

DISCRETE-TIME DIFFERENCE MODEL FOR SIMULATING INTERACTING FISH POPULATION DYNAMICS

C. ALLEN ATKINSON¹

ABSTRACT

The dynamics of interacting fish populations are modeled using a coupled set of discrete-time difference equations. The basic equations describe predator-prey and competitive relationships analogous to the first-order expressions used in standard differential equation models. Population births and aging are represented using a modified Leslie matrix. A spatial representation is also incorporated and consists of a number of separate compartments, each containing interacting population groups which can be interchanged between compartments during a given time period. The potential applicability of the discrete-time formulation is demonstrated via a simulation of the multispecies fish populations within the California Current during the sardine population collapse of 1930-60.

Numerous mathematical models of interacting multispecies fish populations are found in the literature (Riffenburgh 1969; Saila and Parrish 1972; May et al. 1979; Steele 1979). Depending on the nature of a particular ecosystem and the desired resolution level for its components and processes, these models can become extremely complex (Parrish 1975; Anderson and Ursin 1977; Laevastu and Favorite 1978). The major limitation in practical fisheries applications is the lack of sufficient field data to adequately estimate many of the model parameters, particularly the population interaction terms in complex multispecies models (Goodall 1972).

The two objectives in the present multispecies model development are 1) to establish a general mathematical form applicable to a variety of practical fisheries problems and 2) to provide an efficient computational tool for simulating complex multispecies systems. The latter feature has implications for dealing with the problem of model parameter uncertainty via specialized Monte Carlo and nonlinear programming procedures as discussed by Atkinson (1985).

The proposed formulation consists of a unique set of discrete-time difference equations that describe first-order dynamic processes affecting some arbitrary number of interacting fish populations at one or more trophic levels. The discrete equations are particularly well suited for computer implementation. There are no requirements for sophisticated integration routines (e.g., Runge-Kutta, Adams-Moulton), and the equations have inherent numerical

stability. Difference equations are also compatible with fisheries data sets (e.g., eggs and larvae surveys) which are usually sampled seasonally.

The essential biological processes represented in the model are spawning, growth, mortalities, age class structure, nonuniform spatial distributions, and migrations. Certain of these features, such as spawning, sexual maturation, and migrations, are often most conveniently described in a discrete form as assumed in the model. Seasonal time steps are natural increments for consideration as the values of appropriate model parameters can then be easily changed to relate seasonal fish behavior.

The mathematical details of the discrete-time difference model are developed below. The special problem of estimating model parameters in practical applications is also briefly discussed. The dynamics of the California Current fish populations are then modeled and simulation runs performed corresponding to the period of the sardine collapse in 1930-60. Comparisons are made between the simulation results and the actual (estimated) population responses.

DEVELOPMENT OF THE DISCRETE-TIME DIFFERENCE EQUATIONS

The dominant first-order ecological processes affecting fish populations are modeled by discrete-time difference equations. For convenience in the mathematical development, these processes are assumed to occur in the following sequence during a given time period: 1) individual growth and mortalities; 2) spatial redistributions of the surviving members; and 3) births and age class changes of the surviving,

¹System Science Applications, Inc., 121 Via Pasqual, Redondo Beach, CA 90277.

redistributed populations. Consistent with the first-order nature of the formulas, certain simplifications are expected to be incorporated in the ecological representation including implicit modeling of lower trophic levels (e.g., phytoplankton and zooplankton) and functional groupings of less important species as competitors, predators, and prey.

Growth and Mortalities

First-order differential equations of the following general form are typically used to describe the growth and mortalities of a population P_i under competitive and predator-prey influences with itself and other populations:

$$\frac{d P_i}{d t} = (r_i - u_i P - v_i P + w_i P) P_i \quad (1)$$

where r_i = survival/growth parameter
 P = population vector
 = $(P_1, P_2, \dots, P_i, \dots, P_n)$
 u_i = competition coefficient vector
 = $(u_{i1}, u_{i2}, \dots, u_{ii}, \dots, u_{in})$
 v_i = predation coefficient vector
 w_i = prey coefficient vector.

The coefficient vectors u_i , v_i , and w_i contain appropriate zeros such that only the active interactions between populations are defined. (Note that vector multiplication is implied by the forms such as $u_i P$.) The competition terms correspond to the standard Gause model, while the predator-prey terms correspond to the simple Lotka-Volterra model (Pielou 1977). The population variables P_i can be expressed in units of either numbers of individuals or total biomass, with the coefficients defined accordingly.

Assuming a small time step (Δt) relative to the characteristic time of the system ($1/r$), a discrete-time approximation is found directly by integrating Equation (1) to give

$$P_i(\Delta t) = e^{r_i \Delta t} \cdot e^{-u_i P \Delta t} \cdot e^{-v_i P \Delta t} \cdot e^{w_i P \Delta t} \cdot P_i(0) \quad (2)$$

These exponential terms form the basis of the difference model. However, some modification and interpretation of terms is required in order to describe a general form appropriate over a range of population levels.

The most obvious inadequacy of Equation (2) is the positive exponential prey term, $e^{w_i P \Delta t}$, which gets increasingly larger as prey increases without ever reaching a saturation condition. A more ap-

propriate form is the predator feeding model given by Ivlev (1961):

$$F = F_{\max} (1 - e^{-\zeta P}) \quad (3)$$

where F is the predator feeding ration and ζ is an associated prey coefficient, assuming that this form can also be used to describe the predator's growth/survival as a function of prey density.

The proposed difference equation for expressing population growth and mortalities during a Δt time step is

$$P_i(t + 1) = S_i e^{-\alpha_i P} e^{-\beta_i P} (1 - R_i e^{-\gamma_i P}) P_i(t) \quad (4)$$

where S_i = maximum survival/growth rate per time period
 α_i = discrete form of competition coefficient vector
 β_i = discrete form of predation coefficient vector
 R_i = starvation mortality factor
 γ_i = discrete form of prey coefficient vector.

The terms in this generalized form need further discussion and interpretation.

The maximum survival/growth rate factor, S , accounts for population births (if single age class), growth (if biomass units), and certain mortalities such as fishing, disease, and old age. It also accounts for predatory deaths caused by populations not explicitly included in the ecosystem model. It does not account for predation, competition, and prey availability effects associated with the modeled populations, which are explicitly stated by the other terms of Equation (4). Maximum survival/growth is defined under ideal conditions when competition and predation influences are negligible and there is an abundant supply of prey.

The α competition coefficient is the exponential equivalent to the Gause term in Equation (1) and represents a basic damping factor inhibiting population expansion. Self-competition generally relates to the essential environmental resources such as food supply and habitat space. Additional intra-population effects can come into play at the extreme ranges of population densities to complicate this interpretation, such as decreased fecundity caused by crowding (Parrish 1975) and decreased birth rates at very low densities (May 1973). Competition between population groups involves considerations of niche overlap relative to the common resources for which they compete (May 1973). Active competition

interference effects may also be involved (Levine 1976; Vance 1978). Since my model deals only with first-order effects, the components of the coefficient vector α are defined as constants and assumed to be related to the dominant competitive mechanisms acting over the range of population densities expected in the simulation.

The β predation coefficient in Equation (4) corresponds to the Lotka-Volterra term in the differential equation and implies unlimited attack capacity per predator (May 1973). Relative values of these vector components reflect the comparative attack rates of the different predators in the model. The effective β coefficients perhaps should be reduced when there are relatively few predators compared with the size of population P_i because of saturated feeding. However, predation is probably a secondary factor under these conditions as competitive limitations will tend to dominate. Based on first-order arguments, constant β components are assumed to apply over a reasonable range of predator densities. Leslie and Grower (1960) make a similar assumption in the prey equation of their two-component predator-prey model. Their predator response equation, on the other hand, saturates at high relative prey levels as in the present model.

The prey form, represented in Equation (4), reflects Ivlev's form (Equation (3)) and implies some upper bound survival/growth rate under abundant prey conditions. The present form also incorporates a starvation mortality parameter, R , that describes a worst case condition without prey. This parameter would typically equal one unless the Δt time step is short or an alternative food source not explicitly included in the modeling is available to sustain the population.

Component magnitudes of the prey coefficient vector, γ , relate differences in the relative efficiency with which alternative prey are captured and utilized for predator growth and/or survival. At similar prey densities, a predator may utilize different capture methods and feed at higher or lower rates depending on the size and behavioral characteristics of a particular prey (Parsons and Takahashi 1973). Note, however, from the form of the exponential prey term in Equation (4), that any one sufficiently abundant prey population can satisfy the predator feeding requirement.

Finally, in comparing the present development with traditional fishery models, note that Equation (4) can be directly related to the single species recruitment models of Ricker (1958) and Beverton and Holt (1957) if the time step is defined as the maturation time between spawning and recruit-

ment. Also, a comparable fishing term can be broken out of the survival/growth parameter as follows:

$$S = S_f S_0 \tag{5}$$

where S_f is the fishing survival rate and S_0 incorporates the remaining survival/growth effects. A corresponding fishing mortality rate, f , can be defined and related to fishing effort, E_f , as in the Beverton and Holt (1957) model:

$$f = \frac{-\ln S_f}{\Delta t} = \frac{\epsilon_f E_f}{A_f} \tag{6}$$

where ϵ_f is the fishing efficiency and A_f is the fishing area. The general compatibility with traditional fishery models is stressed.

Spatial Redistributions

A simplified picture of fish stock migratory patterns during a typical life cycle is illustrated in Figure 1. Adult fish move from the feeding grounds to the spawning grounds and return; larval fish drift from the spawning to the nursery ground; and recruits join the adult stock on the feeding grounds. The seasonal timing of these events is quite regular as are the spatial regions to which the stock return during the cycle (Cushing 1975).

Large-scale spatial patterns will be represented in the model by a number of "boxes" or compartments, each with a defined size and each contain-

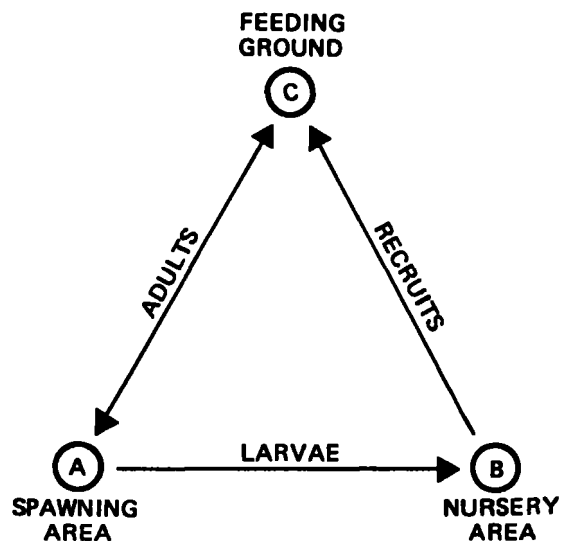


FIGURE 1.—Typical fish migratory pattern (from Cushing 1975).

ing segments of the various ecosystem populations. Population variables will now be uniquely assigned for each box and expressed in density units, such as numbers or kilograms per hectare. Spatial redistributions are assumed to occur during a given time period via migration, net drift, or turbulent dispersion. The resultant redistribution process is expressed by defining population transfers between boxes.

Spatial redistribution is applied to the surviving populations determined from Equation (4) and is described by

$$P_i^k(t + 1, 2) = \sum_{m=1}^M g_i^{mk} P_i^m(t + 1, 1) \quad (7)$$

where

- $P_i^k(t + 1, 2)$ = density of surviving population i in compartment k after spatial redistributions
- $P_i^m(t + 1, 1)$ = density of surviving population i in compartment m before spatial redistributions
- M = total number of spatial compartments
- g_i^{mk} = population i transport coefficient for the exchange from compartment m to compartment k .

The g coefficient defines the population fraction involved in the exchange with an adjustment to account for the difference in area or volume between compartments. If no transit occurs between compartments, the value of the respective coefficient is zero.

Birth and Aging Processes

The larvae and juvenile age classes of fish populations have markedly different survival rates and behavioral characteristics than do adult populations. These differences have potentially important first-order ecological consequences and are, therefore, of concern in the present model development.

A modified version of the Leslie matrix as presented by Lefkovitch (1965) is adopted here. Populations are grouped by stages which can be of unequal duration with no restriction to single year classes. The birth and aging matrix transform for N such stages is given by

$$\begin{bmatrix} P_{i1}^k(t+1,3) \\ P_{i2}^k(t+1,3) \\ P_{i3}^k(t+1,3) \\ \cdot \\ \cdot \\ \cdot \\ P_{iN}^k(t+1,3) \end{bmatrix} = \begin{bmatrix} b_{i1} & f_{i2}^k & f_{i3}^k & \cdot & f_{iN}^k \\ a_{i1} & b_{i1} & 0 & \cdot & 0 \\ 0 & a_{i2} & b_{i3} & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot & 1 \end{bmatrix} \begin{bmatrix} P_{i1}^k(t+1,2) \\ P_{i2}^k(t+1,2) \\ P_{i3}^k(t+1,2) \\ \cdot \\ \cdot \\ \cdot \\ P_{iN}^k(t+1,2) \end{bmatrix} \quad (8)$$

where

- $P_{ij}^k(t + 1, 3)$ = density of population i , age class j after accounting for births and aging in compartment k
- $P_{ij}^k(t + 1, 2)$ = density of population i , age class j before accounting for births and aging, but after accounting for spatial redistributions to compartment k
- a_{ij} = fraction of population i , age class j advancing to age class $j + 1$
- b_{ij} = fraction of population i , age class j remaining in age class j
- f_{ij}^k = fecundity function for population i , age class j in compartment k .

The coefficients a and b are functions of the size of the time step and the division of ages within the population. Equation (8) also implies a fixed age distribution within an age class, such as a uniform distribution.

The fecundity term, f , is a function of the population age class, as well as being time and space dependent. Explicit population crowding effects are neglected here because they would be comingled with the other density-dependent terms in Equation (4).

Composite Ecosystem Dynamics Equations

The above equations are combined and expressed by the general ecosystem dynamics model given below. The final surviving, redistributed, and aged population vector at the end of the time period has been redefined as $P(t + 1) = P(t + 1, 3)$.

$$\begin{aligned}
 P_{ij}^k(t+1) &= \sum_{n=1}^{N_i} \sum_{m=1}^M F_{ijn}^k(t) g_{in}^{mk}(t) S_{in}^m(t) e^{-\alpha_{in} P^n(t)} \\
 &\times e^{-\beta_{in} P^m(t)} [1 - R_{in}^m(t) e^{-\gamma_{in} P^m(t)}] \\
 &\times P_{in}^m(t) \tag{9}
 \end{aligned}$$

where m is summed over all spatial compartments M ; n is summed over all population subgroups N_i ; and $F_{ijn}^k(t)$ is defined by

$$F_{ijn}^k(t) = \begin{cases} f_{in}^k(t); & j = 1, n \geq 2 \\ b_{in}(t); & j \geq 1, n = j \\ a_{in}(t); & j \geq 2, n = j - 1 \\ 0 & ; \text{ otherwise.} \end{cases} \tag{10}$$

The model parameters in Equations (9) and (10) consist of maximum survival/growth rates (S), starvation mortality rates (R), transport terms (g), fecundity factors (f), age class changes (a and b), and population interaction coefficients (α , β , and γ). Time dependency is indicated for all parameters except the interaction terms. Space dependency is assumed to apply to all but age class changes and interaction terms. If the parameters are described by probabilistic functions, the model becomes a stochastic representation.

The above difference model represents a comprehensive description of coupled fish population dynamics and is proposed for general application. The form of Equation (9) is particularly well suited for computer implementation; it provides an efficient time-step simulation capability without requiring a numerical integration scheme. The model can be conveniently programmed on a mini-computer system and used to simulate complex multispecies population dynamics.

MODEL PARAMETER ESTIMATION IN PRACTICAL APPLICATIONS

The predictive power of the difference model in practical applications is obviously dependent on the knowledge of the ecosystem processes and the ability to estimate the associated parameters used in the modeling. This situation is true for any ecosystem model whether it consists of difference equations, differential equations, or any other formulation. In fact, I (1980) showed that difference equations representing multispecies populations can

be used to approximate the complex response modes of differential equations by relating parameters and choosing suitably small differencing time steps. I also showed that the difference model suffers from a similar sensitivity to the parameter estimates; the problem becomes more severe with increasing ecosystem complexity.

Certain parameters in either difference or differential equation models can be roughly estimated from field and/or laboratory studies. Examples include fecundity and growth rates of individual fish which can be observed directly. Population-level parameters, such as interaction and transport terms, are more difficult to estimate given the dynamic, wide-ranging nature of fish behavior. Even with extensive field sampling and the use of multivariate statistical techniques to sort out stochastic environmental features (Reid and Mackay 1968; Mobley 1973; Poole 1976), these parameter estimates will typically have a large degree of uncertainty.

The potential advantage of difference models in dealing with parameter uncertainty is related to their computational efficiency. When parameter uncertainty is represented in a probabilistic framework, Monte Carlo procedures can be applied to statistically describe population response characteristics based on large numbers of simulation runs. Probabilistic descriptions of parameter uncertainty can express both the inherent stochastic nature of the ecosystem and the parameter estimation error. One problem is that the stochastic ecosystem features, which are of primary interest, will typically be masked in the statistics by the large parameter estimation errors if realistic values for the latter are included.

I (1980, in press) used nonlinear programming (NLP) techniques to treat parameter uncertainty in dynamics models for a general class of ecosystem problem. My approach is summarized below; it has been used for resolving parameter estimates in the difference model application discussed in the section that follows.

An NLP problem can be stated in the following general form:

$$\begin{aligned}
 &\text{minimize} && f(x) \\
 &\text{subject to} && g(x) = 0 \\
 &&& x_0 \leq x \leq x_m
 \end{aligned}$$

where x is the variable vector with upper and lower bounds of x_0 and x_m , respectively; $f(x)$ is the so-called objective function; and $g(x)$ is a vector function of implicit constraints.

The problem scenario for my NLP formulation is that of predicting the dynamic response of ecosystem populations to a given perturbation. The response is characterized over some period of interest by the objective function which, depending on the particular problem, can be equated to average population numbers, final population levels, worst-year fishery catch, or some other dynamic feature. The ecological parameters in the dynamics model become the variables with bounds corresponding to the estimated parameter uncertainty range.

Implicit parameter constraints are added to the formulation based on available population history data, ecosystem stability observations, or any known or postulated relationships between parameters. The historical population data are substituted directly into the difference equations, or other assumed dynamics equations. In effect, such constraints force the response modes of the dynamics model to include past population observations, albeit ones that occurred under different (known) conditions than those of interest in the future. Stability observations also infer conditions on the dynamics equations and, hence, model parameters. However, there are practical issues in formulating such conditions. Lyapunov stability analysis techniques (Brogan 1974), while applicable to nonlinear system analysis, are not readily defined for the complex difference equations.

Efficient NLP computational procedures have been applied by me (1980) to solve the special ecosystem formulation described above. A search takes place through bounded parameter space for extreme (minimum and maximum) objective function values while maintaining the equality of the implicit constraints, i.e., the search proceeds on the "constraint surface" in parameter space. The key to an effective problem solution is the computational requirements of the dynamics model which is used in both constraint formulation and for evaluating the objective function at each search step. While the NLP approach does not give definitive estimates of individual model parameters, it strongly delimits their range of values via the interrelationships established by the implicit constraints (Atkinson 1980).

ECOSYSTEM SIMULATIONS USING THE DIFFERENTIAL EQUATION MODEL

The discrete-time multispecies dynamics model given by Equation (9) has been implemented as a FORTRAN computer program and used to perform a variety of simulations of theoretical and applied fisheries scenarios (Atkinson 1980). A case of some practical interest, the collapse of the sardine popula-

tion within the California Current region, will be described and used to demonstrate the potential model utility.

General Description of the Sardine Population Collapse off California

The waters of the California Current flow southward along the west coast of North America covering the general region are illustrated in Figure 2. While the California Current supports a diverse group of fish, the sardine fishery was by far the most important in the early years of this century until the dramatic collapse of the sardine population in 1930-60. A large increase in fishing effort took place during this time and apparently caused, or at least was associated with the sardine population collapse. The estimated history of the sardine population from 1930 to 1960 as derived by Murphy (1966) is shown in Figure 3.

Two sets of anchovy population estimates for the 1930-60 time frame are also presented in Figure 3. Although these data are confused by significant gaps and strong fluctuations from year to year, there does appear to be a significant population increase from levels in the 1940's and early 1950's to that near the end of the 1950's. Since the anchovy is the chief competitor of the sardine with similar food requirements and overlapping habitat boundaries, the general indication is that the anchovy replaced the sardine within the trophic structure (Murphy 1966; Gulland 1971). Murphy's (1966) 3-yr averaged data provides the clearest evidence of this increasing trend. Smith's (1972) yearly estimates show that the anchovy population actually declined from 1940-41 to 1950 (the next year in which data was available), before a sharp rise occurred. The significant variations evident in both anchovy and sardine data are probably caused by random environmental influences on recruitment success (Lasker 1978; Parrish et al. 1981; Methot 1983).

Soutar and Isaacs (1974) presented some interesting longer term data on the sardine and anchovy (plus other pelagic fish) as derived from sedimentary scale depositions in anaerobic basins off Southern California and Baja California. The deposition rate, which is averaged by 5-yr periods, provides a relative picture of the population variations over the last 150 yr (up to 1970). The data for the 1930-60 time frame indicate similar trends to that above, i.e., decreasing sardine levels and increasing anchovy levels. However, significant sardine and anchovy

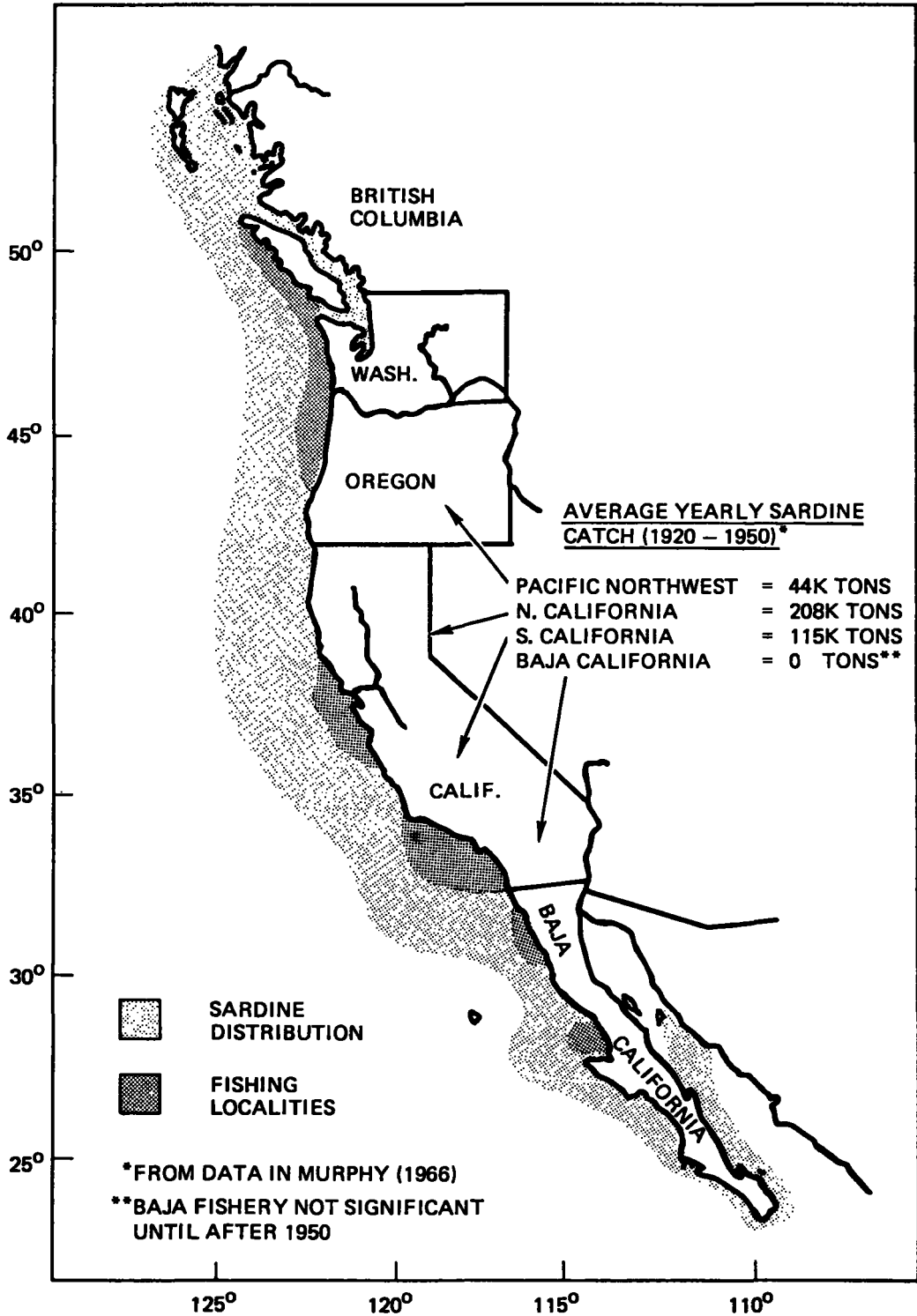


FIGURE 2.—Map of the California Current region showing sardine distribution and major fishing localities in the period before 1950 (from Murphy 1966).

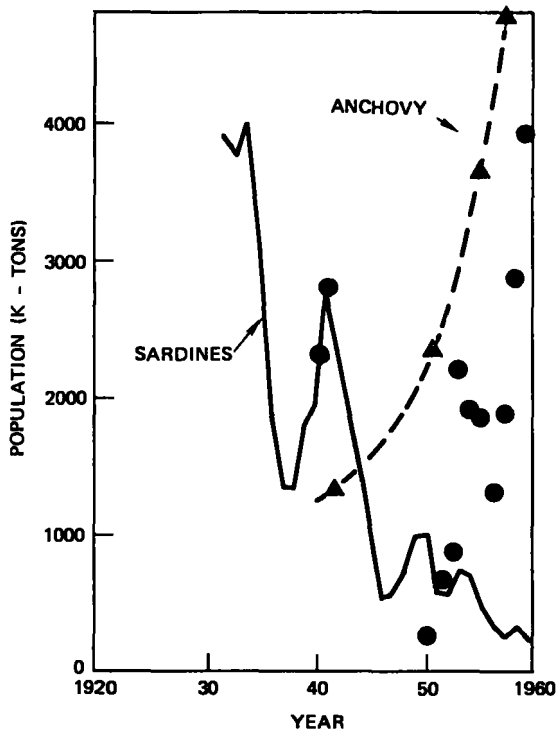


FIGURE 3.—Estimated adult populations of sardine and anchovy during the 1930-60 sardine collapse period. The solid line corresponds to yearly sardine estimates by Murphy (1966). The dashed line with triangles corresponds to 3-yr average anchovy estimates also by Murphy; the initial point is a 2-yr estimate with a data gap until 1951. The circles correspond to yearly anchovy estimates by Smith (1972); a data gap exists between 1941 and 1950.

variations are also evident in earlier times before fishing pressure became a significant factor in the ecosystem. For example, the sardine history showed extremely low levels in 1865-80 comparable to the levels after 1940. The earlier anchovy record, while also having periods of relatively high and low sedimentation rate, appears to have been at consistently higher levels before 1930-60, even higher than the recent increase of the late 1950's. Soutar and Isaacs (1974) stated that relatively unproductive conditions have apparently existed for the past 30 yr or so and have generally affected fish populations of the California Current.

Model Formulation

The waters of the California Current region, with their chemical and biological constituents, can be viewed as an ecological system (Sette 1969). The present model focuses on the sardine and anchovy

subsystem defined by Riffenburgh (1969) and shown in Figure 4. While not a comprehensive description of this ecosystem, I use this representation to demonstrate the application of the difference model in a reasonably complex fishery situation. The sardine ecosystem will be simulated during the period from 1932 to 1952 spanning the years of the major sardine collapse.

The sardine population is divided into three age groups: larval-year stages, yearlings, and adults. The larval year is the most vulnerable period of the sardines' development during which it goes through many fundamental changes. The yearlings are the in-between stage to the sexually mature adult members of the population, which are defined to be 2-yr-olds and above. Early stages of the sardine feed on phytoplankton while the adults feed primarily on zooplankton (Huppert et al. 1980). The adults are also predators of their own larval stages and those of the anchovy as indicated in Figure 4.

The anchovy population is divided into two groups, larvae and adult, which have similar intergroup relationships and feeding habits to the corresponding sardine groups. Competitor and predator groups to the sardine and anchovy are defined as lumped assemblages, both encompassing a broad range of diverse fish species; the competitor group also contains many invertebrates. The pelagic fish competitors (e.g., jack mackerel) are assumed to behave similarly to the sardine and anchovy except that some of the larger members feed on the sardine yearling stage (Riffenburgh 1969). The predators (e.g., hake and baracuda) feed on the adults of the sardine-anchovy-competitor trophic level and also have other prey that have been decoupled from the modeled subsystem. Phytoplankton and zooplankton groups are modeled implicitly as carrying capacity terms.

Additional model assumptions are that 1) spatial features are not critical (i.e., one spatial compartment is used), and 2) seasonal effects can be ignored (i.e., a yearly time step is defined). These two assumptions are probably not justifiable in the time period after 1950 or so, because of the shift of dominance from the northern sardine subpopulation to the southern one. Important differences in such factors as natural survival rates, maturation characteristics, and fishing effort exist for these subpopulations (Murphy 1966).

Discrete-Time Difference Equations

The difference model representing the seven interacting populations of the sardine ecosystem is pre-

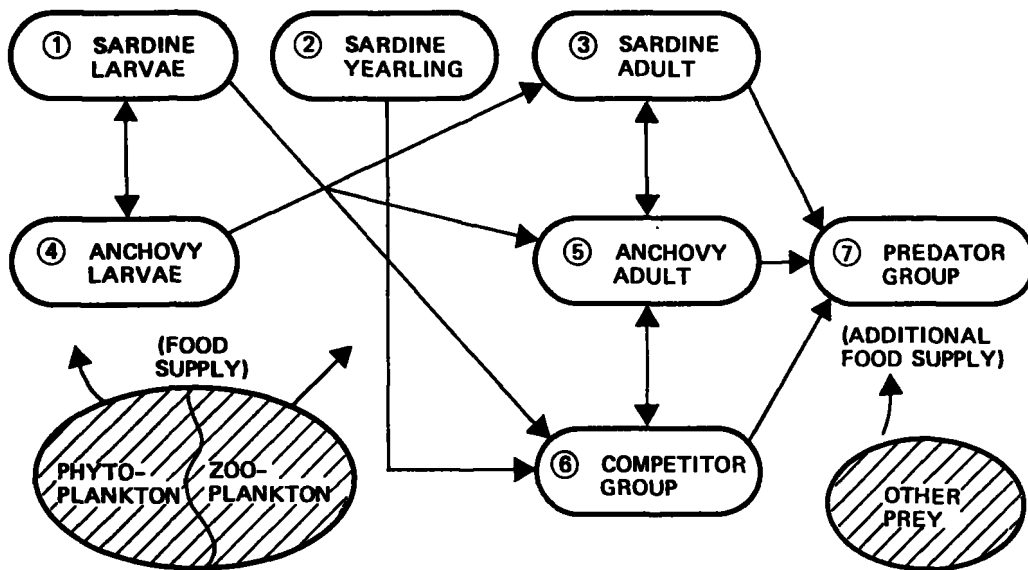


FIGURE 4.—Schematic showing interactions between sardine ecosystem groups as modeled by Riffenburg (1969). Competitive relationships are indicated by the connecting lines with dual arrowheads, while predator-prey relationships are defined by arrows pointing to the predator.

sented in Table 1. These equations reflect the general form of Equation (9) for a single spatial compartment. Parameters are defined for all processes other than transport, including competition, predator-prey, survival/growth, births, and fecundity. These parameters are assumed to be independent of the year during the 1932-52 simulation period, except for 1) the sardine fishing rate, $\delta_3(t)$, and 2) a sardine larvae survival factor, $E_1(t)$. The latter are related to the parameters presented earlier by

$$\delta_3(t) = 1 - S_{f3}(t)$$

$$E_1(t) = S_1(t)/\bar{S}_1$$

where S_{f3} is defined in Equation (5) and \bar{S}_1 is the average (reference) sardine larvae survival rate during 1932-52. The time-varying fishing rate and larvae survival factor represent the "drivers" perturbing the ecosystem during the sardine collapse period. Time-varying representations may also be ap-

TABLE 1—Difference equations describing biomass dynamics of the sardine ecosystem populations. Note that age sub-groups are indexed as separate populations to simplify the nomenclature. Also, all populations in exponentials are assumed to be at time t .

Population 1 - sardine larvae	$P_1(t + 1) = f_3 S_{3,0} [1 - \delta_3(t)] \exp(-\alpha_{33}P_3 - \alpha_{35}P_5 - \alpha_{36}P_6) \exp(-\beta_{37}P_7) P_3(t)$
Population 2 - sardine yearling	$P_2(t + 1) = E_1(t) S_1 \exp(-\alpha_{11}P_1 - \alpha_{14}P_4) \exp(-\beta_{13}P_3 - \beta_{15}P_5 - \beta_{16}P_6) P_1(t)$
Population 3 - sardine adult	$P_3(t + 1) = S_2 \exp(-\alpha_{22}P_2 - \alpha_{25}P_5) \exp(-\beta_{26}P_6) P_2(t) + S_{3,0} [1 - \delta_3(t)] \exp(-\alpha_{33}P_3 - \alpha_{35}P_5 - \alpha_{36}P_6) \exp(-\beta_{37}P_7) P_3(t)$
Population 4 - anchovy larvae	$P_4(t + 1) = f_5 S_5 \exp(-\alpha_{53}P_3 - \alpha_{55}P_5 - \alpha_{56}P_6) \exp(-\beta_{57}P_7) P_5(t)$
Population 5 - anchovy adult	$P_5(t + 1) = S_4 \exp(-\alpha_{41}P_1 - \alpha_{44}P_4) \exp(-\beta_{43}P_3 - \beta_{45}P_5 - \beta_{46}P_6) P_4(t) + S_5 \exp(-\alpha_{53}P_3 - \alpha_{55}P_5 - \alpha_{56}P_6) \exp(-\beta_{57}P_7) P_5(t)$
Population 6 - competitor group	$P_6(t + 1) = S_6 \exp(-\alpha_{63}P_3 - \alpha_{65}P_5 - \alpha_{66}P_6) \exp(-\beta_{67}P_7) P_6(t)$
Population 7 - predator group	$P_7(t + 1) = S_7 \exp(-\alpha_{77}P_7) [1 - R_7 \exp(-\gamma_{73}P_3 - \gamma_{75}P_5 - \gamma_{76}P_6)] P_7(t)$

propriate for other population parameters such as anchovy larvae survival but are ignored here. The modeling emphasizes those features directly impacting the adult sardine population because it is the only population for which detailed data are available for making comparisons.

Initial Conditions: State of the Ecosystem

The sardine ecosystem will assumed to be in an approximate equilibrium state prior to 1932, ignoring random population fluctuations. The sardine population appears to be consistently near virgin levels for the few years that data are available before 1932 (Fig. 3), and I speculate that the other populations are at reasonably consistent levels as well. There is some justification for overall stability at the sardine-anchovy-competitor trophic level and the predator trophic level, if not for individual fish species or population groups (Sette 1969; Steele 1979).

Estimates of population biomasses prior to the 1932-52 collapse period were summarized by Atkinson (1980) from data given by Murphy (1966) and Riffenburgh (1969). The biomasses presented below correspond to the assumed equilibrium state at the start of a fishing year. A fishing year is defined to begin in the summer after the main spring spawning season of the sardine and anchovy.

- sardine larvae $\bar{P}_1 = 1,600$ kilotons
- sardine yearling $\bar{P}_2 = 300$ kilotons
- sardine adult $\bar{P}_3 = 4,000$ kilotons
- anchovy larvae $\bar{P}_4 = 400$ kilotons
- anchovy adult $\bar{P}_5 = 1,000$ kilotons
- competitors $\bar{P}_6 = 3,000$ kilotons
- predators $\bar{P}_7 = 2,000$ kilotons

The initial state in 1932 is also defined by this biomass vector, \bar{P} .

Parameter Estimation for the Sardine Ecosystem Model

First, I point out that the above model representation is not intended to be a comprehensive description of the sardine ecosystem or to have general application for predicting future population dynamics, at least not as developed here. However, it is proposed as a reasonable representation to demonstrate the similarity between simulated results and observed system dynamics during the 1932-52 time frame provided appropriate parameter estimates

can be determined. The value of the difference formation in dealing with the parameter uncertainty issue will be illustrated in the discussion below of parameter estimation procedures.

Two model parameters in the equations of Table 1 were estimated directly from available data in the literature (Murphy 1967; MacCall 1979; Clark and Phillips 1932; Huppert et al. 1980): adult sardine survival, $S_{3,0} = 1.40$ (excludes fishing mortality effects), and adult anchovy survival, $S_5 = 1.20$. The driver terms in the model, $\delta_3(t)$ and $E_1(t)$, were also estimated from available data during the simulation period. These terms could not, of course, be definitized without the benefit of present hindsight. In a predictive situation, such terms would generally have a large degree of uncertainty, because projected fishing pressure is highly speculative while larvae survival has a strong stochastic component. Here, however, the available data will be used to the extent possible to resolve model terms.

Estimates of sardine fishing parameter, $\delta_3(t)$, were derived from Murphy's (1966) data and are shown plotted in Figure 5. The simplified model used in the simulations ignores detailed yearly variations and focuses on the major trends. A linear increase is assumed during the period from a rate of about 0.1 in 1932 to a rate >0.4 in 1936. The fishing rate is assumed to remain constant for the remainder of the simulation period.

The assumed model for the sardine larvae survival term, $E_1(t)$, is presented in Figure 6 along with Sette's (1969) data from which it was derived. These data represent numbers of fish at age class two versus the year spawned. The survival rate model assumes that these observed fluctuations in the data primarily reflect random survival effects during the first year of life. $E_1(t)$ was obtained by normalizing Sette's data with respect to the spawning population biomass and defining a relative scale such that the integrated value over the 20-yr period from 1932 to 1952 was equal to one.

The remaining model parameters, which represent the great majority of those in the equations of Table 1, could not be directly estimated to any degree of accuracy from available literature data. Instead, these estimates were derived from the special nonlinear programming analysis of mine (1980, in press) mentioned previously. I treated these ecosystem model parameters as variables with upper and lower bounds reflecting their uncertainty ranges. The bounds established by me for the sardine ecosystem parameters were typically an order of magnitude. Implicit parameter constraints were

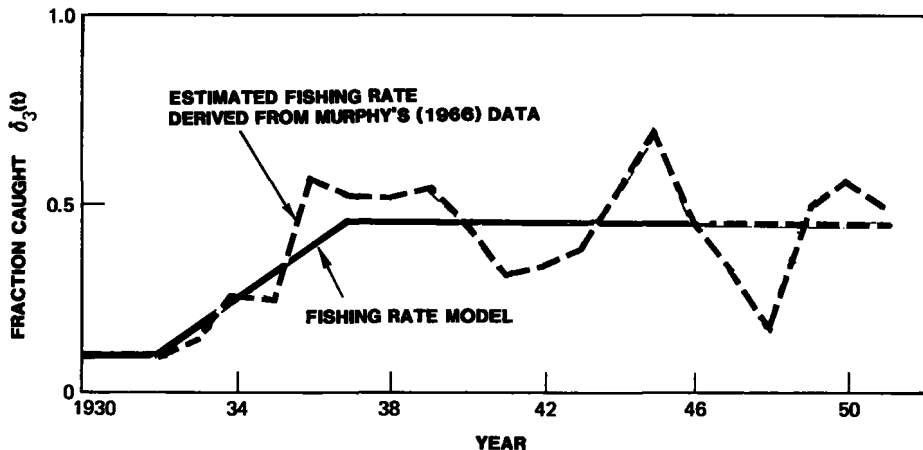


FIGURE 5.—Model of sardine fishing rate, $\delta_3(t)$, used in the sardine ecosystem simulations.

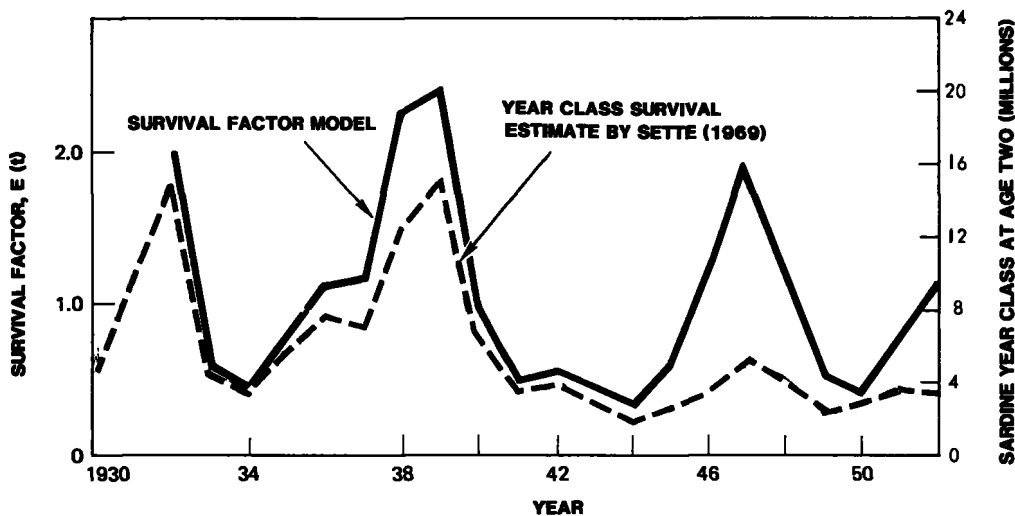


FIGURE 6.—Model of sardine larvae survival, $E_1(t)$, used in the sardine ecosystem simulations.

defined by the assumed equilibrium condition prior to 1932-52. Setting the time-varying fishing rate at its pre-1932 value ($\delta_3 = 0.10$) and fixing the time-varying larval survival factor at its reference value ($E_1 = 1.0$), a set of seven equality constraints were specified corresponding to the seven population equations in Table 1 with $P(t + 1) = P(t) = \bar{P}$. While there is still significant degrees-of-freedom in the model (i.e., more parameters than equality constraints), I was able to greatly resolve their values based on my nonlinear programming procedures.

The parameters in Table 2 represent the “nominal” estimates presented by me (1980) based on my

NLP analyses. In searching for minimum and maximum population response levels throughout bounded parameter space, a series of intermediate search steps were taken that produced suites of interdependent parameter values satisfying the pre-1932 equilibrium condition. Population response levels were equated to the average sardine population during the 1932-52 simulation period in this analysis. The selected nominal parameter suite in Table 2 gives response levels approximately midway between the determination of minimum and maximum levels.

Note that the parameter values in Table 2 were not derived from statistical procedures using the

TABLE 2.—Estimated values of the sardine ecosystem model parameters (from Atkinson 1980).

Population	Parameter type	Symbol	Nominal value	Population	Parameter type	Symbol	Nominal value
1 Sardine larvae	Survival/growth	S_1	7.26	5 Anchovy adult	Survival/growth	S_5	1.30
	Competition	α_{11}	5×10^{-6}		Competition	α_{53}	2.0×10^{-5}
	Competition	α_{14}	2.5×10^{-6}		Competition	α_{55}	3.0×10^{-5}
	Predation	β_{13}	7.6×10^{-4}		Competition	α_{56}	1.0×10^{-5}
	Predation	β_{15}	3.8×10^{-4}		Predation	β_{57}	1.0×10^{-4}
	Predation	β_{16}	7.6×10^{-5}	Fecundity	f_5	0.432	
2 Sardine yearling	Survival/growth	S_2	2.10	6 Competitor group	Survival/growth	S_6	1.65
	Competition	α_{22}	3.7×10^{-5}		Competition	α_{63}	5.0×10^{-5}
	Competition	α_{25}	1.8×10^{-5}		Competition	α_{65}	5.0×10^{-5}
	Predation	β_{26}	1.8×10^{-5}		Competition	α_{68}	5.0×10^{-5}
3 Sardine adult	Survival/growth	$S_{3,0}$	1.40	7 Predator group	Survival/growth	S_7	1.23
	Competition	α_{33}	1.5×10^{-5}		Mortality	R_7	0.5
	Competition	α_{35}	1.0×10^{-5}		Competition	α_{77}	5.2×10^{-5}
	Competition	α_{36}	5.0×10^{-6}		Prey	γ_{73}	2.5×10^{-4}
	Predation	β_{37}	1.0×10^{-4}		Prey	γ_{75}	2.5×10^{-4}
	Fecundity	f_3	0.468		Prey	γ_{76}	1.25×10^{-4}
4 Anchovy larvae	Survival/growth	S_4	0.50				
	Competition	α_{41}	2.5×10^{-6}				
	Competition	α_{44}	5.0×10^{-6}				
	Predation	β_{43}	1.5×10^{-4}				
	Predation	β_{45}	3.0×10^{-4}				
	Predation	β_{46}	3.0×10^{-5}				

population data during the simulation period (Fig. 3). The estimates are uncoupled from these data and, hence, reflect strictly a priori knowledge as would exist in applications where predictions are required. Furthermore, the parameter values are not proposed as best estimates of these parameters, but simply provide a consistent set of values for use in the simulation demonstration. The nonlinear programming approach of mine is structured in general to bound future ecosystem response characteristics given only a priori population data.

Ecosystem Simulations

The simulated sardine ecosystem histories are presented and compared with estimated sardine and anchovy population data in Figure 7. The adult sardine population simulation is in reasonably good agreement with the data of Murphy (1966) giving the many approximations and simplifying assumptions used in the modeling. The major dynamic features of the adult sardines decline are consistent, including the sharp rebounds associated with the favorable conditions for sardine larvae survival in 1938 and 1939 and again in 1947 (Fig. 6).

The simulated anchovy response in Figure 7, which ignores any fluctuating larvae survival component, appears to track the 3-yr averaged estimates of Murphy (1966). The anchovy population increases along with the competitor group to fill the ecological void in this trophic level. The predator biomass decreased slightly because the decline of the sardine

results in a less desirable food supply, at least according to estimated input parameters. Unfortunately, there are no available data for comparing with the predicted competitor and predator group responses.

Another simulation run was made to investigate the speculation that fluctuating larval survival rates, by themselves, might have caused the sardine collapse. The sardine fishing rate was held at the relatively low levels that existed before 1932 ($d_s = 0.10$), and the fluctuating larvae survival model in Figure 6 was applied. The resulting simulation run is presented in Figure 8 and shows the predicted history of the adult sardine population, along with that of the anchovy, competitor, and predator groups. The adult sardine population again fluctuates markedly but now remains at relatively high levels, in no apparent danger of collapsing. It would appear from these runs that the added fishing pressure is necessary to explain the actual event during this period.

CONCLUSIONS

A general set of discrete-time difference equations have been developed for use in simulating the important dynamic processes effecting fish populations, including

- interactions between competitors, predators, and prey
- birth, growth, and aging processes within a

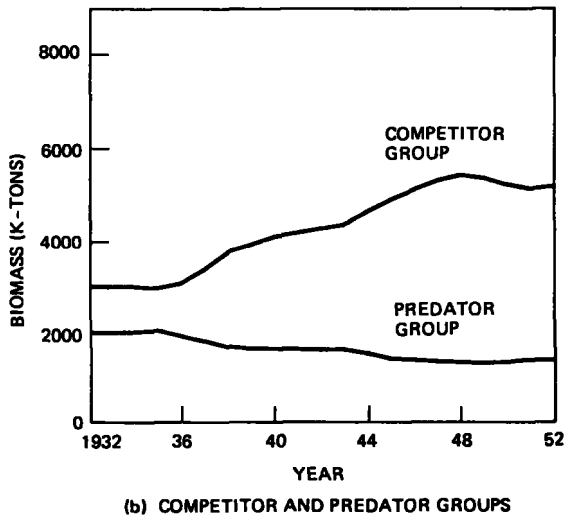
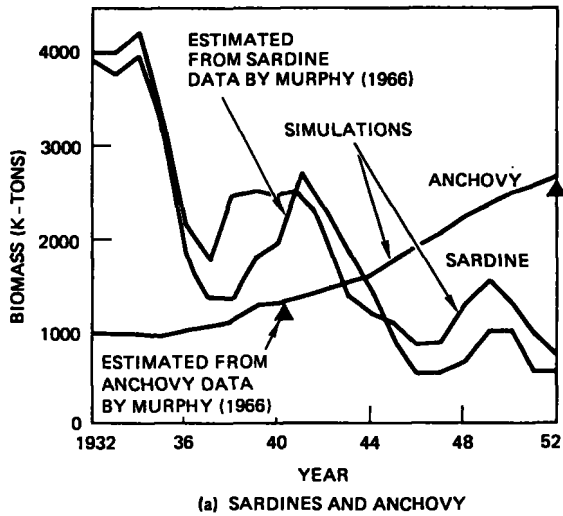


FIGURE 7.—Simulation run for assumed models of increased sardine fishing rate and fluctuating sardine larvae survival rate.

- single population group
- spatial and temporal variations.

The sardine subsystem within the California Current region was modeled using the multispecies difference model and simulations computed for the sardine's collapse period of 1932-52. Input drivers perturbing the system included representations of the increased sardine fishing pressure and the fluctuating sardine larvae survival rates during this period. Simulation results were shown to compare favorably with the available population history data. The increased fishing pressure was indicated to be

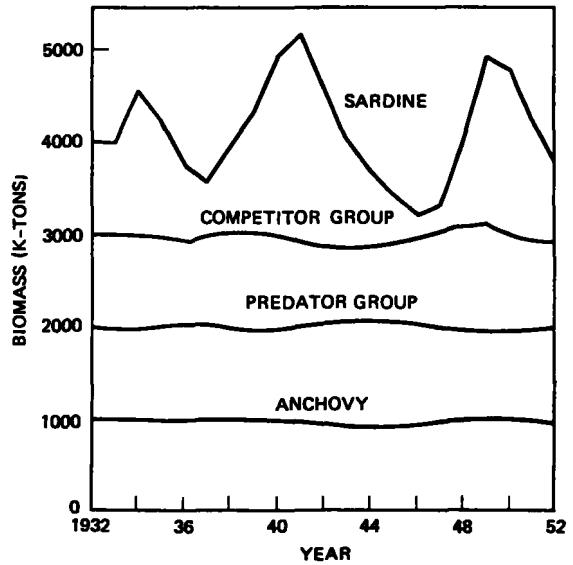


FIGURE 8.—Simulation run for assumed constant pre-1932 fishing rate but with fluctuating sardine larvae survival rate.

the fundamental cause for the sardine collapse; the estimated yearly fluctuations in sardine larvae survival could not by themselves have caused this sudden event.

These simulation results demonstrate the use of the discrete-time difference model as an efficient simulation tool. There appear to be many applications for the model in theoretical and applied multi-species fisheries studies.

ACKNOWLEDGMENTS

This work was based on a part of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree at the University of California, Los Angeles. S. E. Jacobsen, chairman of the dissertation committee, provided guidance and encouragement throughout these studies. D. A. Kiefer of the Department of Biological Sciences, University of Southern California, reviewed early versions of this paper and made helpful comments.

LITERATURE CITED

ANDERSON, K. P., AND E. URSIN.
1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Medd. Dan. Fisk. Havunders.* 7:319-435.

ATKINSON, C. A.
1980. Analysis of perturbed dynamic systems under param-

- eter uncertainty - a nonlinear programming approach with applications to marine ecosystems. Ph.D. Thesis, Univ. California, Los Angeles, 198 p.
- In press. A nonlinear programming approach to the analysis of perturbed marine ecosystems under model parameter uncertainty. Ecological Modeling.
- BEVERTON, R. J. H., AND S. H. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.). Ser. II, 19, 533 p. (See p. 21-135.)
- BROGAN, W. L.
1974. Modern control theory. Quantum Publishers, Inc., N.Y., 393 p. (See p. 262-283.)
- CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy in the California fishery. Calif. Fish and Game 38:189-207.
- CUSHING, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, 278 p. (See p. 85-247.)
- GOODALL, D. W.
1972. Building and testing ecosystem models. In J. N. R. Jeffers (editor), Math models in ecology. The 12th symposium of the British Ecological Society, Grange-Over-Sands, Lancashire, 23-26, March 1971. p. 173-183. Blackwell Sci. Publ. Lond.
- GULLAND, J. A.
1971. Ecological aspects of fishing research. Adv. Ecol. Res. 7:115-176.
- HUPPERT, D. D., A. D. MACCALL, G. F. STAUFFER, J. A. MCMILLAN, AND H. W. FREY.
1980. California's northern anchovy fishery: biological and economic basis for fishery management. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-1.
- IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 p.
- LAEVASTU, T., AND F. FAVORITE.
1978. Fluctuations in Pacific herring stock in the Eastern Bering Sea as revealed by ecosystem model (DYNUMES III). Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 177:445-459.
- 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.
- LEFKOVITCH, L. P.
1965. The study of population growth in organisms grouped by stages. Biometrics. 12:1-18.
- LESLIE, P. H., AND J. C. GROWER.
1960. The properties of a stochastic model for the predator-prey type of interactions between two species. Biometrika 47:219-234.
- LEVINE, S. H.
1976. Competitive interactions in ecosystems. Am. Nat. 110:903-910.
- MACCALL, A. D.
1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20, p. 72-82.
- MAY, R. M.
1973. Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton, NJ, 265 p. (See p. 13-171.)
- MAY, R. M., J. R. BEDDINGTON, C. W. CLARK, S. J. HOLT, AND R. M. LAWS.
1979. Management of multispecies fisheries. Science 205: 267-277.
- METHOT, R. D., JR.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741-750.
- MOBLEY, C. D.
1973. A systematic approach to ecosystems analysis. J. Theor. Biol. 42:119-136.
- MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34:1-84.
- PARRISH, J. D.
1975. Marine trophic interactions by dynamic simulation of fish species. Fish. Bull., U.S. 73:695-716.
- PARRISH, R. H., C. S. NELSON, AND A. BARUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceano. 1:175-203.
- PARSONS, T. R., AND M. TAKAHASHI.
1973. Biological oceanographic processes. Pergamon Press, Oxford, 186 p. (See p. 149-155.)
- PIELOU, E. C.
1977. Mathematical ecology. John Wiley and Son, N.Y., 385 p. (See p. 8-110.)
- POOLE, R. W.
1976. Empirical multivariate autoregressive equation predictors of the fluctuations of interacting species. Math. Biosci. 28:81-97.
- REID, M. H., AND R. S. MACKAY.
1968. A review and discussion of some methods for system identification and modeling. Med. Biol. Eng. 6:231-268.
- RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can. Bull. 119, 300 p.
- RIFFENBURGH, R. H.
1969. A stochastic model of interpopulation dynamics in marine ecology. J. Fish. Res. Board Can. 26:2843-2880.
- SAILA, S. B., AND J. D. PARRISH.
1972. Exploitation effects upon interspecific relationships in marine ecosystems. Fish. Bull., U.S. 70:383-393.
- SETTE, O. E.
1969. A perspective of a multi-species fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 13, p. 81-87.
- SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.
- SOUTAR, A., AND J. D. ISAACS.
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.
- STEELE, J. H.
1979. Some problems in the management of marine resources. Appl. Biol. 4:103-140.
- VANCE, R. R.
1978. Predation and resource partitioning in one predator-two prey model communities. Am. Nat. 112:797-813.