

POPULATION MODELS FOR THE NORTHERN ANCHOVY
(*ENGRAULIS MORDAX*)¹

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INTRODUCTION

The northern anchovy (*Engraulis mordax* Girard) is abundant off the coast of California and Baja California. The central subpopulation, or central stock, extends from 30°N to 38°N, and has been estimated at 3 to 4 million short tons' spawning biomass in recent years (Vrooman and Smith, 1972; Smith, 1972). The combined U.S. and Mexican harvests in 1977 were approximately 290 000 short tons and show prospects for increase. The Mexican industry is unilaterally undertaking a major fishery expansion designed to provide domestic self-sufficiency in fish meal. This is estimated to require a 300 000 to 500 000 t harvest from the central stock. Simultaneously, the U.S. legislation which created the 200-mile fishery conservation zone requires all affected fisheries to be managed for "optimum yield". The resource will have to be allocated between U.S. and Mexican commercial fishermen, who wish to maximize their portions of the allowable catch, and the recreational fishermen, who wish to maintain the largest possible anchovy biomass to provide forage which will support large populations of predatory fish. Determination of optimum yield requires an analysis of the trade-offs between yield and stock size.

A surplus production curve would provide the basis for such an analysis, but no large fishery has previously exploited the resource in such a way that traditional fishery methods can be applied. However, the California Cooperative Oceanic Fishery Investigations (CalCOFI) program has conducted rigorous egg and larval surveys since 1950, providing an independent source of population size estimates. MacCall, Stauffer, and Troadec (1976) applied the Gulland potential yield formula (Gulland, 1970) to these biomass estimates, and concluded that the resource may have a

potential yield of over 2 million t. An alternative to this crude and imprecise method is afforded by the time series of CalCOFI survey estimates itself (Fig. 1). The anchovy spawning biomass was remarkably small in the early 1950s, and grew over the following twenty years to an apparent equilibrium of nearly 4 million t. Since population growth at given initial size is a nearly direct measure of surplus production, the CalCOFI time series provides the makings of a surplus production model based on observed growth rates.

Before such a growth model can be constructed, we must examine the conditions under which that growth occurred. In particular, we must consider the reasons for the low biomass in 1951. A popular hypothesis has been that the decline of the California sardine (*Sardinops sagax caerulea*) left a void which the anchovy later filled. This hypothesis requires that the anchovy not be abundant before 1951 when the sardine biomass was large, and that sardine and anchovy abundances be negatively correlated. Results of recent work have been contrary to these assumptions. Soutar and Isaacs (1974) examined rates of scale deposition in anaerobic sediments off southern California for the past 150 years, and obtained a rank-correlation coefficient of +0.34 between sardine and anchovy scales. Assuming that scale deposition rates are proportional to population size, this strongly argues against an inverse relationship between population sizes. Further evidence is given by Smith (1972), showing that larval census estimates made from CalCOFI-like surveys in 1940 and 1941 indicate an anchovy spawning biomass of between 2 and 3 million t. At the same time, the sardine spawning biomass is estimated to have been 1.3 to 2 million t, so large populations of both species were existing simultaneously.

I offer an alternative hypothesis: the anchovy encountered a prolonged series of poor recruitments during the late 1940s, and the subsequent CalCOFI records document the recovery to more normal levels of abundance. While this hypothesis cannot be proved,

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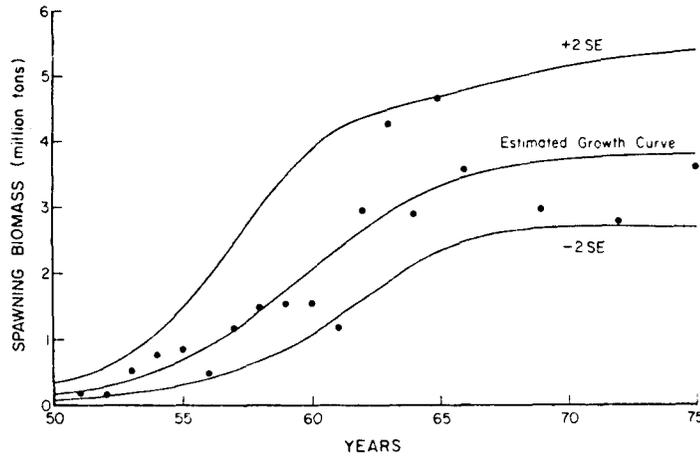


Figure 1. Historical increase in northern anchovy spawning biomass, with fitted growth curve and approximate confidence limits.

it is supported by two sets of evidence. The upwelling index of Bakun (1973) for $33^{\circ}\text{N } 119^{\circ}\text{W}$ (the Southern California Bight) in the second quarter of the year (April-June) shows a remarkable set of anomalies extending from 1947 to 1952 (Fig. 2). Upwelling during this period appears to have been much weaker than at any subsequent time. Lasker (1973) discusses some possible mechanisms for recruitment failure in the anchovy fishery. He indicates that insufficient upwelling in the spring may be a contributing factor, as the plankton blooms necessary for larval survival may not form in sufficient concentrations. If this actually occurred, we might expect to have seen poor recruitments in other pelagic species during the same period. Such was the case. The 1949 and 1950 year classes of the Pacific sardine were extremely weak, and contributed significantly to the final collapse of that fishery. The 1949, 1950, and 1951 year classes of Pacific mackerel (*Scomber japonicus*) were the smallest on record until the final collapse of that fishery in the 1960s (Parrish and MacCall, 1978). The Pacific bonito (*Sarda chiliensis lineolata*) virtually disappeared from southern California waters in the late 1940s until they returned in 1954 (Collins and MacCall, 1977). It appears reasonable that the northern anchovy, which shares the same environment, may have experienced similar recruitment difficulties.

In the following population growth model, I assume that events of the type described above are unusual. The sedimentary scale record of Soutar and Isaacs (1974) suggests that anchovy abundance was high and fairly constant from 1810 to 1925, but it appears to have been lower, and more variable, in recent years. The present model is based on conditions prevailing

since 1951, and may therefore be optimistic. However, until adverse conditions occur, it is appropriate to base harvest rates on the current productivity of the resource. Safeguards can be incorporated into the resource management policy which will minimize the impact of unanticipated recruitment failures and rehabilitate the fishery at an optimal rate. Such a management policy will be described in a later section, after the population model is developed.

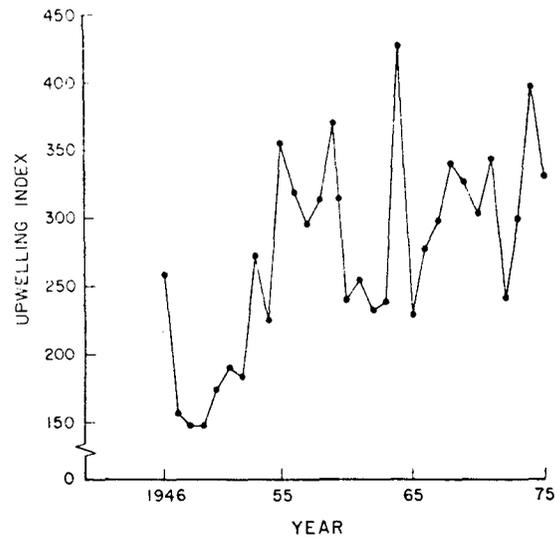


Figure 2. Mean upwelling index for April, May, and June, at $33^{\circ}\text{N } 119^{\circ}\text{W}$ (from Bakun, 1973).

DETERMINISTIC MODEL

The growth of the northern anchovy central sub-population since 1951 followed a pattern empirically similar, if one allows for random variability, to the Verhulst-Pearl logistic growth curve. Many of the assumptions underlying the traditional logistic growth model cannot be met by the northern anchovy. However, it is quite reasonable as an empirical description of population growth, and has already been used in a variety of standard fishery production models. Whereas in those traditional models the nature of population growth is inferred from the response to fishery removals, the present model must infer the response to fishery removals, given a pattern of population growth. The basic components of the model are standard fishery equations, which were reassembled to describe annual population processes, and the effects of a fishery.

Spawning biomass is defined as the total weight of male and female fish in the population which have spawned at least once in their lives. In practice, only female fish, which produce detectable spawning products, are counted; males are assumed to be present in equal quantities. The spawning biomass is assumed to be proportional to the abundance of anchovy larvae (Smith, 1972). Since anchovy spawning usually reaches peak intensity in the spring, but can occur throughout the year, the annual census will be assumed to measure the spawning biomass on March 1 of each year. Recruitment is the addition of spawning biomass to the population by the entry of those individuals spawning for the first time. Recruitment is assumed to occur on the first birthday, since anchovies appear to spawn at age 1 (E. Knaggs, personal communication). Fish are assumed to become fully available to the fishery at the time they are recruited to the spawning biomass; however, they are partially available for the preceding few months.

The actual variation of spawning biomass throughout the year may look like the sinusoidal curve in Figure 3A. At "A", recruitment and somatic growth rates exceed the mortality rate so the population rapidly increases as new spawners enter the pool. At "B", the combined rates equal zero and the spawning population reaches peak biomass for the year. At "C", the recruitment rate has become very low so that mortality is the dominant force, causing the spawning biomass to fall until the next season's recruitment begins to enter the population. At "D", an autumn spawning is described, which would appear as a ripple in the main population cycle.

To be useful, a population model must simplify the events described above and relate them to quantities which we can measure. The model proposed here

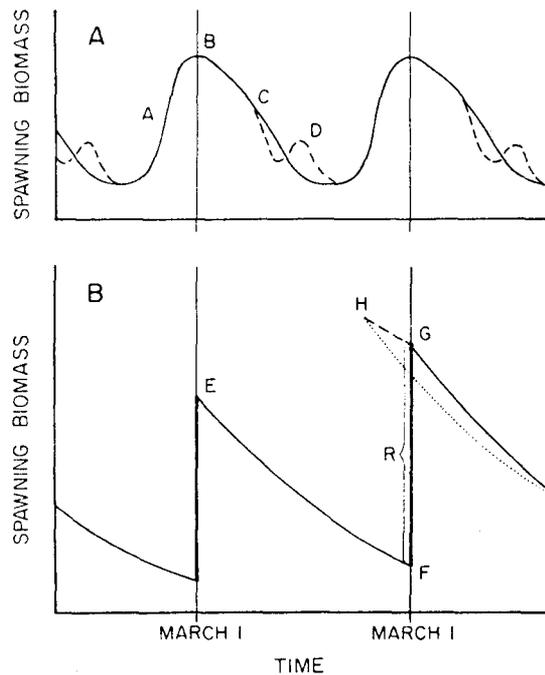


Figure 3. Diagrams of annual anchovy population processes: A, actual; B, model. Not drawn to scale.

assumes that recruitment can be described as entering the spawning biomass *en masse* on March 1 of each year (Fig. 3B). The ichthyoplankton survey gives a spawning biomass estimate which is shown at "E". Subsequently, the cohort consisting of all spawners included in "E" declines in biomass owing to natural and fishing mortality, which is partially offset by somatic growth. "F" shows the remaining biomass at the end of the year which is augmented by the next recruitment (R) to give a new spawning biomass cohort at "G". "H" represents partial availability to the fishery before first spawning. The mathematical relationships between the biomasses at points "E", "F", and "G" are easily described by standard fishery equations.

The population at "F" is a function of the population at "E" and the combined rates of growth and fishing and natural mortality. If the rate of growth is expressed in similar fashion to rates of mortality, the equations become very straightforward. Letting G be the instantaneous or specific rate of growth:

$$G = \frac{dW}{Wdt}$$

where W is fish weight. The combined instantaneous rate of loss of cohort biomass is $F+M-G$. In this analysis the quantity $M-G$ is used as an instantaneous rate of loss of biomass. Such an approximation must be used with caution, and should be discarded if better information is available. The survival of biomass (B) from March 1 (τ) to time $\tau+\Delta t$ is given by

$$B_{\tau+\Delta t} = B_{\tau} e^{-(F+M-G)\Delta t} \quad (1)$$

and the yield (Y) during the period is

$$Y = B_{\tau} \frac{F}{(F+M-G)} \left[1 - e^{-(F+M-G)\Delta t} \right] \quad (2)$$

The biomass at "C" is the sum of the biomass at "F" and recruitment. In the absence of fishing, "F" and "G" are points on the logistic growth curve exactly 1 year apart. This relationship is described by

$$B_{\tau+1}^* = B_{\tau-1} + R_{\tau-1} \\ = \left[\frac{1}{B_{\infty}} + \left(\frac{1}{B_{\tau}} - \frac{1}{B_{\infty}} \right) e^{-r} \right]^{-1} \quad (3)$$

where B_{∞} is the asymptotic maximum biomass, r is the intrinsic rate of increase, and $B_{\tau+1}^*$ represents a new cohort formed from the surviving biomass of the old cohort $B_{\tau+1}$, given by Equation (1), augmented by recruitment $R_{\tau+1}$. Recruitment is therefore given by (3) minus (1) where $F=0$:

$$R_{\tau+1} = \left[\frac{1}{B_{\infty}} + \left(\frac{1}{B_{\tau}} - \frac{1}{B_{\infty}} \right) e^{-r} \right]^{-1} - B_{\tau} e^{-(M-G)} \quad (4)$$

Thus the only independent variable in this spawner-recruit relationship is the spawning biomass 1 year prior to recruitment. In reality, the recruitment at time $\tau+1$ is provided by the previous year's spawning at time τ , but also to some extent those at $\tau-1$ and possibly at $\tau-2$. Since the spawning biomasses at times $\tau-1$ and $\tau-2$ are relatively near that at time τ , the error resulting from simplification to a 1-year cycle should be small.

The harvest of prespawners was included in the model to reflect more accurately actual fishery behavior. Fish were assumed to become partially available to the fishery (with ϕ as the coefficient of relative availability) for a length of time τ before spawning on March 1 (time τ). The quantity $(M-G)$ is assumed to be the same as that for spawners. The equivalent of fish alive at time $\tau-\tau$ would have been

$$R_{\tau+1-\tau} = R_{\tau+1} e^{(M-G)\tau} \quad (5)$$

where $R_{\tau+1}$ is as given in Equation (5) and $R_{\tau+1-\tau}$ denotes equivalent recruitment at that time earlier than March 1 when prespawners first become available to the fishery ("H" in Fig. 3B). Since fishing begins at time $\tau+1-\tau$, the recruitment remaining at time $\tau+1$ ($R_{\tau+1}^*$) is

$$R_{\tau+1}^* = R_{\tau+1-\tau} e^{-(\phi F+M-G)\tau} \\ = R_{\tau+1} e^{(M-G)\tau} e^{-(\phi F+M-G)\tau} \\ = R_{\tau+1} e^{-\phi F\tau} \quad (6)$$

and the biomass at $\tau+1$ is

$$B_{\tau+1}^* = B_{\tau} e^{-(F+M-G)} + R_{\tau+1-\tau} e^{-(\phi F+M-G)\tau} \quad (7)$$

$$= B_{\tau} e^{-(F+M-G)} + R_{\tau+1} e^{-\phi F\tau} \quad (8)$$

The total yield of fish during the year is

$$Y = B_{\tau} \frac{F}{F+M-G} \left[1 - e^{-(F+M-G)} \right] + \omega R_{\tau+1} e^{(M-G)} \\ \frac{\phi F}{\phi F+M-G} \left[1 - e^{-(\phi F+M-G)\tau} \right] \quad (9)$$

where ω is a coefficient of prespawner body weight in units of adult fish body weight.

Stochastic forms of the above model will be considered after the next section.

PARAMETER ESTIMATION

Two methods of estimating the logistic growth parameters, B_{∞} and r , were used. First, approximate values were estimated by fitting the logistic growth equation to larval census estimates using a curvilinear least-squares regression procedure. This method requires us to ignore the effects that actual harvests may have had on the population growth, and therefore tends to bias the parameter estimates. An advantage of the method is that it gives approximate standard errors and covariances for the estimated parameters. The second estimation procedure was an iterative least-squares estimate using catch-corrected biomass estimates, in which the growth model was used to estimate yearly transitions. While providing better parameter estimates, this method does not provide estimates of standard errors, and requires the assumption that actual biomasses are equal to observed biomasses with respect to the impact of the fishery. Spawning biomasses (P. Smith, personal communication) and catches are given in Table 1, and parameter estimates are given in Tables 2 and 3.

Table 1. Catch, equivalent catch, and spawning biomass. Values in thousand short tons

	Total catch	Equivalent catch at year-end	Spawning biomass
1951	8.4	5.4	180
1952	42.7	26.9	156
1953	45.6	26.6	510
1954	28.5	17.4	768
1955	28.0	15.3	846
1956	36.3	21.1	485
1957	19.9	11.6	1 172
1958	9.5	6.0	1 479
1959	9.0	5.5	1 514
1960	7.6	4.5	1 540
1961	9.9	6.3	1 159
1962	8.8	5.5	2 985
1963	7.2	4.6	4 254
1964	12.7	8.0	2 901
1965	23.7	14.1	4 659
1966	66.4	40.7	3 572
1967	47.7	29.7	-
1968	40.6	27.5	-
1969	93.0	64.3	2 999
1970	107.9	78.7	-
1971	60.5	37.5	-
1972	59.1	40.9	2 784
1973	162.6	103.3	-
1974	142.9	95.7	-
1975	-	-	3 603

Table 2. Estimates of logistic growth parameters

Parameter	Curvilinear regression (no catches)	Iterative solution (corrected for catches)
B_{∞} (GM)	3.611×10^6 t 36.85×10^{12} larvae	3.619×10^6 t
B_{∞} (AM)	3.841×10^6 t 39.19×10^{12} larvae	3.828×10^6 t
r	0.3369	0.3638
A	3.231	3.195
$B(t=0)$ (GM)	137.3×10^3 t 1.401×10^{12} larvae	143.6×10^3 t
$B(t=0)$ (AM)	146.0×10^3 t 1.490×10^{12} larvae	153.1×10^3 t
RSS	1.976	2.035
GM to AM correction factor	1.0637	1.0657

Logistic parameters - first method

The logistic growth curve

$$B_t = \frac{B_{\infty}}{1 + e^{-rt+A}} \tag{10}$$

where A is a constant relating to B_t at time $t = 0$ [$B(t = 0)$], is a special case of the Richards growth curve (Richards, 1959; Pella and Tomlinson, 1969)

$$B_t = \left\{ B_{\infty}^{1-m} + \left[B(t=0)^{1-m} - B_{\infty}^{1-m} \right] e^{-r(1-m)t} \right\}^{1/(1-m)} \tag{11}$$

where the skewness parameter (m) is equal to 2. Equations (10) and (11) are continuous equivalents to the annual transition Equation (3), but the former are more suited to regression because the independent variable, t , is not subject to large random error.

Regression also assumes that the residual variance is constant with respect to t , an assumption which is not met by the biomass data (Fig. 1). There may be several reasons for the increase in variance for the later years, including a change from monthly to quarterly cruises, and statistical properties associated with the increase in biomass itself. Much of the error

in larval survey estimates arises from the clumped distribution of the spawning products. Taft (1960) showed the negative binomial distribution applied to such survey samples, with the characteristic that the variance increases rapidly with increases in the mean (abundance). Zweifel and Smith² (MS) give a preliminary estimate of CalCOFI larval survey sampling error based on the negative binomial distribution, in which a 95% confidence interval is described by a multiplicative factor of 1.2. Logarithmic transformation equalized the variance at high and low biomasses, supplying the condition of homoscedasticity necessary for proper regression estimates.

The parameters of the log transformations of Equations (10) and (11) were estimated by the curvilinear least-squares regression (Marquardt algorithm) given by Conway, Glass, and Wilcox (1970). Various values of m were tried, giving a minimum residual sum of squares (RSS) at approximately $m = 1.6$ (Fig. 4). Since the RSS for $m = 2$ gives only a slightly higher RSS, the extra parameter in Equation (11) does not provide a statistically significant improvement in fit, and was therefore unnecessary. This justifies the use of the logistic growth curve in Equation (3) and simplifies estimation of the parameters.

Since the use of log-transformed variables results in the regression being fitted to the geometric mean of the raw data, a correction described by Beauchamp and Olson (1973) was applied to estimate the appropriate arithmetic mean. This correction consists of multiplying the antilog estimate of the mean by $e^{(s^2/2)}$ where s^2 is the variance of the estimate ($RSS/n-3$). In terms of the logistic growth Equation (10), the

² James Zweifel and Paul E. Smith, NMFS, La Jolla, California, USA.

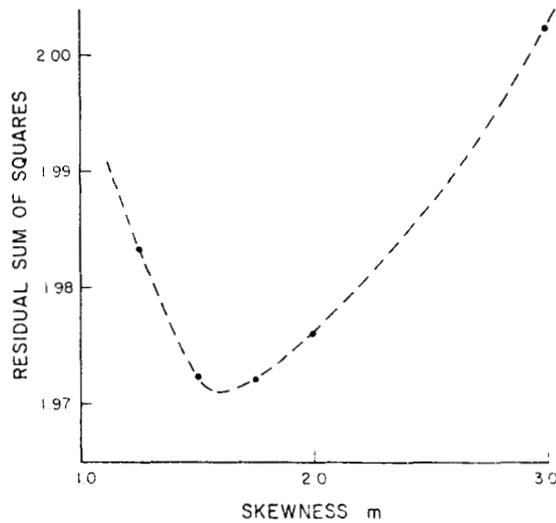


Figure 4. Minimum residual sums of squares as a function of the skewness parameter m .

correction is applied to B_{∞} . The parameter estimates are given in Table 2, and their standard errors and covariances are given in Table 3.

Approximate confidence limits for the growth curve (10) are obtained by the "delta method", which is basically a Taylor series approximation (Seber, 1973). In Seber's notation, the approximate variance of a function g which has parameters x_i ($i = 1, 2, \dots, n$) is given by

$$V \left[g(x_1, x_2, \dots) \right] = \sum_{i=1}^n V[x_i] \left(\frac{\partial g}{\partial x_i} \right)^2 + 2 \sum_{ij} \text{cov}[x_i, x_j] \left(\frac{\partial g}{\partial x_i} \right) \left(\frac{\partial g}{\partial x_j} \right) \quad (12)$$

Since the log transform of Equation (10) was used in the regression, function g is the logarithm of (10), and the partial derivatives must be calculated appropriately. Also, B_{∞} and its covariances do not yet incorporate the geometric mean correction factor, which in this case must be applied after taking antilogs of the estimated confidence limits. The approximate 95% confidence limits were calculated by the regression estimates ± 2 standard errors (Fig. 1).

Confidence limits for the rate of population growth are more interesting, as these have a direct bearing on the precision of the surplus production curve on which fishing strategy will be based. Annual growth rate is obtained by subtracting B_T from Equation (3), and approximate confidence limits were again calculated by the delta method. In this case the parameters used in the calculation were already corrected for the geometric mean. While the instantaneous growth rate function underlying the logistic growth curve is a symmetrical parabola, the corresponding annual growth rate (Fig. 5) as a function of initial biomass is skewed slightly to the right. The highest annual growth rate occurs at an initial biomass slightly smaller than $\frac{1}{2}B_{\infty}$, such that the peak of the instantaneous growth rate curve is encompassed by the year's growth.

Logistic parameters - second method

The above estimates of logistic growth parameters were made under the assumption that actual harvest of anchovies during the period had negligible effect on population growth. Such an assumption was necessary in order to obtain parameter error estimates by the curvilinear regression procedure. The following parameter estimates for harvest-corrected growth incorporate a catch correction but do not have error estimates; errors are probably similar to those given previously (Table 3).

The second method employs the deterministic model (Equation 3) to give expected biomasses each year,

Table 3. Variance-covariance matrix for growth parameters estimated by curvilinear regression

		B_{∞}		B_{∞}		r	A
		10^{12} larvae		10^3 t			
		GM	AM	GM	AM		
B_{∞}	$(10^{12}$ larvae)	GM	$(6.513)^2$	-	-	-	-
		AM	-	$(6.927)^2$	-	-	-
B_{∞}	$(10^3$ t)	GM	-	-	$(638.2)^2$	-	-
		AM	-	-	-	$(678.9)^2$	-
r		-221.6	-235.7	-21.71	-23.10	$(0.0560)^2$	-
A		546.8	581.6	53.6	57.0	0.00677	$(0.271)^2$
		$n = 19$		$df = 19-3$		$t_0 = 1950$ A.D.	

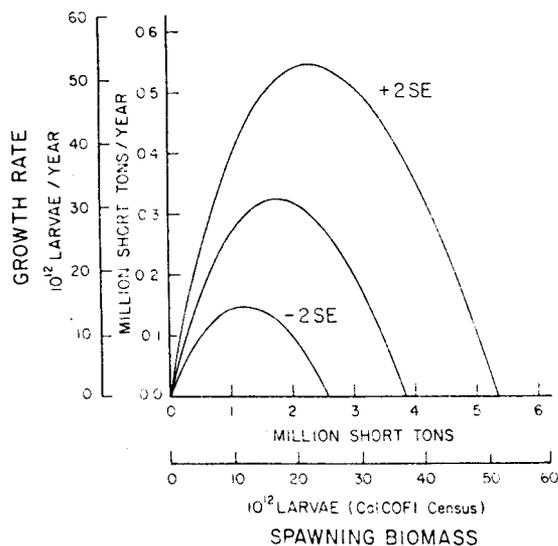


Figure 5. Logistic growth-rate curve and approximate confidence limits, with biomass measured alternatively in short tons or in CalCOFI larval census values.

allowing the time series to be fitted analogously to the first method. In order to correct for harvests, a quantity equal to the net year-end effect of the previous year's catch (Table 1) was subtracted from the expected population size. This quantity was determined by an application of cohort analysis. Equations (1) and (2) are analogues of the usual catch equations which employ only M and F . In this case, G is a constant instantaneous rate and can therefore be combined with F and M which are also constant instantaneous rates. Using the value of the specific growth rate constant developed in a later section, the quantity $(M-G) = 0.8$ was substituted for M in the cohort analysis equations (Tomlinson, 1970) allowing cohort analysis of a population measured in weight rather than numbers.

Monthly catches in weight were compiled for a March-to-February year. California landings by month were obtained from the California Marine Fish Landings series of *Fish Bulletins* from the California Department of Fish and Game. Bait landings were also obtained from the above source, but only annual totals are given. The bait catch was arbitrarily divided equally among June, July, August, and September, the months of maximum bait harvest. Mexican catches were obtained from MacCall, Stauffer, and Troadec (1976), and from recent unpublished fishery reports. Since no data are available on Mexican catches before 1962, arbitrary values of 100 t in 1956 increasing by

100 t annually to 500 t in 1960 were used. Again, only annual totals are available, so the Mexican catches were divided into the same 4-month period as the bait catch. This division is consistent with the Ensenada-based fishery which operates mainly during the summer months.

A "forward solution" form of cohort analysis was used to find the surviving biomass of the spawners at the beginning of the next spawning season. An initial value of fishing mortality was obtained by solving Equation (2) for F , given the total March landings and the larval survey estimate of spawning biomass (March 1). Monthly biomasses were then estimated sequentially to give biomass on the following March 1. This final biomass was then subtracted from the biomass which would be indicated by Equation (1) had there been no fishing. This difference is the catch correction factor applied to biomasses predicted by Equation (3). It can be viewed as the catch which would have the same net effect as the true catches, had it been taken entirely on the last day of February. Annual catches and year-end equivalent catches are given in Table 1.

Parameter values were estimated by an iterative procedure based on searching the response surface for the minimum residual sum of squares (Stauffer, 1973). Three trial values of each of the parameters r , $B\infty$ and $B(t=0)$ were selected, giving 27 combinations in all. The 19 biomass estimates corresponding to the CalCOFI surveys from 1951 to 1975 were predicted by each combination of three trial parameter values, and a residual sum of squares (RSS) for the logarithm of the biomasses was calculated. A multiple linear regression program (BMD02R) was utilized to estimate coefficients of the following equation used to model the residual sum of squares response surface:

$$RSS = b_0 + b_1 B\infty + b_2 r + b_3 B(t=0) + b_4 B\infty^2 + b_5 r^2 + b_6 B(t=0)^2 + b_7 r B\infty + b_8 B\infty B(t=0) + b_9 r B(t=0) \quad (13)$$

The values of r , $B\infty$, and $B(t=0)$ that minimize the RSS are the solution to the three first order partial derivatives of (13), with respect to r , $B\infty$, and $B(t=0)$, set equal to zero, i.e.,

$$\frac{\partial RSS}{\partial B\infty} = b_1 + 2b_4 B\infty + b_7 r + b_8 B(t=0) = 0$$

$$\frac{\partial RSS}{\partial r} = b_2 + 2b_5 r + b_7 B\infty + b_9 B(t=0) = 0$$

$$\frac{\partial RSS}{\partial B(t=0)} = b_3 + 2b_6 B(t=0) + b_8 B\infty + b_9 r = 0.$$

These can be rewritten in terms of matrix algebra as

$$Dx = d$$

where the matrix $D = \begin{bmatrix} 2b_4 & b_7 & b_8 \\ b_7 & 2b_5 & b_9 \\ b_8 & b_9 & 2b_6 \end{bmatrix}$

the vectors $x = \begin{bmatrix} B \\ r \\ B(t=0) \end{bmatrix}$ and $d = \begin{bmatrix} -b_1 \\ -b_2 \\ -b_3 \end{bmatrix}$

From this, the values of r , B , and $B(t=0)$ that minimize RSS can be expressed as

$$x = D^{-1}d \quad (14)$$

Since Equation (13) only approximates the response surface, about four iterations of the above parameter estimation procedure with successively closer delineations of the trial parameter region gave results precise to three significant digits in most cases. An independent test of accuracy is furnished by the previous curvilinear regression estimates. An iterative solution was run for the case of "no catches", giving results very similar to the regression estimates. It is interesting to note that this solution, which includes the effect of actual harvests, gives a slightly larger minimum RSS than does the previous regression solution (Table 2). This suggests that the small fishery which has existed does not account for a detectable portion of the variance in biomass which has been observed.

Other parameters

The parameters M and G always appear in combination as $(M-G)$, which can be interpreted as instantaneous rate of natural decrease in biomass, and which were estimated as such by the following approximation (Table 4). Growth from age 2 to age 3 was considered typical of the population. Mean length at age (Spratt, 1975) was expanded by the length-weight relationship (Collins, 1969) to obtain approximate mean weight. Survival was assumed to be 1.0 at age 2, and 0.346 at age 3, based on $M = 1.06$ (MacCall, 1974). The difference of the logarithm of approximate cohort biomasses was 0.75, and was rounded to 0.8 as a functional estimate of the quantity $(M-G)$.

Table 4. Approximation of $(M-G)$

Age	Mean length (mm-SL)	Weight (g)	Numbers in cohort	Weight of cohort	In weight of cohort
2	112	14.2	1.000	14.25	9.55
3	124	19.3	0.346	6.69	8.81
					Difference = 0.75

Table 5. Mean weight data for estimation of ω and ϕ

Season	Ratio mean weight	Ratio catch
	Age 0 to mean weight age 1+	Age 0 to catch age 1+
1965/1966	0.542	0.0254
1966/1967	0.501	0.0370
1967/1968	No data for southern California	
1968/1969	0.765	0.1740
1969/1970	0.636	0.2347
1970/1971	0.639	0.0270
1971/1972	0.639	0.0812
1972/1973	0.815	0.0852
1973/1974	0.642	0.0478
Mean	0.647	0.0890
Standard deviation	0.103	0.0764

The quantity ω is the ratio of the weight of an average prespawner (age 0) to that of an average spawner (age 1 and older). By dividing total weight landed by total number of fish landed for each category, average weights for these two groups were obtained from the landings reports. The average ratio of these average weights gives an estimate of $\omega = 0.647$ (Table 5).

Prespawning anchovies are assumed to be partially (ϕ) available to the fishery for a short period (τ) before they spawn on their first birthday. Relative availability is defined as

$$\phi = F_0/F_{1+} \quad (16)$$

for the same reason. Harvest of prespawners is given by

$$Y_0 = F_0 \bar{B}_0 \tau \quad (17)$$

where \bar{B}_0 is the average biomass of prespawners during the period of availability preceding spawning. Harvest of adult anchovies is given by

$$Y_{1+} = F_{1+} \bar{B}_{1+} \quad (18)$$

where time is unity, being one fishing year. Therefore, (17) and (18) are substituted into (16) to obtain

$$\phi = (Y_0/Y_{1+}) (\bar{B}_{1+}/\bar{B}_0 \tau) \quad (19)$$

The quantity Y_0/Y_{1+} can be obtained from fishery data (Table 5), and the theoretical ratio of mean biomasses can be obtained from the model.

The mean biomass of adult fish is given by

$$\begin{aligned} \bar{B}_{1+} &= \int_{t=0}^{\infty} B' e^{-(F+M-G)t} dt \\ &= \frac{B'}{F+M-G} \end{aligned} \quad (20)$$

where $t = 0$ denotes time of first spawning, and B' denotes the biomass at that time. This equation uses

the approximation that the biomass of all adult cohorts in a single season is equivalent to the biomass of a single cohort over its lifetime. The mean biomass of prespawners during the period of partial availability is

$$B_0 = \frac{1}{\tau} \int_{t=-\tau}^{t=0} \omega B' e^{-(\Phi F + M - G)t} dt$$

$$= \frac{\omega B' [e^{(\Phi F + M - G)\tau} - 1]}{\tau(\Phi F + M - G)} \quad (21)$$

Equations (20) and (21) are now substituted into (19) to obtain

$$\Phi = \frac{Y_0}{Y_{1+}} \cdot \frac{\Phi F + M - G}{\omega(F + M - G) [e^{(\Phi F + M - G)\tau} - 1]} \quad (22)$$

The quantity Φ can now be estimated by iteration, given values of the remaining variables. The historical average value of Y_0/Y_{1+} has been 0.039 (Table 5). The fishing mortality rate F has averaged 0.03, and $(M - G)$ was estimated above to be 0.8. Age 0 anchovies first appear in January, about 0.2 years before spawning on March 1, so for $\tau = 0.2$, Φ is estimated to be 0.76.

DISCUSSION OF THE DETERMINISTIC MODEL

The deterministic model described above allows equilibrium yield to be described as a function of spawning biomass (Fig. 6). Equilibrium yield is defined as that yield which is expected to maintain the spawning biomass at the same level in the following year. Note that this is not equivalent to sustainable yield, because natural fluctuations in recruitment success will not allow a given biomass to be maintained. Sustainability decreases with increasing variability and will be discussed in more detail later.

A somewhat surprising result of the model is that the equilibrium yield is considerably greater than the expected population growth in the absence of a fishery (560 000 t per year as opposed to 353 000 t per year). This is contrary to the assumption of equality often made in production modeling, and arises from the fact that reproduction is periodic rather than continuous with immediate recruitment. Qualitatively, the phenomenon arises from the competing risk of death from fishing and natural causes, so that many fish taken by the fishery would not have reproduced at the next spawning in any case. A simple correction factor can easily be derived from guesses of mortality rates, and could significantly improve the performance of catch-transition production models (e.g., Schaefer, 1957; Pella and Tomlinson, 1969), particularly when

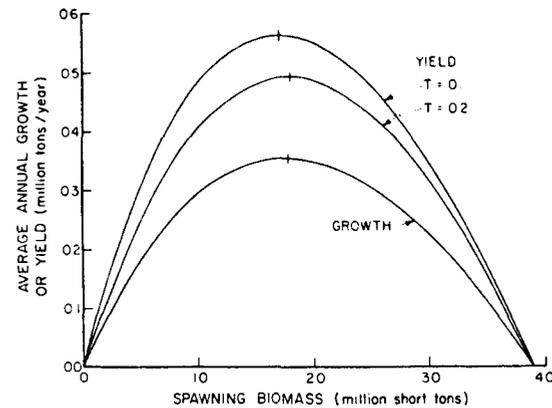


Figure 6. Equilibrium yield and growth rates for the northern anchovy central stock. Growth is mean population growth in the absence of fishing. Equilibrium yield is given for no harvest of prespawners ($\tau = 0$), and for partial availability of prespawners ($\tau = 0.2$).

applied to stocks in which reproduction is seasonal (MacCall, 1978).

Another rather surprising property of the equilibrium yield curve is the fact that yield decreases when prespawners are harvested (484 000 t per year as opposed to 560 000 t per year). Yield per recruit considerations indicate that maximum yield per recruit is obtained by fishing the resource intensively with a small size at entry (MacCall, Stauffer, and Troadec, 1976). The present model, which includes reproduction, indicates that harvesting anchovies immediately before spawning results in a twofold loss to the population: loss of the fish and of its progeny. The model predicts that yield will generally be near a maximum when fish are taken as soon after spawning as possible. Whether these are valid conclusions remains to be seen. For comparison, the Peruvian anchoveta fishery was highly productive under intensive fishing of prespawners in the 1960s. However, the above two considerations may also help explain the unexpectedly slow recovery of the anchoveta resource since the population collapse of the early 1970s.

STOCHASTIC MODEL

While the above deterministic model is useful for estimating the approximate long-term productivity of the northern anchovy central stock, it is unable to provide a realistic and useful description of short-term productivity and variability. Spawning biomass has shown large fluctuations about the hypothesized trend (Fig. 1). A simple stochastic model can be derived from the second method (iterative least squares) of

logistic parameter estimation described above. Equation (3) of the population growth model can be re-written as

$$\ln B_T = \ln (B_T + R_T) \\ = \ln \left[\frac{1}{B_\infty} + \left(\frac{1}{B_{T-1}} - \frac{1}{B_\infty} \right) e^{-r} \right]^{-1} + \epsilon \quad (23)$$

or more simply

$$\ln B_T^* = \ln \hat{B}_T^* + \epsilon$$

where ϵ is a stochastic error term with mean = 0, B_T^* is surviving biomass plus recruitment, and \hat{B}_T^* is predicted from B_{T-1} by the deterministic growth model. There are three principal sources of this error: 1) variability of population processes, particularly recruitment, 2) error of observation of biomass at time t , and 3) error of observation at time $t-1$. A more complicated model could be constructed with stochastic errors in recruitment and in observed population size respectively. Such a model would allow simulations of population and fishery behavior over long periods. However, there is at present no definitive way to separate the components of the error term in (23). Thus there would be a wide spectrum of simulation model results depending on the portion of the variability assigned to recruitment.

The simple stochastic model (23) does not require that the error term be separated into components, but requires the assumption that the effect of the fishery on a population of the observed biomass would be a close approximation of the effects of a fishery on a population of the actual biomass. This assumption also occurs in the second method of logistic parameter estimation, so the parameters inherently reflect this assumption. On the other hand, there is a definite non-linearity in the model, such that responses to an underestimated biomass are not equal and opposite to responses to an equally overestimated biomass. This problem should not be severe except when large catches are being taken from small biomasses.

A plot of $\ln B_T^*$ against $\ln \hat{B}_T^*$ from 1952 to 1966, where the latter variate is corrected for catches according to the second logistic parameter estimation method, shows the deterministic model to be a good description of the average year-to-year behavior of the observed spawning biomasses (Fig. 7). The residual error term ($\epsilon = \ln B_T^* - \ln \hat{B}_T^*$) is well behaved when plotted against $\ln \hat{B}_T^*$ (Fig. 7), with a mean of 0.016 and a standard deviation of 0.496. The mean is sufficiently near zero to justify acceptance of the parameter estimates of B_∞ (arithmetic mean) and r for predictive purposes. The residuals show no distinct

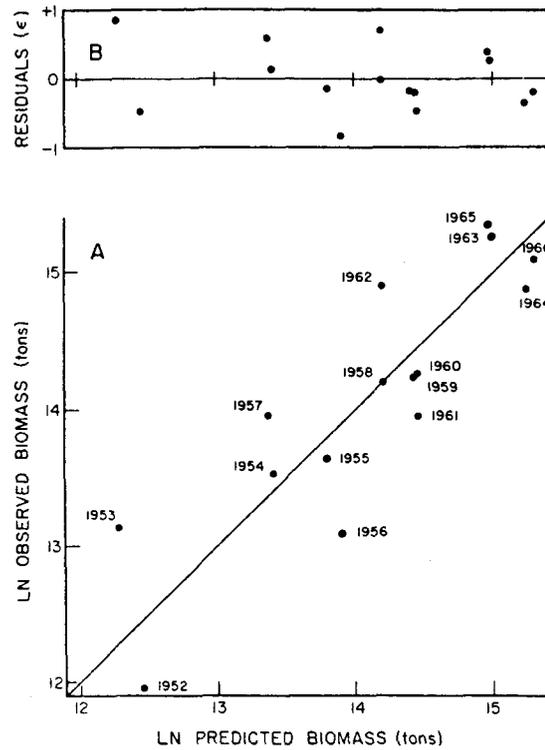


Figure 7. Comparison of predicted and observed spawning biomasses, including a plot of residuals.

changes in pattern over the range of observed biomasses. Therefore, ϵ will be assumed to be normally distributed ($\mu = 0$, $\sigma = 0.496$) in the stochastic model.

Equation (23) is equivalent to

$$B_{T+1}^* = B_{T+1} + R_{T+1} = \\ e^\epsilon \left[\frac{1}{B_\infty} + \left(\frac{1}{B_T} - \frac{1}{B_\infty} \right) e^{-r} \right]^{-1} \quad (24)$$

so if there is no fishing, R_{T+1} can be obtained by the analogue of (4):

$$R_{T+1} = e^\epsilon \left[\frac{1}{B_\infty} + \left(\frac{1}{B_T} - \frac{1}{B_\infty} \right) e^{-r} \right]^{-1} \\ - B_T e^{-(M-G)} \quad (25)$$

Note that R_{T+1} is not actual recruitment, but apparent recruitment, since the observation error of B_T and B_{T+1} is included in the stochastic error term. For this reason, apparent recruitment can become negative for low values of e^ϵ . Equation (25) can be used to estimate

Table 6. Conditions for negative apparent recruitment, and probabilities of occurrence based on an assumed normal distribution ($\sigma_\epsilon = 0.496$)

Spawning biomass B_T (1 000 t)	Minimum ϵ for positive apparent recruitment	Probability $\epsilon \sim \epsilon_{\min}$
1	-1.16	0.0096
500	-1.11	0.0125
2 000	-0.96	0.0262
4 000	-0.79	0.0559
6 000	-0.65	0.0951
10 000	-0.41	0.2033

values of ϵ which give negative apparent recruitment for various levels of B_T . Some sample values, with their probabilities, are given in Table 6. While no instances of negative apparent recruitment have occurred in the time series of CalCOFI spawning-biomass estimates, there appears to be no reason, other than low probability, for such a condition not to be observed in the future.

Catch will be given as a function of spawning biomass, which could either reflect levels of nominal fishing effort, or in this case, be controlled by a variable quota management system of the form

$$Q = \begin{cases} a(B_T - b), & B_T - b > 0 \\ c, & \text{otherwise} \end{cases} \quad (26)$$

where Q is a reduction fishery quota, b is minimum spawning biomass for a quota to be established, and a is a fraction of the excess spawning biomass over level b . The quantity c is a small maintenance fishery for non-reduction uses such as live bait.

When we include exploitation of prespawners in the stochastic model, the equations become lengthy. The quantity R_{T+1} which is given by (25) is substituted into (9) to give an expression relating catch to B_T , ϵ and F :

$$Y = \frac{F}{F + M - G} B_T [1 - e^{-(F+M-G)}] + \omega \left\{ c^\epsilon \left[\frac{1}{B_\infty} - \left(\frac{1}{B_T} - \frac{1}{B_\infty} e^{-r} \right)^{-1} - B_T c^{-(M-G)} \right] c^{(M-G)\tau} \frac{\Phi F}{\Phi F + M - G} [1 - c^{-(\Phi F + M - G)\tau}] \right\} \quad (27)$$

MARKOV MODEL

While the stochastic model could be investigated by Monte Carlo simulation methods, the model is uniquely adaptable to treatment as a Markov process, which can directly provide probability distri-

butions of observed biomass. Various discrete levels of biomass can be treated as states. Since the model contains no time lags, transition probabilities between states are stationary.

For a vector of n discrete observed biomass values B_1, \dots, B_n (in ascending order), we wish to calculate the elements of a matrix containing the probabilities that a population of observed size B_i at time τ will become a population of observed size B_j at time $\tau+1$. The probabilities of each possible transition are associated with the corresponding error term ϵ_{ij} , which has the properties described in the stochastic population model.

Since we are given that the observed biomass at time τ is B_i and the observed biomass at time $\tau+1$ is B_j , Equation (8) provides us with

$$B_j = B_i e^{-(F+M-G)} + R_{T+1} c^{-\Phi F \tau} \quad (28)$$

where R_{T+1} is given by (25). Therefore,

$$B_j = B_i c^{-(F+M-G)} + \left\{ c^{\epsilon_{ij}} \left[\frac{1}{B_\infty} - \left(\frac{1}{B_i} - \frac{1}{B_\infty} \right) e^{-r} \right]^{-1} - B_i c^{-(M-G)} \right\} c^{-\Phi F \tau}$$

or

$$\ln \left(\frac{\epsilon_{ij} = [B_j - B_i c^{-(F+M-G)}] c^{\Phi F \tau} + B_i c^{-(M-G)}}{\left[\frac{1}{B_\infty} - \left(\frac{1}{B_i} - \frac{1}{B_\infty} \right) e^{-r} \right]^{-1}} \right) \quad (29)$$

In implementing the Markov model on a computer, (29) can be substituted for ϵ in (27), so that F can be estimated iteratively given B_i , B_j , and Y_i . This value of F then gives ϵ_{ij} from (29), and a probability can be computed for the transition. Note that Y_i is determined by B_i and the quota formula (26). Each different quota formula will give a different and unique transition probability matrix.

The Markov model was based on a 30×30 probability matrix. Discrete biomasses were a geometric series from $B_1 = 200\,000$ t to $B_{30} = 16\,000\,000$ t, with an element ratio (s) of 1.16312. The probability associated with ϵ_{ij} was calculated from a fixed value of B_i , and an interval centered about B_j :

$$P(\epsilon_{ij}) = \mathfrak{F}(B_j | s B_i) - \mathfrak{F}(B_j | s B_i) \quad (30)$$

where \mathfrak{F} is the cumulative density function for the normal distribution. The probabilities corresponding to the tails of the distribution were assigned to $\epsilon_{i,1}$ and $\epsilon_{i,30}$, respectively. The quantity \mathfrak{F} was calculated by a polynomial approximation.

Each harvest policy (26) generates a unique transition probability matrix. Any probability vector associated with the vector of discrete observed population sizes B can be multiplied by the transition probability matrix to obtain a new vector of probabilities reflecting the likelihood of observing the corresponding population sizes in the following year. This multiplication can be used to investigate the probable near-term effects of management decisions. In the case of an infinite time horizon, which could be appropriate to long-term management policy, we can find the stable probability distribution to which all beginning probability distributions tend to converge after repeated multiplication by the transition probability matrix. This stable probability distribution is that eigenvector of the transition probability matrix whose eigenvalue is 1. Actually, after about 10 multiplications by the transition matrix, most initial probability vectors converge to very nearly the stable probability distribution given by the eigenvector.

While the model is at present used to evaluate alternative pre-specified quota policies, other uses are possible. If an objective function can be specified, the Markov model could serve as a basis for determining the optimum harvest policy (Mendelsohn³, MS). In a management mode, the model can provide an *a priori* probability distribution so that biomass could be estimated by efficient Bayes methods.

Example Application

Three fishery management policies will be examined and compared (Fig. 8, Table 7). A "no fishery" policy (Case I) allows only 10000 short tons' annual harvest for live bait and fresh-fish markets. This policy allows the biomass to remain at virgin levels and forms a basis for comparison. The "present" fishery (Case II) was recently adopted by the United States as an optimum yield policy, wherein the greatest overall benefit arises from maintaining a biomass somewhat larger than that resulting from a strictly maximum yield policy. A maximum yield or "heavy fishing" policy (Case III) passes through the peak of the equilibrium yield curve. Theoretically the largest yield would be obtained by a policy with a very steep slope and a fishery cutoff at about 1.5 million short tons. That policy would produce a highly variable fishery, whereas our Case III seeks to stabilize the fishery by virtue of a shallower slope and a lower fishery cutoff point.

When plotted on a log scale, the stable probability distributions resemble normal density functions (Fig. 9). The discontinuity at the tails of the distributions

Table 7. Comparison of resource characteristics under three harvest policies, and under the special case of an unequal sex composition in the landings. Values in million short tons

Harvest	Minimal (I)	Optimal (II)	Heavy (III)	Optimal (II) (sex ratio 1.73:1♂)
Slope (<i>a</i>)	-	0.33	0.33	0.33
Cutoff (<i>b</i>)	-	1.00	0.50	1.00
Maintenance (<i>c</i>)	0.01	0.01	0.01	0.01
Assumed maximum	0.01	1.00	1.00	1.00
Spawning biomass characteristics				
Median	3.35	2.05	1.66	1.84
Mean	4.12	2.75	2.35	2.48
Standard deviation	2.95	2.32	2.19	2.15
Probability (percentage of years)				
$B < 0.5$	1.3	4.4	8.7	5.7
$B < 1.0$	6.6	18.4	28.2	22.3
$B < 1.5$	14.9	34.5	45.3	39.8
$B < 2.0$	24.6	48.4	58.3	54.1
$B < 2.5$	34.4	59.6	67.9	65.0
Yield characteristics				
Median	-	0.351	0.387	0.280
Mean	-	0.442	0.467	0.373
Standard deviation	-	0.379	0.362	0.370
Probability (percentage of years)				
$Y = 0.01$	100	18.4	8.7	22.3
$Y < 0.1$	100	28.2	15.9	33.1
$Y < 0.5$	100	59.6	58.3	65.0
$Y < 1.0$	100	80.0	80.3	83.7

is slight. Under a minimal fishery (Case I), the highest probabilities are associated with biomasses near B_{∞} , as expected. However, the variability of the biomass is high, with a 25% probability of observing a biomass of less than 2 million short tons in any given year (Table 7). As fishing becomes more intense, the peak biomass shifts to lower values, and the probability distributions become flatter. Mean yield from Case III is only 6% greater than that from Case II; however, the mean biomass is 14% smaller, showing little marginal value from the heavy policy, especially if benefits arise from increased biomass. The lower fishery cutoff point of Case III results in fewer years of fishery closures, but at the same time would delay recoveries from periods of low abundance. Expected values and variances of more complicated fishery measures, such as economic yield, are easily calculated if the measure can be expressed in terms of biomass and catch.

³ Roy Mendelsohn, NMFS, Honolulu, Hawaii, USA.

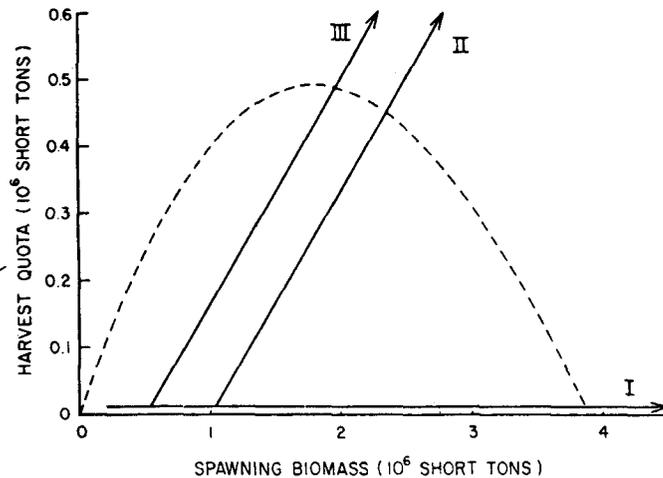


Figure 8. Three harvest policies examined by the model: I, minimal fishing; II, optimal fishing; III, heavy fishing.

DISCUSSION OF THE STOCHASTIC MODEL

Previous estimates of potential yield from the northern anchovy central stock have been based on the Gulland (1970) approximation formula. A wide range of potential yields was given, depending on the base years for determining "virgin biomass" (MacCall, Stauffer, and Troadec, 1976). Reasonable estimates ranged from 1 to 2 million short tons per year. The model developed in this paper suggests a much smaller potential yield of about 450000 short tons per year. In view of the historical low biomasses of anchovy, the Gulland potential yield estimates seem high, and are clearly not sustainable. The present estimate of potential yield seems somewhat low when compared with fisheries on similar species. However, many of those fisheries have subsequently experienced severe depletion, and the expectations may have been too high.

This model emphasizes the role of natural population variability in fishery projections. While the equilibrium yield curve from the deterministic model indicates a maximum yield of 484000 short tons, the stochastic model shows that somewhat less than this can be expected, and only under a highly fluctuating fishery. Yields of 200000 to 300000 t are more nearly sustainable in the strict sense.

In any particular year, abundance is determined by natural variations in recruitment, and a fishery will have little effect. However, over the long term, a fishery strongly modifies the probability distribution of biomasses. When a period of low abundance occurs under a fishery, one must not simply blame it on the fishery nor explain it away as an unavoidable natural

event. In actuality, low abundance must be interpreted as a natural event which has become more likely because of the fishery. Management policies which do not reduce fishing pressure at low population sizes greatly increase the probabilities of low population sizes, often to the point of virtual certainty. The California sardine fishery, which had no effective constraint on fishing pressure or harvest, is such a case. An inflexible constant quota, even if set at a level below maximum equilibrium yield, contains a large risk of prolonged or possibly irreversible low population sizes.

The management policy adopted for the northern anchovy central stock (Fig. 8, Table 7) attempts to maintain an average population somewhat larger than that producing strictly maximum yield, by means of a harvest quota formula (26). Biomass was seen as contributing benefits by providing forage to other consumable and non-consumable predators, by providing more readily available supplies of live bait for recreational fishing, and by reducing harvesting costs of the reduction fishery. A reserve spawning biomass of 1 million short tons serves to preserve the reproductive capacity of the resource during adverse periods, and should help maintain some stability of trophic relationships in the ecosystem. When the resource is abundant, the allowable harvest will increase.

This variable quota policy is very resistant to errors in the model predictions. If the resource is more productive than anticipated, a larger biomass will obtain, and allowable harvest will increase. Similarly, if the resource is less productive, there will be a smaller average biomass and a smaller harvest. Random

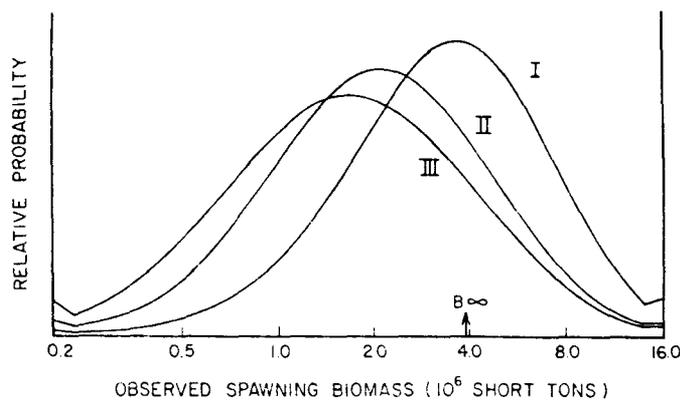


Figure 9. Spawning biomass probability distribution for three harvest policies.

variability is likely to produce periods of apparent high productivity and periods of apparent low productivity. Biomasses are serially correlated, protracting these periods somewhat longer than might be expected from random runs alone. A very large number of years will have to pass before the model can be adequately tested against actual resource performance.

There is considerable imprecision in the variability predicted by the model. The small number of observations results in a wide confidence interval. The substitution of observed biomass for actual biomass in the calculations results in an overestimate of resource variance, the actual biomass being less variable than our imprecise estimates. However, positive serial correlation in recruitment strengths is likely, although none was detected in the short time series which was available. As an extreme case of serial correlation, we must consider possible changes in the oceanic "regimes", as may have occurred in the late 1940s and early 1950s. Such serial correlation will increase the variability of population size, and the model predicts a lowering of average population size and yield.

A further error in the model predictions arises from the assumption that the fishery impact on the spawning biomass is measured by total yield. The fishery for the northern anchovy is peculiar in that the sex ratio of landings has averaged 1.73 females to each male by weight, whereas the population itself appears to be evenly distributed between the sexes (Klingbeil, 1978). Thus it appears likely that the fishery may have a disproportionate impact on the biomass of female fish, and therefore on the spawning potential of the population. If this hypothesis is true, the expected yield and biomass will be less than anticipated (Table 7), and the resource may be overfished with respect to the stated goal of optimum yield. As a

corollary, management which encourages the harvesting of male fish could potentially increase yield at little loss to population size, and a more optimal utilization of the resource would result.

SUMMARY

The low anchovy central stock biomass in the early 1950s was probably due to a series of reproductive failures rather than to competition from the Pacific sardine. The pattern of anchovy population growth since 1951 can be empirically described by a logistic growth curve, which forms the basis of a population growth model. Estimated maximum equilibrium yield (484000 short tons/year) is higher than maximum growth rate (353000 short tons/year) due to competing risk of death and discontinuous reproduction. Asymptotic maximum spawning biomass is 3.9 million tons. A stochastic population growth model was derived from the deterministic logistic model by considering error in annual population size predictions. This model was implemented as a Markov process with various biomasses as states, and stationary transition probabilities based on a given harvest policy. The stable probability distribution indicates that the resource is highly variable in a natural unharvested state. Management policies can be examined by the model, providing expected values, variances, and probabilities of various events or conditions. The present management policy of allowing a reduction fishery to harvest one third of the excess over 1 million short tons' spawning biomass could be expected to have a mean annual yield of 443000 short tons and a mean spawning biomass of 2.75 million short tons. Because the fishery harvests a disproportionate amount of females, there may be a corresponding disproportio-

nate impact on spawning potential, in which case the above management policy may result in overfishing with respect to the desired goal of optimum yield.

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REFERENCES

- Bakun, A. 1973. Coastal upwelling indices, West Coast of North America, 1946-1971. NOAA Tech. Rep., NMFS SSRF-671, 103 pp.
- Beauchamp, J. J., and Olson, J. S. 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology*, 54: 1403-1407.
- Collins, R. A. 1969. Size and age composition of northern anchovy (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67 and 1967-68 seasons. Calif. Dept. Fish and Game, Fish. Bull., 147: 56-74.
- Collins, R. A., and MacCall, A. D. 1977. California's Pacific bonito resource, its status and management. Calif. Dept. Fish and Game, Mar. Res. Tech. Rep., 35: 1-39.
- Conway, G. R., Glass, N. R., and Wilcox, J. C. 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. *Ecology*, 51: 503-507.
- Gulland, J. A. 1970. Preface. In *The fish resources of the oceans*, pp. 1-4. Ed. by J. A. Gulland. FAO Fish. Tech. Pap., 97: 425 pp.
- Klingbeil, R. 1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off southern California. Calif. Fish Game, 64: 200-209.
- Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 173: 212-230.
- MacCall, A. D. 1974. The mortality rate of *Engraulis mordax* in southern California. Mar. Res. Comm., Calif. coop. oceanic fish. Invest., Rep. 17: 131-135.
- MacCall, A. D. 1978. A note on production modeling of populations with discontinuous reproduction. Calif. Fish Game, 64: 225-227.
- MacCall, A. D., Stauffer, G. D., and Troadec, J. P. 1976. Southern California recreational and commercial marine fisheries. Mar. Fish. Rev. 38(1): 1-32.
- Parrish, R. H., MacCall, A. D. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dept. Fish and Game, Fish Bull., 167: 1-110.
- Pella, J. J., and Tomlinson, P. K. 1969. A generalized stock production model. Bull. Inter-Amer. Trop. Tuna Comm., 13: 419-496.
- Richards, F. J. 1959. A flexible growth function for empirical use. J. Exp. Botany, 10(29): 290-300.
- Schaefer, M. B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm. 2(6): 245-285.
- Seber, G. 1973. The estimation of animal abundance and related parameters. Hafner Press, New York, 506 pp.
- Smith, P. E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull. (U.S.), 70: 849-874.
- Soutar, A., and Isaacs, J. D. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. (U.S.) 72: 257-273.
- Spratt, J. D. 1975. Growth rate of the northern anchovy *Engraulis mordax* in southern California waters, calculated from otoliths. Calif. Fish Game, 61: 116-126.
- Stauffer, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. thesis. University of Washington, 213 pp.
- Taft, B. 1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. Limnol. Oceanogr. 5(3): 245-264.
- Tomlinson, P. K. 1970. A generalization of the Murphy catch equation. J. Fish. Res. Bd Can., 27: 821-825.
- Vrooman, A. M., and Smith, P. E. 1971. Biomass of the subpopulations of northern anchovy *Engraulis mordax* Girard. Mar. Res. Comm., Calif. coop. oceanic fish. Invest., Rep. 15: 49-51