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AN OVERVIEW OF PRODUCTION MODELING[1/]

By

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1.0 INTRODUCTION

The production model approach to fish stock assessment is an application of the simple population equations of Lotka (1925) and Volterra (1926) to mathematically describe the response of fish populations to predation by man. The approach ignores, for the most part, the age structure of the population and the individual population dynamics components of growth in weight, natural mortality, and reproduction. The individual components are represented as a net resultant production of biomass (occasionally as numbers), hence, the term "production modeling." The benefit in treating the exploited population in this very simplistic manner is largely the drastic reduction in data requirements for assessing the effects of exploitation on a fish population. The costs accrued in obtaining this benefit are the creation of numerous assumptions, many of which are known *a priori* to not be fully satisfied, and the lack of being able to analyze the effects of altering certain driving variables available for control by fisheries management (e.g., fishing season, size at first capture, relative rates of fishing mortality among age groups, etc.).

1.1 Data Requirements

The basic data requirements for implementing a production model analysis of a particular fish population are:

- Total catch in weight (perhaps numbers) by year.
- Total fishing effort in standardized units by year.

While these basic data requirements appear to be rather simple, this appearance is only superficial, especially for fishing effort. Effort must be adequately separated when more than one species is being sought and must be standardized to some common units when different gear types (and characteristics) are utilized--this is especially difficult when there are different gear types exploiting relatively different age groups and/or strong efficiency interactions among population densities, time-area strata, gear types (and characteristics), and the amount of effort employed. Detailed examinations of these problems will appear in other Workshop documents; however, the population density question is addressed in this document.

As a rule of thumb, my experience indicates that in order to obtain reliable parameter estimates, a minimum of 10 years of complete data is required for a fish population and fishery with the characteristics as follows: (1) life-span of 4-8 years, (2) the number of year classes contributing significantly to the catch about 2-4, (3) the age at first capture about 1-3 years, (4) a fishing effort development rate, such that the average change in catch per unit effort is about 3-4% per year over the 10 years of data; and (5) a fairly stable environment. Exceeding any or all of these characteristics will require a longer data series, as will a slower effort development rate. Other considerations more difficult to assess are relative rates of fishing effort development by different gear types and peculiar life history strategies. The amount of required data is highly subjective; however, further guidance can be obtained from Pella and Tomlinson (1969).

1.2 Model Formulation

The general production model for a single species system is given by:

$$dP/dt = g(P)-h(P) \qquad (1)$$

where P is population size, $g(P)$ is the net resultant natural production rate and $h(P)$ is the rate of catch. Pella and Tomlinson (1969) have proposed the most flexible simple function for $g(P)$ as:

$$g(P) = HP^m-KP \qquad (2)$$

where H, K, and m are constant parameters. The usual assumption about the rate of catch is:

$$h(P) = FP \qquad (3)$$

where F is the instantaneous fishing mortality coefficient. Substituting (2) and (3) into (1) the equilibrium ($dP/dt = 0$) relationships of Figure 1 are obtained--interpretive parameters derived from the equilibrium relationships are given in Table 1.

1.3 Assumptions

The assumptions required in production model analysis may be partitioned into two categories: (1) those required for employing the approach and (2) those required because of the nature of the data available for fitting the model.

1.3.1 Approach Assumptions

1.3.1.1 Equilibrium conditions. It is assumed that given a constant rate of fishing (including zero), a population will achieve a state where, on the average, it will not change in size or characteristics. This presumes that the main controlling factor of population size is the amount of fishing mortality applied to the population.

1.3.1.2 Single population. It is assumed that the model is applied to a single population in the genetic sense or to single stock in the sense that the biological unit responds as if it were a single population. The approach to date, therefore, has ignored multiple stock and species interactions, although initial applications of the approach were to aggregate species and stocks (Graham, (1935).

1.3.1.3 Fishable population constant. It is assumed either that the age-specific fishing mortalities have been and will remain constant relative to one another, or more strongly, that the total catch and stock production in weight are independent of age.

1.3.2 Data Assumptions

1.3.2.1 Constant catchability. It is assumed (1) that fishing effort has been standardized to adjust for differences in efficiency of different gear types and classes and (2) that it has been adjusted for temporal changes in efficiency due to technological or population-dependent causes; such that fishing effort is proportional to the instantaneous fishing mortality coefficient

$$F_i = qf_i \qquad (4)$$

where f_i is the fishing effort in year i.

1.3.2.2 No lags. It is assumed (1) that the age structure shifts to its stable age distribution simultaneously and instantaneously with changes in population size or, more strongly, that the total catch and stock production in weight are independent of age, and (2) that time lags in recruitment or in density-dependent growth, natural mortality and reproduction do not occur--alternatively it can be assumed that the effects cancel out in terms of net population production. This assumption is required in the use of transitional state data for fitting the model.

Additional discussion of the assumptions can be found in Schaefer and Beverton (1963) and Pella and Tomlinson (1969).

1.4 Fitting Methods

There are three basic approaches to fitting the production model to fishery data. The first method involves fitting the derived equilibrium relationships

$$U = (a + bf)^{\frac{1}{m-1}} \qquad (5)$$

or

$$Y = f(a + bf)^{\frac{1}{m-1}} \qquad (6)$$

directly to observed equilibrium data points, where U is the catch per unit effort, f is fishing effort, and Y is equilibrium yield (see Table 1 for parameter conversions). Rarely, if ever, are there three or more periods of stable effort, however, making necessary the use of transitional state data. The second method, due to Schaefer (1954, 1957) but culminating in Pella and Tomlinson (1969), involves the integral of equation (1) to predict the population changes and yield--the transition prediction approach. The third method, developed by Gulland (1961, 1969), involves adjusting the fishing effort so as to estimate equilibrium data and then fitting equation (5) or (6)--the equilibrium approximation approach (Fox, In Press).

It is impossible *a priori* to select the transition prediction or equilibrium approximation approach as being better in general. It depends upon the characteristics of the population, fishery, and available data, upon the complexion of the fishery management situation, and upon the statistical philosophy of the individual. Fox (In Press) has compared the two approaches (computer programs PRODFIT and GENPROD) under very limited conditions (Table 2). Additional work is required before any significant specific guidance can be offered.

1.5 Perspective of Approach and Scope

As can be easily observed from the model formulation, the assumptions made, and the fitting methods used, that the production model is a crude representation of the dynamics of an exploited population. At best the approach provides only a rough approximation of the response to exploitation that might be expected from a population. Therefore, the proper perspective of production model analysis is that it is little more than a simple regression model and, while useful for deriving preliminary estimates, it should not be continued as the sole means for monitoring of the status of the stock and for making management decisions.

Table 1. Parameter conversions

Interpretive parameters	Pella and Tomlinson (1969) formulation	Fox (*In Press*) formulation	Density-dependent q formulation
1. Catchability coefficient	q	q	αP^{β}
2. Maximum population size (P_{max})	$\left(\frac{K}{H}\right)^{\frac{1}{m-1}}$	$\frac{1}{q}(a)^{\frac{1}{m-1}}$	$\left(\frac{1}{\alpha}\right)^{\frac{1}{\beta+1}} \times \left(\frac{c'}{a'}\right)^{\frac{1}{m-1}}$
3. Optimum population size (P_{opt})	$\left(\frac{K}{mH}\right)^{\frac{1}{m-1}}$	$\frac{1}{q}\left(\frac{a}{m}\right)^{\frac{1}{m-1}}$	$\left(\frac{1}{\alpha}\right)^{\frac{1}{\beta+1}} \left(\frac{c'}{a'm}\right)^{\frac{1}{m-1}}$
4. Optimum fishing effort (f_{opt})	$\frac{K(1-m)}{mq}$	$\frac{a(1-m)}{mb}$	$\frac{c'(1-m)}{m}\left(\frac{c'}{a'm}\right)^{\frac{\beta}{1-m}}$
5. Maximum equilibrium yield (Y_{max})	$H\left(\frac{K}{mH}\right)^{\frac{m}{m-1}} - K\left(\frac{K}{mH}\right)^{\frac{1}{m-1}}$	$\frac{a(1-m)\ (a/m)^{\frac{1}{m-1}}}{mb}$	$\frac{c'(1-m)\left(\frac{c'}{a'm}\right)^{\frac{1}{m-1}}}{m}$

Table 2. Summary of Y_{max} estimates by alternative strategies with the equilibrium approximation and transition prediction approaches for five replicated stochastic catch histories. Empirical value of Y_{max} is 5.60. (Fox, *In Press*, Table 10)

Method/strategy	$\hat{Y}_{max}$ Mean	Standard error of mean	Average percentage error	Range
Equilibrium approximation approach[1]				
1. Estimate m	6.39	0.62	17.8	5.07-8.65
2. Assume m ⟶ 1	5.57	0.14	3.6	5.05-5.80
3. Assume m = 2	6.16	0.09	10.0	5.86-6.35
4. Least-squares, m = 1 or 2	5.57	0.14	3.6	5.05-5.80
Transition prediction approach[2]				
1. Estimate m	7.24	0.84	31.7	5.26-9.34
2. Assume m ⟶ 1	5.72	0.31	10.0	4.66-6.39
3. Assume m = 2	6.17	0.25	12.4	5.30-6.63
4. Least-squares, m = 1 or 2	5.89	0.24	8.5	5.30-6.63

[1] Program PRODFIT.

[2] Program GENPROD.

Traditionally, tropical tunas have been very difficult to age and production models have been applied continually due to the paucity of reliable additional detailed information. This reliance has led to interpretive problems in the eastern Atlantic and Pacific yellowfin fisheries as the complexions of the fisheries have changed (Joseph, 1970; IATTC, 1972; Fox and Lenarz, 1972, 1973). Therefore, this document provides several simple expansions of the production model for examining, with catch and fishing effort data, deviations from the basic assumptions.

2.0 ASSUMPTION FAILURES

Each of the five assumptions has been the object of some research, which will be briefly summarized. Two of the assumptions, single population and constant catchability, will receive additional work in this document.

2.1 Equilibrium Conditions

Most tuna stocks appear to respond to exploitation with a reasonably regular relationship between their indices of stock size and the amount of fishing effort. At least two notable exceptions appear to be eastern Pacific skipjack tuna (Joseph, 1970) and, perhaps, North Atlantic bluefin tuna (Sakagawa and Coan, 1973). Year class fluctuations are moderate in size for yellowfin tuna (Davidoff, 1969; Fonteneau and Lenarz, 1973) and residuals analysis of the eastern Pacific yellowfin fishery showed moderate, periodic, auto-correlated deviations from the predictions of the production model (Fox, 1971).

Particular care must be taken when applying the production model approach to populations with peculiar life histories. For example, Fox (1973, and In Press) has shown that a pandalid shrimp population (protandric hermaphrodites) with random mating collapses at a particular level of fishing mortality (Figure 2).

2.2 Single Population

Lord (1971) formulated a general multiple species production model with inter-specific interaction terms and performed some mathematical analysis of the logistic form (m = 2). However, there has been no attempt to apply the model to an actual fishery. Similarly, Larkin (1963) mathematically examined the competition equations of Lotka and Volterra, the logistic form, for two species in detail.

The mixing of multiple stocks is of specific interest to tuna stock assessment in applying production model analysis. If the "stocks" in question are actually genetically distinct and occupy a space sympatrically, then the competition equation analysis of Larkin (1963) is analogous. However, if this were the case, then the "stocks" would be separate species by definition. The problem in tuna stock assessment is one of stocks of the same species occupying different, though not necessarily distinct, spaces with some degree of mixing among them (IATTC, 1972). For simplicity, I will consider only two stocks and the logistic form of population production (m = 2).

2.2.1 The Mixing Model Formulation

Consider two logistic stocks of the same species which occupy distinct spaces, such that fishing mortality (or fishing effort) can be applied to each stock separately (F_1 and F_2), but between which there is some mixing at intrinsic rates T_1 and T_2. Consider also that these stocks are not different, other than in their origin, such that once a part of stock 1 transfers to the area of stock 2 it is indistinguishable in all aspects from stock 2 (and vice versa). The mixing model is, therefore, the set of equations:

$$\frac{dP_1}{dt} = (K_1P_1 + T_2P_2)\left(\frac{P_{max(1)} - P_1}{P_{max(1)}}\right) - T_1P_1\left(\frac{P_{max(2)} - P_2}{P_{max(2)}}\right) - F_1P_1 \qquad 7(a)$$

$$\frac{dP_2}{dt} = (K_2P_2 + T_1P_1)\left(\frac{P_{max(2)} - P_2}{P_{max(2)}}\right) - T_2P_2\left(\frac{P_{max(1)} - P_1}{P_{max(1)}}\right) - F_2P_2 \qquad 7(b)$$

where 1 and 2 are the designations for stocks 1 and 1 (for parameter conversions see Table 1).

It can be seen that the model assumes that the rates of mixing are determined by the population size in the area of origin and the amount of space available in the area of transfer--when both populations are at their carrying capacities, P_{max}, (with $F_1 = F_2 = 0$) there is no mixing. Many additional mixing models could be formulated under alternate hypotheses, but I will restrict my analysis in this document to equation set (7).

2.2.2 Mixing Model Analysis

Rigorous mathematical analysis of the mixing equations (7) could be presented (c.f. Larkin, 1963; Pielou, 1969); however, such will be presented in a future paper and it will suffice to illustrate simply a few of the implications of the model.

Figure 3 provides the locus of equilibrium points ($dP_1/dt = 0$, $dP_2/dt = 0$) for equation set (7)--the concave upward curves for equation (7a) and concave downward curves for equation (7b)--with an arbitrary set of parameters which approximate those obtained by Fox (1971) for the early eastern Pacific yellowfin tuna fishery. Additionally,

$$P_{max(1)} = 0.5 \, P_{max(2)},$$

$$K_1 = K_2 = K = 5.6$$

and

$$T_1 = T_2 = T.$$

Four combinations of fishing mortality at 0 and 1 are plotted for two cases of the mixing coefficient relative to the intrinsic rate of increase coefficient (T/K). Points of stability occur at the intersections of the concave upward and concave downward curves (heavy dots).

Figure 3A illustrates the relationships when mixing is slow relative to population productivity, $T/K = 0.1$. At $F_1 = F_2 = 0$ both populations achieve their respective P_{max} (point labelled A). Applying fishing mortality to either stock has little affect on the stock not being exploited (point B or C). However, applying fishing mortality simultaneously to both stocks results in slightly lower stock sizes (point D) than exploiting just one or the other (points B and C) due to an increase in export and a loss of supporting import.

Figure 3B illustrates the relationships when mixing is relatively high. With no fishing mortality, point L is the same as point A (Figure 3A). An obvious difference between the low and high relative mixing rates is that the curves become more coincident as the relative rate of mixing increases, approaching a common curve as the mixing rate becomes infinite. Furthermore, the degree of synergistic lowering of both stock sizes when both are exploited (point O), as opposed to each being exploited alone (points M and N), is much greater than when the mixing rate is low (Figure 3A).

2.2.3 Mixing and the Yield-Effort Relationship

The major question is: what impact does the mixing of stocks have on the shape of the yield-effort curve? Figure 4 illustrates the combined equilibrium yield and combined fishing effort curves (assuming catchability = 1) for four rates of mixing and three ratios of effort applications to the two stocks. All parameters are the same as in the previous section. On the vertical axes is the combined equilibrium yield from the two stocks ($Y_1 + Y_2$) and the combined fishing effort ($F_1 + F_2$) is on the horizontal axes. The dash-dot lines represent all the effort being exerted on P_1 alone, the dashed lines represent 75% of the total effort being distributed on P_1 and 25% being distributed on P_2, and the heavy lines represent an equal amount of effort being distributed on both P_1 and P_2.

When there is no mixing between the stocks, $T_1 = T_2 = 0$ (Figure 4, upper left panel), obviously the total maximum sustainable yield (TMSY) increases to the sum of the MSY's of the two stocks when fished separately. Because of the nature of the parameters selected, the MSY of each stock occurs at the same F, but the MSY of P_2 is twice as large as that of P_1. Any other effort ratio produces a lower TMSY.

When the mixing rate is very large, $T_1 = T_2 = 56$ (Figure 4, lower right panel), the model behaves as if it were one large stock, $P_1 + P_2$, as expected. The total sustainable yield is nearly the same regardless of the effort ratio.

In the case where mixing is intermediate between the two extremes, $T_1 = T_2 = 0.56$ (Figure 4, upper right panel) and $T_1 = T_2 = 5.6$ (Figure 4, lower left panel) some very interesting relationships are implied from which several important scenarios can be derived. Depending on the effort ratio: (1) curves resembling m = 0 to m = 2 can be derived, (2) TMSY can vary widely at about the same level of total effort, and (3) the TMSY can be the same but at widely varying values of total effort.

Let us consider two scenarios where effort develops first on P_1 and then transfers in part to P_2.

2.2.3.1. Scenario 1. When the mixing rate is relatively low (Figure 4, upper right panel) a fishery developing on P_1 would follow the dash-dot curve out to a maximum of 1.5 units of yield at 4-5 units of fishing effort. If 1 to 1.25 units of the 4-5 effort units were shifted to P_2, the equilibrium yield would increase markedly, and if an additional 1 to 1.25 units were transferred to P_2 the TMSY would be double that originally observed and for exactly the same amount of total effort. However, since the equilibrium catch rates differ between P_1 and P_2 at the same fishing effort (that of P_1 is one-half that of P_2) an unequal effort ratio would be trended towards.

When the mixing rate is moderately high (Figure 4, lower left panel), the same manner of fishery development would have the opposite consequences. A fishery developing on P_1 would follow the dash-dot curve out to an TMSY of 3 units at 10 units of fishing effort. Any redistribution of fishing effort to P_2 would cause the total equilibrium yield to plummet.

2.2.3.2 Scenario 2. Development of a fishery on P_2 may occur through the addition of effort rather than through its re-distribution. When the mixing rate is relatively low (Figure 4, upper right panel) development of a fishery on P_1 would follow the dash-dot curve. Additional effort being placed on P_2 could initially cause the overall fishery to begin following the dashed curve with increased equilibrium yield. Trouble would arise if total effort exceeds 8 units and greater effort were added to P_2 such that the effort ratio were even--total equilibrium yield would decrease. With a higher mixing rate (Figure , lower left panel) the same trouble could occur, but it would occur at lesser effort being placed on P_2 than for the lower mixing rate situation.

2.2.4 Summary

The formulation of the mixing model has considerable impact on the yield-effort relationship. The model formulation presented here, along with the assumed parameter values, indicates that knowledge of the mixing relationship can be critical to good management and is highly dependent upon how fishing effort is distributed. It remains to be seen how well such a model can describe an actual fishery situation. To this end, work is underway to investigate other model formulations and to develop methods for fitting the models to actual fishery data.

2.3 Fishable Population Constant

One of the major shortcomings of the production model approach is that the impact on the shape of the yield curve, by altering (1) the size selectivity of a particular type of fishing gear or (2) the relative rates of fishing of gear exploiting different size groups, cannot be assessed *a priori* from the basic production model or basic total catch and effort data. Lenarz, et al. (1974) discussed this in relation to the minimum size regulation for Atlantic yellowfin tuna and showed how the shape of the curve is dependent upon the size regulation.

A major problem can occur when the fishable population has changed substantially within the data that one is attempting to fit to a production model. The result could be a composite of two or more production models, which describes neither the former nor the recent realtionship (Figure 5). When the underlying models are dome-shaped and the more recent situation (curve 2) is more productive than the former (curve 1), the resulting composite (curve 1 & 2) could easily lead to overfishing.

Further work is required to forecast alterations in the shape of the production model due to changes in the fishable population. However, some work to relate the parameters H, K, and m (equation 2) to age distribution matrix model characteristics has been initiated (Smith, 1973).

2.4 Constant Catchability

The usual assumption is that fishing effort is proportional to the instantaneous fishing mortality coefficient (equation 4) such that catch per unit effort, U, is proportional to population size. This may not be true for a variety of reasons, some of the major ones are:

1) Since U is really a measure of population density rather than population size, the deployment of effort relative to gradients in population density will cause changes in the effective q.

2) The catchability of fish may change with age such that the effective overall catchability can increase or decrease with changes in fishing mortality.

3) The behavior of fish may be such that they are more or less catchable at a lower population size than at a higher population size.

These problems have been previously addressed (e.g., Rothschild, 1971 and Radovich, 1973). Also, these and other problems are certain to be discussed in other Workshop documents. However, a simple extension of the production model to include changes in catchability due to density-dependence in q will be examined.

2.4.1 Density-Dependent Catchability Model

A simple general model for catchability is the power function:

$$q = \alpha P^{\beta} \qquad (8)$$

When $\beta = 0$, q is constant (the usual assumption), q increases with decreasing population size when $\beta<0$, and q decreases with decreasing population when $\beta>0$ (Figure 6). The power function has been shown to fit the relationship between catchability and population size as determined by cohort analyses for the California sardine (MacCall, personal communication).[1] The density-dependent catchability (DDC) production model therefore, is

$$\frac{dP}{dt} = HP^{m} - KP - \alpha P^{\beta} fP \qquad (9)$$

At equilibrium and in terms of catch per unit effort, U, equation (9) may be manipulated to:

$$f = a'U^{b'} + c'U^{d'}$$

where

$$a' = H/(\alpha)^{\left(\frac{\beta+2}{\beta+1}\right)}$$

$$b' = (m-1-\beta)/(\beta+1)$$

$$c' = -K/(\alpha)^{\left(\frac{\beta+2}{\beta+1}\right)}$$

and

$$d' = -\beta/(\beta+1)$$

2.4.2 DDC and the Yield-Effort Relationship

The equilibrium relationships for catch per unit effort vs fishing effort and for yield vs fishing effort are shown in Figure 7 with different values of β for an underlying logistic model (m=2). Several things are readily apparent.

1) The maximum equilibrium yield, Y_{max}, is independent of β, but the optimum fishing effort, f_{opt}, is not.

2) The apparent yield curve can resemble the non-density-dependent generalized stock production model for $m > 2$ when $\beta < 0$ and for $0<m<2$ when $\beta > 0$, even though the real population model is $m = 2$, the logistic model. This is also true for any value of $m > 1$ but for different ranges in β.

3) The yield curve bends back towards the origin at some $\beta<0$ such that there are critical values for equilibrium yield, Y*, catch per unit effort, U*, and fishing effort, f.*

The implications of the first two points are obvious and parallel a discussion of the implications for models with different values for m. The third point, however, is somewhat more interesting. The critical catch per unit effort, fishing effort, and yield values at equilibrium are:

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[1]Alec MacCall, California Department of Fish and Game, Long Beach, California

$$U^* = \left(- \frac{c'd'}{a'b'}\right)^{\frac{1}{b'-d'}}$$

$$f^* = a' \left(- \frac{c'd'}{a'b'}\right)^{\frac{b'}{b'-d'}} + c' \left(\frac{c'd'}{a'b'}\right)^{\frac{d'}{b'-d'}}$$

and $$Y^* = a' \left(-\frac{c'd}{a'b'}\right)^{\frac{b'+1}{b'-d'}} + c' \left(-\frac{c'd'}{a'b'}\right)^{\frac{d'+1}{b'-d'}}$$

Therefore, there is a critical point for all $\beta < 0$ (i.e., the catchability increases with decreasing population size) if the underlying population production model is $m \geq 2$. A critical point also occurs for $1 < m < 2$ at certain values of $\beta < 0$. Should a fishery exceed f* for a period of time such that the catch per unit effort falls below U*, the fishery will begin responding apparently in an illogical fashion and attempts at management, based on the assumption that the fishery responds as a simple Schaefer model (or generalized stock production model), will appear to be fruitless--hence, management without understanding the density-dependence in catchability would be futile. If such a fishery becomes overfished (i.e., equilibrium yield begins to decrease), it will require a much greater fishing effort reduction to restore the productivity of the fishery than a fishery without density-dependent catchability.

Several economists have published steady-state yield models which bend back toward the origin as in Figure 7 and have analyzed the steady-state economic implications--Southey (1972) by simple graphical analysis and Hannesson by somewhat more rigorous mathematical analysis. Hannesson (1974) argues that the bending back of the yield curve would most likely be due to the production function, g(P),--equation (2)--as in the pandalid shrimp example (Figure 2). While Hannesson (1974) notes the possibility of obtaining a bent-back yield curve through coalescence of the population as it decreases (the DDC production model with $\beta<0$), he states that it does not seem likely. I disagree with his opinion.

2.4.3 Some Examples

A computer program, PRODQ, was written to fit equation (10) for any selected values of m and β to fishery catch and effort data with the equilibrium approximation approach (Fox, In Press). Two contrasting examples were chosen--the California sardine fishery and the eastern Pacific yellowfin tuna fishery.

2.4.3.1 California sardine. Catch and fishing effort data for the 1932-33 through 1954-55 fishing seasons were obtained from Marr (1960) and the corresponding numbers of significant year classes in the catch were obtained from Wolf (1961). Two values for m were selected (1 and 2). Table 3 provides the least-squares estimates of β to the nearest 0.1 for each of the two values for m. No estimates could be made for the entire data series for $\beta = 0$; as is obvious in Figure 8. The marginal best fit is obtained with the logistic model (m = 2) for $\beta = -0.3$, indicating a strongly density-dependent catchability. The critical fishing effort, f*, is 22% greater than the optimum fishing effort (Table 3) and it was exceeded consistently for the 1943-44 through 1947-48 fishing seasons as the fishery collapsed (Figure 8).

While the DDC production model fits the California sardine data reasonably well and the collapse of the fishery can be described in terms of it, one is still uncertain as to the true causes. These are still the confounded effects of multiple stocks (or populations), competing species, and physical environment alterations. On the other hand, MacCall (personal communication)[1] has shown that the relationship between population size and catchability estimated from simple total catch and effort data (Figure 8, Table 3) can also be deduced from a more rigorous analysis of the age composition data.

2.4.3.2 Eastern Pacific Yellowfin tuna fishery. Catch and fishing effort data for the 1934 through 1967 fishing seasons were obtained from Pella and Tomlinson (1969). The parameter β was estimated to the nearest 0.1 for the logistic (m = 2) and exponential ($m \to 1$) production models (Table 4). The marginal best fit was obtained for the logistic model (m = 2) with a β of 0.4, indicating an inverse density-dependent catchability, i.e., catchability decreases as population size decreases. Also, it may be noted that the fits of the exponential production model ($m \to 1$) with no density-dependence ($\beta=0$) and the best fit are nearly identical (Table 4). Figure 9 shows the best fit relationship.

For the eastern Pacific yellowfin tuna fishery, an apparently decreasing catchability with decreasing population size could be due to a variety of reasons, among them being: 1) a change in the average age through increased exploitation causing a reduction in the average effective catchability (Davidoff, 1969); 2) an expansion of fishing onto additional stocks thereby increasing the fishable population size (IATTC, 1972); 3) gear interference as fishing effort has increased; etc.

Table 3.--Estimated parameters of the DDC production model for the California sardine fishery 1932-55[1]

m	β	Y_{max} (10^3 short tons)	U_{max} (10^3 tons per month)	f_{opt} (months fishing)	f* (months fishing)	Residual sum of squares (x10^6)
1.0001	-0.4	692	1.306	966	1349	1.523
2.0[2]	-0.3	623	0.901	1123	1370	1.468

[1]Data from Marr (1960, Tables I and II) and Wolf (1961, Table 22).

[2]Least-squares best fit.

Table 4.--Estimated parameters of the DDC production model for the eastern Pacific yellowfin tuna fishery, 1934-67[1]

m	β	Y_{max} (10^6 lbs)	U_{max} (10^3 lbs per day)	f_{opt} (10^3 days fishing)	Residual sum of squares (x10^9)
1.0001	0.0	169	14.4	31.9	1.1123
2.0	0.0	176	12.5	28.0	1.1862
	0.4[2]	169	14.0	31.9	1.1120

[1]Data from Pella and Tomlinson (1969, Table 6).

[2]Least-squares best fit.

2.5 No Lags

There are two major sources of error in the production model approach due to time lags--(1) differences between the stable age structure and transitional state age structure and (2) density-dependent adjustments in the dynamic components--growth, natural mortality, and reproduction rates. For the most part these problems arise out of the necessity for using transitional state catch and effort data to estimate the production model parameters.

2.5.1 Age Structure Lags

Pella and Tomlinson (1969) present a good discussion of the effects of lags in shifting the age structure to the stable age structure as fishing mortality changes from year to year. In short, the greater the change in fishing mortality from year to year and the more age groups in the fishable population, the greater the difference will be between the observed transitional age structure and the stable age structure at any particular population size; hence, the representation of the equilibrium yield-effort relationship by the fitted production model will likely be poorer.

2.5.2 Lags in the Dynamic Components

The major source of concern here is that reproduction is necessarily lagged, the higher the age at first capture the greater the apparent lag in reproduction. If recruitment to the fishable population depends, for the most part, on the size of the parent stock, then the effects of reproduction lag can become very pronounced as the age at first capture increases. Ricker (1958, p. 260) provides Pacific halibut as an example where a year class makes its greatest contribution to the catch at an age of about 9 years--plotting surplus production on population size in the same year indicates overfishing occurred, while plotting surplus production on the population size 9 years previous does not indicate overfishing. If, on the other hand, there is strong density-dependence (competition, cannibalism, etc.), then production through recruitment would involve much less of a lag, or no lag in the extreme case.

2.5.3 Time-Lag Production Model

The logistic (m = 2) and exponential (m→1) production models with time lagged terms have been mathematically analyzed by Wangersky and Cunningham (1957) and Walter (1973). They show that, depending upon the lag time, a population may cycle with constant, decreasing, or increasing amplitude even under a constant fishing mortality rate. Walter (1973) demonstrates further, that if the population does cycle, then the maximum long-term yield is achieved with a population size-dependent fishing effort.

3.0 RESEARCH REQUIREMENTS

From the preceding section it can be seen that there are three critical areas which require the utmost attention when employing the production model approach to fish stock assessment:

- Definition of fishing effort
- Definition of stock
- Definition of fishable population

Obviously, these are critical areas for fish stock assessment period. Frequently, however, they are ignored in production model analysis, particularly in interpreting the analysis for management advice.

3.1 Definition of Fishing Effort

The interpretation of production model analysis depends heavily on the relationship between fishing effort and fishing mortality. The catchability coefficient in the production model can be replaced by a simple function as in Section 2.4.1 and the parameters estimated as in Section 2.4.3. However, there is no sufficient way to statistically test the hypothesis $\beta \neq 0$ without considerable ancillary information on the age composition of the catch.

For any fishery in question, theoretical models of the fishing process and schooling and distributional behavior of the fish could be utilized to determine an array of expected relationships between overall effective fishing mortality (in biomass) and the fishing effort variables which can be recorded in logbooks. This is particularly relevant in the case of tuna purse seining operations which fish schools of yellowfin and skipjack tunas opportunistically, and take varying fractions of the schools encountered. The situation is even more complex in the eastern Pacific where fishing occurs for yellowfin tuna in association with porpoise schools as well as yellowfin not associated with porpoise schools.

3.2 Definition of Stock

Further work is needed on the definition of tuna stocks. A primary candidate for the failure of the original production model in the eastern Pacific yellowfin fishery to describe the catch and effort relationship is an expansion of fishing onto additional stocks which mix to some unknown degree. It is usually assumed that if effort is relatively uniform over the stocks then stock definition is not a critical problem. This is true for the mixing model in Section 2.2 if the growth coefficients, K, and mixing coefficients, T, are the same for each stock. However, this is not true if the coefficients are very different.

3.3 Definition of Fishable Population

Production model analysis of the Atlantic longline fishery through the early 1960's when it was primarily a longline fishery led to the conclusion that the fishery was nearly fully exploited with a maximum sustainable yield in the neighborhood of 50 thousand metric tons (FAO, 1968). It was noted in the FAO (1968) report that the presence of a surface fishery would likely increase the total catch, somewhat. Subsequent further development of the surface fishery has resulted in catches of 50-70 thousand tons for the eastern Atlantic surface fishery alone, 1968-73, and to catches of 90-100 thousand tons for the total Atlantic longline and surface combined. While these catches may not be sustainable, recent production model analysis (Fox and Lenarz, 1973) indicates a total Atlantic MSY of 80-90 thousand tons under the present constitution of the fishery. This development underlines the necessity for further work to elicit some greater understanding of the relation between altering the age composition of the catch and the parameters of the production model.

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FIGURES

Figure 1. Equilibrium relationships of the generalized stock production model for three values of m. (A) Equilibrium yield and population size; (B) Population size and fishing effort; (C) Equilibrium yield and fishing effort.

Figure 2. Fit of the generalized stock production model (solid line) to simulated equilibrium values (open circles) of (A) Catch per unit effort and (B) Yield by computer program PRODFIT. Shaded areas represent non-equilibrium.

Figure 3. Locus of equilibrium points for the production model with mixing of two species (equations 7a and 7b). (A) Low relative mixing rate; (B) High relative mixing rate.

Figure 4. Total equilibrium yield-total fishing effort curves for the production model with mixing of two species (equations 7a and 7b) at four rates of mixing.

Figure 5. Hypothetical results of changing the fishable population from curve (1) to curve (2) and the resultant relationship, curve (1 & 2).

Figure 6. Density-dependent catchability model (equation 8).

Figure 7. Equilibrium relationships for the density-dependent catchability production model (equation 10) with m = 2 for differenct values of β. (A) Catch per unit effort on fishing effort; (B) Yield on fishing effort.

Figure 8. Density-dependent catchability production model fit to the California sardine fishery for the 1932-33 through 1954-55 fishing seasons.

Figure 9. Density-dependent catchability production model fit to the eastern Pacific yellowfin tuna fishery for the years 1934-67.

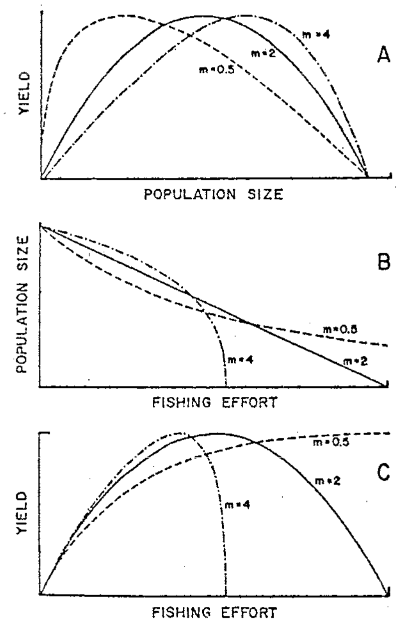


FIGURE 1

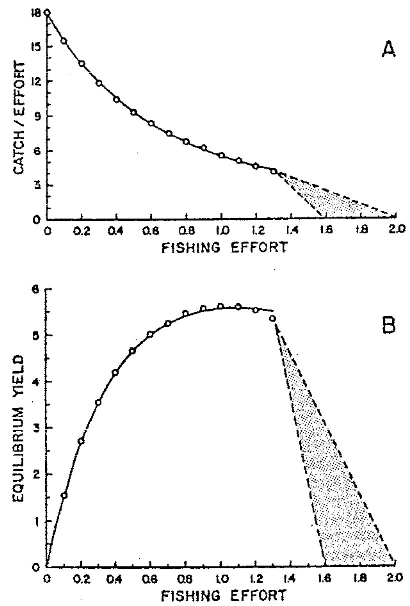


FIGURE 2

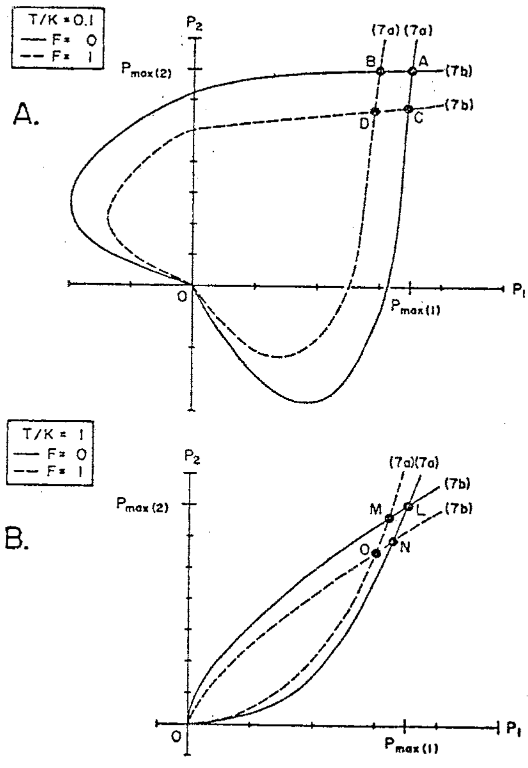


FIGURE 3

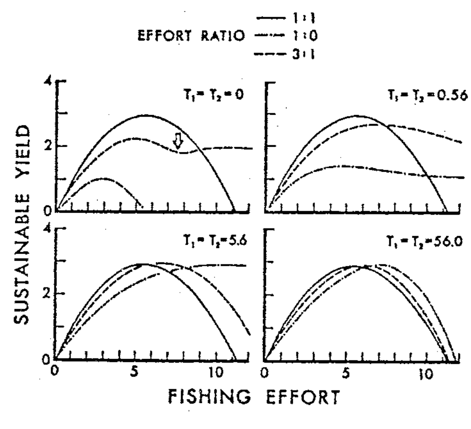


FIGURE 4

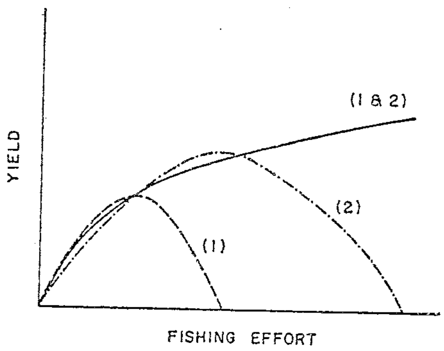
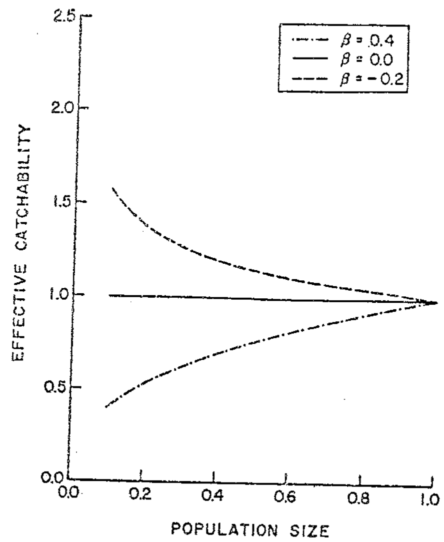


FIGURE 5



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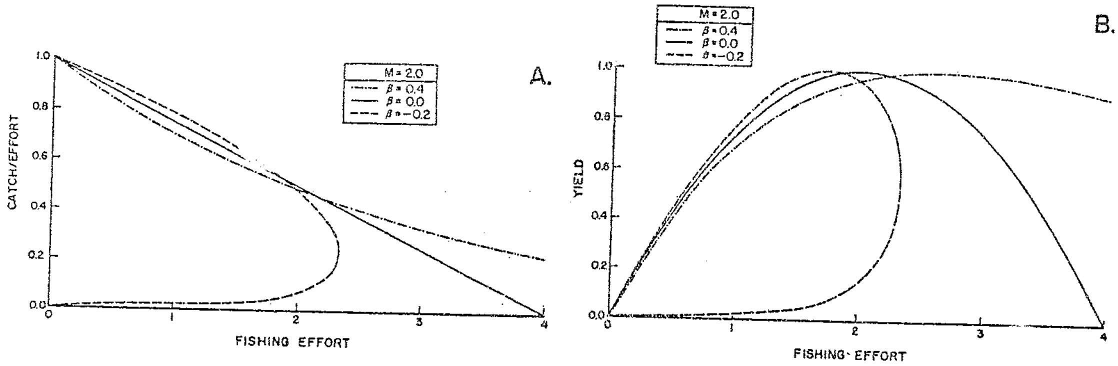

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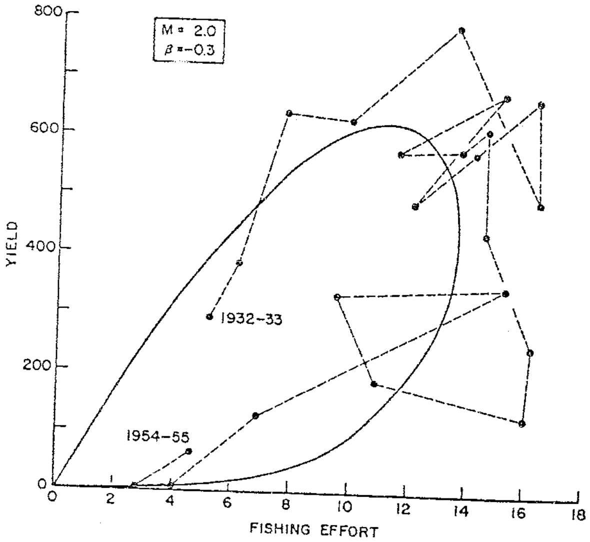

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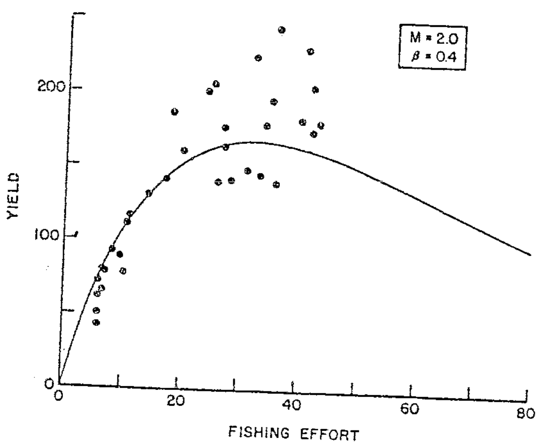

FIGURE 9