( r \). We now present simple ways in which \( F \) and \( r \) can be modeled.

We assume that the value of \( r \) can be modeled as a function of the area where fishing occurs. Let \( s \) be the surface area covered by the fishery and \( S \) be the surface area occupied by the whole population \( (s \leq S) \). Several possible scenarios can be contemplated by letting \( r \) be a simple power function of the ratio \( s/S \):

\[
 r = \left( \frac{s}{S} \right)^c; \quad c \geq 0. \quad (12)
\]

A value of \( c \) equal to 1.0 would encompass cases in which an increase in \( s \) would lead to a proportional increase in \( r \). Cases in which \( 0 < c < 1 \) would apply if the rate of change of the fraction of the stock potentially affected by fishing decreases as the fishery expands. The opposite would be true if \( c > 1 \) (Figure 2).

When nominal fishing effort is used as an index of fishing mortality, it is possible to allow for gradients of biomass concentration within the area inhabited by the stock. Thus, the same amount of fishing effort does not generate the same fishing mortality when effort is exerted in areas with different biomass densities. This concept is similar to that of "concentration profiles" discussed by Clark (1985). Consideration of such concentration gradients is possible only under the assumption that the areal distribution of relative biomass densities would remain unchanged for any population size.

If fishing is random within the area \( s \), annual average catch per unit of effort, \( U \), can be modeled as

\[
 U = \frac{Y}{f} = \rho ad; \quad (13)
\]

\( f \) is the nominal fishing effort, \( \rho \) is the probability of capturing fish that are in the path of the fishing gear (gear efficiency), \( a \) is the area swept by one unit of \( f \), and \( d \) is the average density of fish in the area swept. (For references on using catch per unit of effort as an index of abundance, see Gulland 1964). Furthermore, \( d \) can be expressed as

\[
 d = \frac{P_1}{s}, \quad (14)
\]

Equations (13) and (14) imply that fishing mortality is not a simple linear function of the nominal fishing effort; fishing mortality also depends on the exploited area. This is the underlying assumption in Munro's (1977) treatment of effort per unit area for sedentary (no-mixing) substocks. Thus,

\[
 F_1 = \frac{\beta f}{s}; \quad (15)
\]

\( \beta = \rho a \).

The relationship between equilibrium yield and the two explanatory variables \( (s \) and \( f \)) for the no-mixing case is obtained by incorporating equations (12) and (15) into equation (4):

\[
 Y = \frac{\beta P}{S} e^{-s'f} - \frac{\beta^2 P}{S' K} e^{-s'^2 f^2}. \quad (16)
\]

The linear parameters in the above equation can be combined for simplicity:

\[
 Y = a_s s'^{-1} f - b_s s'^{-2} f^2. \quad (17)
\]

Here the subscript I is used to indicate that the parameters correspond to the no-mixing case. From equation (17),

\[
 f_{msy} = \frac{sa_I}{2b_I}, \quad (18)
\]

and

\[
 MSY = \frac{s'^2 a_I^2}{4b_I}. \quad (19)
\]

The parameters of interest can be estimated in the traditional fashion (e.g., see Fox 1975) by treating \( U \) as the dependent variable and \( f \) and \( s \) as the independent variables. Such models containing two independent variables can be fitted with nonlinear regression.

For the high-mixing case, the relationship among yield, effort, and area is obtained in similar fash-
ion, by incorporating equations (12) and (15) into equation (9):

\[ Y = \frac{\beta P}{S} s^{n-1} f - \frac{\beta^2 P}{S} s^{2n-2} f^2. \]  

(20)

Combining the linear parameters in the above equation leads to

\[ Y = a_0 s^{n-1} f - b_0 s^{2n-2} f^2; \]  

(21)

\[ f_{mn} = \frac{s^{1-a}}{2b_n}, \]  

(22)

and

\[ MSY = \frac{a_n^2}{4b_n}. \]  

(23)

**Example**

We now illustrate the application of the model with data from the fishery for yellowfin tuna in the eastern Pacific. The data should be adequate for this purpose because the fishery has experienced large changes in effort and areal coverage over the past two decades (Figure 3).

The time-series data used (Table 1) were obtained from the Bulletin and Annual Reports of the Inter-American Tropical Tuna Commission (Alverson 1960, 1963; Calkins and Chatwin 1967, 1971; IATTC 1972–1986; Calkins 1975). Catch is in metric tons and effort is in number of fishing days of class 6 purse-seiners. The 1967–1984 efforts listed in the IATTC (1984) Annual Report were extended to cover the period 1961–1984. For this purpose, we regressed effort values in class 6 units against effort in class 3 units for the period 1967–1973 (from the 1973 Annual Report) and used this relationship to convert earlier data. The areas listed in Table 1 are the number of 1° squares that had catches in any given year, inside and outside the Commission’s yellowfin tuna regulatory area. Although better annual estimates for the area under exploitation could be obtained with a weighted average of quarterly data, we decided to use the values in Table 1 as a useful proxy for illustrative purposes only.

The following four models were fitted to the data.

\[ U = a_0 - b_0 f \]  

(Schaefer 1954);  

(24a)

\[ U = (a_0 + b_0 f)^{(1/(1+n-1))} \]  

(Pella and Tomlinson 1969).  

(24b)

\[ U = a_1 s^{n-1} - b_1 s^{2n-2} f \]  

(Case I: No mixing).  

(24c)

\[ U = a_1 s^{n-1} - b_1 s^{2n-2} f \]  

(Case II: High mixing).  

(24d)

The data were modified to approximate equilibrium according to the method described by Fox (1975). This method assumes that the catch per unit of effort in a year’s catches is related to the amount of effort in every year since the cohort entered the fishery, up to the present. The value of fishing effort for year \( i \) is computed as a weighted average over the number of years, \( k \), that a year-class contributes significantly to the catches:

\[ f_i = [k f_i + (k - 1) f_{i-1} + \ldots + f_{i-k+1}]/[k + (k - 1) + \ldots + 1]. \]  

(25)

Because catch per unit of effort in our model is also related to the area occupied by the fishery (equations 13 and 14), the same averaging technique was used to approximate equilibrium levels of \( s \):

\[ s_i = [k s_i + (k - 1) s_{i-1} + \ldots + s_{i-k+1}]/[k + (k - 1) + \ldots + 1]. \]  

(26)

For our example, the number of year-classes contributing to the yellowfin tuna fishery each year were estimated from the age structures of catches reported by Davidoff (1969) and IATTC (1986). These values represent a fishery that progressively caught older animals as it expanded offshore. Evidence for offshore–inshore stratification by size (age) of eastern Pacific yellowfin tuna was reported by Suzuki et al. (1978).

The four models in equations (24a)–(24d) were
fitted to the eastern Pacific yellowfin tuna data with the weighted nonlinear least-squares algorithm developed by Marquardt (1963). The weights used were:

\[ W_i = 1/(\bar{U}_i^2); \]

\( \bar{U}_i \) is the predicted catch per unit of effort for the \( i \)th data point. This procedure gives greater weights to the points with lowest \( U \), which are usually the most recent and the better estimated data points. Additional considerations for the use of this procedure were given by Fox (1971).

The standard errors of the parameter estimates thus obtained for the no-mixing model (discussed more extensively than the others in the following section) were approximated by the Monte Carlo bootstrap (Efron 1982; Diaconis and Efron 1983). This method assumes that the data provide an estimate of the cumulative density function of a parent distribution, without making any theoretical assumptions about its form. The application of the method proceeded by sampling the input data 1,000 times with replacement. Every sample consisted of 23 randomly selected triplets of \( U \), \( s \), and \( f \), which were then used to estimate the model’s parameters. The standard errors of \( \tilde{a}, \tilde{b}, \) and \( \tilde{c} \) were then approximated by the sample standard deviations of the corresponding 1,000 estimates from bootstrapping.

**Results**

The residual sums of squares were very similar for the Schaefer, generalized, and high-mixing models (Table 2). Calculated \( R^2 \) values, adjusted for the number of parameters \( (R^2_{adj} = 1 - (n - 1)(1 - R^2)/(n - p)) \), were similar for these three fits (0.52, 0.53, and 0.54, respectively). The values for maximum sustainable yield differed among the three models, being about 200,000 tonnes for the Schaefer fit, 280,000 tonnes for the generalized fit, and 230,000 tonnes for the high-mixing fit.

A significantly improved fit was obtained with the no-mixing model (Table 2). For this reason, the results from this model are emphasized in this section. The model was able to explain nearly 75% of the variability in the relationship between catch per unit of effort and the two explanatory variables, area and effort (Figure 4a).

The values for \( S_{msy} \) and MSY predicted with the no-mixing model depend on the surface area exploited by the fishery (equation 18 and 19; yield curve in Figure 4b). The MSY values increase as
TABLE 2.—Results obtained by fitting four production models to data on the eastern Pacific yellowfin tuna fishery. RSS = residual sum of squares; $R^2_{adj}$ = coefficient of determination adjusted for the number of parameters in the model; $f_{msy}$ = optimum fishing effort; MSY = maximum sustainable yield; $s$ = surface area covered by the fishery.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Schaefer (1954)</th>
<th>Generalized</th>
<th>No mixing</th>
<th>High mixing</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d_0$</td>
<td>0.044</td>
<td>0.044</td>
<td>0.044</td>
<td>0.044</td>
<td>0.044</td>
</tr>
<tr>
<td>$h_0$</td>
<td>2.11 x 10^-4</td>
<td>3.61 x 10^-4</td>
<td>3.61 x 10^-4</td>
<td>3.61 x 10^-4</td>
<td>3.61 x 10^-4</td>
</tr>
<tr>
<td>$m$</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>$d_1$</td>
<td>562.83</td>
<td>562.83</td>
<td>562.83</td>
<td>562.83</td>
<td>562.83</td>
</tr>
<tr>
<td>$b_1$</td>
<td>8.60</td>
<td>8.60</td>
<td>8.60</td>
<td>8.60</td>
<td>8.60</td>
</tr>
<tr>
<td>$d_{11}$</td>
<td>4.51</td>
<td>4.51</td>
<td>4.51</td>
<td>4.51</td>
<td>4.51</td>
</tr>
<tr>
<td>$b_{11}$</td>
<td>2.21 x 10^-5</td>
<td>2.21 x 10^-5</td>
<td>2.21 x 10^-5</td>
<td>2.21 x 10^-5</td>
<td>2.21 x 10^-5</td>
</tr>
<tr>
<td>$c$</td>
<td>0.458</td>
<td>0.458</td>
<td>0.458</td>
<td>0.458</td>
<td>0.458</td>
</tr>
<tr>
<td>RSS</td>
<td>172.98</td>
<td>167.87</td>
<td>94.67</td>
<td>163.56</td>
<td>163.56</td>
</tr>
<tr>
<td>$R^2_{adj}$</td>
<td>0.52</td>
<td>0.53</td>
<td>0.74</td>
<td>0.54</td>
<td>0.54</td>
</tr>
<tr>
<td>$f_{msy}$</td>
<td>(undefined)</td>
<td>32.71</td>
<td>102.139C</td>
<td>0.225</td>
<td>0.225</td>
</tr>
<tr>
<td>MSY</td>
<td>198,553</td>
<td>277,296</td>
<td>9,2036.458</td>
<td>230,323</td>
<td>230,323</td>
</tr>
</tbody>
</table>

a function of $s^{0.458}$ (i.e., approximately as the square root of the areal coverage of the fishery), whereas $f_{msy}$ increases with increasing $s$, giving a seemingly good explanation of how the equilibrium relationship has changed with the expansion of the fishery. Because $c = 0.458$ lies between 0 and 1, the analysis suggests that the fishery has expanded from more productive to less productive areas.

The variance-covariance matrix for the parameters in the no-mixing model, as estimated by the bootstrap with 1,000 samples from the data, was

<table>
<thead>
<tr>
<th></th>
<th>$c$</th>
<th>$a_1$</th>
<th>$b_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c$</td>
<td>$2.67 \times 10^{-3}$</td>
<td>$-13.149$</td>
<td>$-0.209$</td>
</tr>
<tr>
<td>$a_1$</td>
<td>$-13.149$</td>
<td>$72,546.73$</td>
<td>$1,182.98$</td>
</tr>
<tr>
<td>$b_1$</td>
<td>$-0.209$</td>
<td>$1,182.98$</td>
<td>$19.635$</td>
</tr>
</tbody>
</table>

The coefficients of variation (CV = 100 [SD/mean]) of the bootstrap estimates, useful as an indication of the precision in the parameter estimates, were 12.2, 35.4, and 37.2% for $c$, $a_1$, and $b_1$, respectively. The relatively high precision of these estimates is partly due to the large time series and to the fact that both independent variables, area and effort, have experienced great changes throughout the development of the yellowfin tuna fishery. Such contrast usually leads to more precise and robust parameter estimates in nonlinear models than when the independent variables remain relatively constant (Loehle 1988).

Uncertainty in the estimates of $f_{msy}$ and MSY was also studied by computing these values from the 1,000 bootstrap estimates of $c$, $a_1$, and $b_1$. For a surface area of 850 1° squares (around which the fishery fluctuated for the last 10 years of data), the mean values of $f_{msy}$ and MSY are 27,349.6 (SD, 1,364.16) and 198,965 (SD, 8,394.5), respectively. Thus, the estimates of $f_{msy}$ and MSY (CV of $f_{msy} = 5.0%$; CV of MSY = 4.2%) are more precise than are those of the individual parameters $c$, $a_1$, and $b_1$.

Figure 5 shows the equilibrium yield-effort relationship for the no-mixing model with $s = 850$ 1° squares. The solid line is the relationship obtained with the initial estimates of the no-mixing model (Table 2). The cloud of points constitutes the 1,000 MSY-$f_{msy}$ pairs that resulted from the bootstrap procedure. This cloud of points is shown.
instead of the more popular ellipsoid because it requires no assumptions about the parametric nature of the \( f_{\text{MSY}} \) and MSY estimates. The dashed lines in Figure 5 represent the 95% confidence limits for the yield–effort relationship calculated according to the percentile method. This method consists of calculating, for every value of effort, the 1,000 bootstrap values of yield (equation 15) and then obtaining the 0.025 and 0.975 percentiles of the resulting cumulative distribution of yield. Obviously, the uncertainty depicted by Figure 5 is conditional on the applicability of the model to the data. Nevertheless, the results indicate that the parameters of interest are estimated with a relatively high precision despite the variability of the data.

Discussion

The general assumption that production models deal with a single biological unit is often violated when the data are gathered from expanding or contracting fisheries. The two models that we have presented offer two simple alternatives to this assumption. In both models, the single biological unit is still referenced, but the fishery only affects a (changing) part of it. In addition, by utilizing some measure of the spatial extent of a fishery, the models inherently allow for a relationship between catch per unit of effort and the area occupied by the fishable stock. This relationship has long been recognized, but often ignored, and implies that the probability of capturing a fish with a unit of effort (catchability coefficient) is proportional to the density of the exploited stock (Pa-loheimo and Dickie 1964; Winters and Wheeler 1985).

The best fit to the yellowfin tuna data was obtained with the no-mixing model. Only a slight improvement over the Schaefer (1954) model was obtained with the generalized production model of Pella and Tomlinson (1969). Whereas the additional shape parameter used in the generalized model \( m \) in Pella and Tomlinson’s [1969] notation gives flexibility to the form of the function that describes population growth, the additional parameter in the no-mixing model is associated with a second explanatory variable (area). The use of independent variables other than fishing effort is not a new concept in production modeling. In general, other explanatory variables could be added to the simple stock production model. For example, Laloe (1988) incorporated an index of river runoff in a production model for Spanish sardine Sardinella aurita. Naturally, the fits of models such as those presented in this paper would improve with the use of an additional shape parameter like \( m \), but this would involve the estimation of yet another parameter.

A power curve (equation 12) was chosen to express the relationship between the fraction of the stock potentially available to fishing and the area covered by the fishery. This relationship can be much more complex because it is entirely dependent upon the historical development of the fishery. Clark (1985) offers detailed discussion of a concept similar to this stock fraction–area fraction relationship, which he termed “concentration profiles.” Because fish are not necessarily uniformly distributed throughout their geographical range, fisheries tend to develop by initially exploiting the areas with the highest concentrations. The development could also proceed from inshore to offshore areas, regardless of the distribution of fish densities. Functional relationships other than the power curve presented here could offer more flexibility (e.g., a cumulative beta function), but this would, in general, increase the number of parameters that need to be estimated.

The estimation of the \( f_{\text{MSY}} \) and MSY values for the whole stock requires knowledge of the total area occupied by the population, \( S \), but \( S' \) is estimated together with other parameters in the model and cannot be isolated with the present formulation. Knowledge of \( S \) must then come from
ancillary information such as resource mapping (Caddy and Garcia 1986). Otherwise it would only be prudent to use a value of \( s \) approximately equal to the largest observed \( s \) because the use of unreasonable values could lead to vastly misleading results.

We used yellowfin tuna data for convenience because the IATTC Annual Reports contain information on areal coverage. However, less-detailed historical information on the evolution of \( s \) should also explain a significant amount of variability. To demonstrate this with the yellowfin tuna example, we assumed that the available information on the fishery's areal development was limited to the following. (1) During the initial 10 years of the data series, the area remained constant at an arbitrary value of one unit (\( s = 1 \)). (2) During the next 4 years, the areal coverage was doubled (\( s = 2 \)). (3) In later years, the fishery exploited an area roughly three times as large as it did during the initial years (\( s = 3 \)). This constitutes a very rough approximation to the changes in \( s \) given in Table 1. However, the fit obtained with the no-mixing model was almost as good (\( R^2 = 0.71 \)) as the fit with the complete data set (\( R^2 = 0.74 \); Table 2). Estimates of MSY and \( f_{\text{msy}} \) for \( s = 3 \) were only 6% higher and 3% lower, respectively, than the corresponding values for the complete data set with \( s = 850 \). It is apparent, then, that very crude estimates of the areal coverage of the fishery may greatly improve the fit of a production model. This is a very encouraging result in light of the difficulties encountered in obtaining detailed information on the areal distribution of catch and effort for many fisheries.

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References


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