PAPER

A Nonlinear Biodynamic Model For Age-Structured Multicohort Populations

by

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Abstract

A second order nonlinear differential-equation model coupling abundance and population density is used to study the interacting dynamics of **n** cohorts. The model explicitly considers mechanisms that affect life stages: (i) resource assimilation rates, (ii) environmental carrying capacities, (iii) basal metabolic rates, (iv) optimal weights, (v) density-dependent mortality, (vi) density-dependent intraspecific competition, and (vi) density-dependent net fecundity and birth rates. The deterministic model exhibited limit cycles, and failed to converge to asymptotic stable equilibrium points, in some cases.

Introduction

Traditional population models are generally recognized as reliable demographic descriptors over a spectrum of stock classes. However, these mathematical models have embedded implicit assumptions which require constant life history parameterization,

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and do not consider intra-cohort and inter-population interactions. In contrast, all populations have interactions between individuals at any given age strata and total population level (Murdoch et al. 1975; Guckenheimer et al. 1977; Botsford & Wickham 1979; Rothschild & Mullin 1987).

Traditional density-independent stock assessment models (e.g., logistic assessment and dynamic pool) may be inadequate for expressing marine fishery stock ·dynamics because they either condense or completely neglect age-structured interactions and feedbacks (Ault, 1988). Their inadequacy stems further from neglect of numerous age classes and multiple spawnings per year recognized as adaptations that reflect the difficulty of ensuring survival in unstable physical or hostile marine environments (Rothschild 1986; Sinclair 1989). It is typically uncertain whether we are dealing with genuine "single species" situations given the scope of the population dynamics processes we are attempting to describe (May 1981), and that populations generally show little or no tendency to converge to expected equilibrium states.

There are a paucity of theoretical or research models on which to base expectations of population productivity where intraspecific and/or interspecific competition are involved. Most mathematical models of competition have been in large based on the work of Lotka and Volterra (Lotka 1925, 1932; Volterra 1928, 1938). In these equations, but two species, of population sizes N_1 and N_2, are considered to compete according to an extended Verhulst-Pearl scheme:

$$\frac{1}{N_i} \dot{N_i} = \rho_i - \mu_i \left(a N_1 + b N_2 \right) . \tag{1}$$

This system of equations ordinarily leads to extinction of one species and dominance of the other at some static population level (Kerner 1961; Haimovici 1979a,b). The most serious deficiency of analogs Eq(1) is that no recognition of age classes, nor any other vital statistic which may be pertinent, including time-lagged behavior, are made (Larkin 1963). Although the probability that interspecific and intraspecific competition influences the productivity of populations has been widely recognized, the difficulty has been in determining how to assess their importance.

In this paper we assume that demographic characteristics of most populations are inter-related, strongly density-dependent, and evolve continuously with respect to time. Our objectives are three-fold 1) to formally develop a mathematical model of continuous deterministic nonlinear age-structured multiple cohort interactions and interdependencies, 2) to derive a dynamic numerical model to simulate the system of equations, and 3) to elucidate the properties of the mathematical model for single

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multicohort populations as a first step towards understanding what is going on and how these systems are expected to evolve with respect to time and perturbations.

Background to Study

There is a tendency among many population dynamicists to interpret apparently erratic data as either stochastic "noise" or random experimental error. Another possibility is that some simple deterministic models can give rise to apparently chaotic dynamics (May & Oster 1976; Thompson & Stewart 1986; May 1987; Briggs 1987; Grebogi et al. 1987; Giollub & Baker, 1991) (see Figure 1). That is, the variability observed is the result of perfectly deterministic underlying dynamics that lead to stochastic results.

Determinants of abundance in multi-species, multi-age group population environments may be more well defined by population interactions among age-strata and species types. However, in general, there is insufficient quantitative knowledge about the manner in which the demographic characteristics of a given species changes with changes in population densities (Beverton & Holt 1957; Paulik 1972; Pielou 1977; Keyfitz 1977). Traditional management models may not be entirely suitable because interactions and dependencies among multicohort populations suggest the lack of asymptotic, stable-point equilibria, which may vitiate the traditional concepts. To further complicate matters, simultaneous harvesting of large numbers of species in multiple species systems may often manifest complex "catastrophic" system behavior whereby the system is discontinuously transformed to multiple equilibrium states or chaos as the harvest rates or environmental perturbations vary (Schaffer 1985).

In this paper we address three topics. First, we note the strong importance of addressing the multiple interactions that cohorts within a given population are believed to exhibit, and the possibility that these ideas could in fact be extended to a multiple species conceptual framework. In fact, our development of multiple cohort interactions are different from traditional Lotka-Volterra approaches. Secondly, the interactions within and between populations necessitate that we develop a physiological link in the equations. Lotka-Volterra dynamics are physiologically-independent between cohorts or populations. On the other hand, the von Bertalanffy equations are density-independent. We endeavored to develop a hybrid set of equations that link physiology (through the base weight equations) and density (through the base abundance equations) providing a new set of logistic density-dependent and metabolic constraints. While the new equations contained Lotka-Volterra like terms, they only come to bear through the interaction in the local cohort, and the possible interactions with others. Our model represents a diversion away from the more traditional equations, in that they are not exclusively dependent upon simple Lotka-Volterra or von Bertalanffy concepts, but in fact can be

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solved to return the logistic equations. The mathematical details of the model are developed below.

The Multiple Cohort Model

Consider a continuous model of a long-lived organism and its population dynamics, given the underlying desire to understand the individual ensemble mean characteristics of weight as well as the total population density of each age strata as a function of time. For continuously-breeding populations the intrinsic population dynamics structure consists of j-cohort life stages which exhibit dependence upon the timing of their entrance into the population. Each cohort life stage is affected by certain exogenous mechanisms: (i) the resource assimilation rate, (ii) the size- or age-specific metabolic requirements, (iii) environmental carrying capacities for each age strata, (iv) competition between cohorts, and (v) population densities within and among cohorts, all of which contribute to the composite populations increases or decreases. Assume that the mean individual weight, W_i, of the ith individual in the jth "age" ($\doteq$ size) class is governed by the balance between the competition for available environmental resources and the age-specific basal metabolic rate. Consider the general governing equation from the classic energy balance equations:

$$\dot{W}_i = (r_i - \alpha_i) W_i, \tag{2}$$

where a dot denotes differentiation with respect to time, and

r_i $\equiv$ resource assimilation or growth rate.

α_i $\equiv$ intrinsic basal metabolic costs rate.

The term r_i represents the intrinsic rate of increase which would be approached if no limitations were placed on the increase in weight of the respective cohorts if they were living in isolation. If we now consider that the age-specific weight of the ith individual can be influenced by its local cohort density, and the individual abundances of the other j cohort life stages, then the balance Eq(2) can be transformed to:

$$\dot{W}_i = W_i r_i - a_i W_i N_i - \sum_{i \ne j} b_{ij} W_i N_j - \alpha_i W_i. \tag{3}$$

If we set $K_i = r_i / a_i$ and $B_i = \sum_{i \ne j} b_{ij} / a_i$, we find that after a little rearranging:

$$\dot{W}_i = r_i W_i \{K_i - N_i - (B_i \cdot N_j)\} / K_i - \alpha_i W_i, \tag{4}$$

a_i $\equiv$ environmental carrying capacities (i.e., intraspecific checks on the rate of increase) for the ensemble individual mean characteristics.

Σb_{ij} $\equiv$ competition coefficient between ensemble individual

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i and the specific j cohort densities (i.e., provides for the effects of each cohort on its competitor). By definition $b_{ij} \geq 0 \; \forall_{ij}$.

N_i ≡ population abundance for the ith individual in cohort j.

N_j ≡ population abundance for the jth cohort.

The term, B_i, represents the ratio of how much damping is generated by a competitor relative to the damping effect that a cohort strength has on itself. The values of the interaction parameters, b_{ij}, represent fixed interactions between cohorts. However, changes in b_{ij}'s may be represented as a quasi-simulation of habitat modification, or perhaps population genetic changes (Larkin, 1963). Eq(4) has a competition form reminiscent of the Lotka-Volterra family of equations; however, the effect of competition is now expressed through the mean weight equation. Note that no provision has been allowed for interspecific competition, a condition which may have importance in the analysis of tropical reef fish ecology and tropical multispecies fisheries. However, the interspecific competition feature can be accomplished by adding an averaged term, $-\Sigma\Sigma c_{ijk}(t)$, with the brackets to account for the j-cohort, k-species interactions. The basal metabolic costs term, $-\alpha_i W_i$, has been added which allows for the effect of physiological mechanisms. The linear parameterization is the simplest means of addressing the growing scientific acceptance that physiological processes play important roles in regulating fish growth, survivorship, and recruitment (Hoar et al., 1979, 1983; Caddy & Sharp, 1986 Ware).

We now endeavor to develop a simple population balance equation such that population growth can be represented as the outcome of the gains from births and/or recruitments which are offset by losses from all sources of mortality

$$\dot{N}_i = R_{ij} - Z_i N_i, \tag{5}$$

so,

$$Z_i = M_i \left(1 - \frac{W_i}{W_i^{\bullet}}\right) + F_i, \tag{6}$$

M_i ≡ instantaneous natural mortality for the ensemble individual of the jth cohort.

$W_i^{\bullet}$ ≡ maximum weight (biomass) for the ith aged (size) individual of the jth cohort.

F_i ≡ fishing and/or predatory pressure for the ith aged (size) individual of the jth cohort. Note that

tradeoff here is that while bigger fish at any given age may be less susceptible to natural mortality or predation, they are on the other hand more susceptible to fishing predation.

Eq(5) varies from standard fishery representation of the change in cohort abundance with respect to time because of the form of the recruitment term. The recruitment term allows communication between adjacent cohort population regions, as well as additions that may flow between strata to strata in terms of either births and/or immigration or emigration. The mortality term is also structured into an alternative form with endogenous and exogenous population forcing components, i.e.:

$$R_{i \cdot 0} = \sum_{j=1}^{n} \left(\sum_{i=1}^{m} f_{ij} \left(1 - \frac{W_i^* - W_i}{W_i^*} \right) \right),$$ (7)

R_{ij} ≡ instantaneous rate of recruitment from the jth to the ith population cell, which in the case for recruitment to the initial age becomes,

f_j ≡ fecundity of the jth age (size) class.

Fecundity per unit of parental biomass may be highly variable and dependent upon the nutritional state and size structure of the stock (Parrish et al., 1986). Eq(7) would imply that the ensemble weight of a specific jth cohort may be suboptimal which would allow for dependency of age-specific reproductive input on the density-dependent factors which influence growth. If weight is suboptimal then the average cohort reproductive value will decrease, while on the other hand if weight is supraoptimal, then the reproductive value of a cohort will increase accordingly. The question of recruitment to the adult population should properly be dealt with by writing down balance equations analogous to Eq(5) for the populations of all the various stages in the life history of the species concerned

$$\dot{N}_i = R_{ij} - \left[M_i \left(1 - \frac{W_i}{W_i^*} \right) + F_i \right] N_i.$$ (8)

The natural mortality then reflects the degree of metabolic stress the population undergoes reflecting endogenous constraints and provides the couple back to the mean weight equation. The biological mechanism for the density-dependent inter-age mortality could be viewed as competition for food and space in which young cannot compete favorably with older members of the population (Botsford & Wickham, 1979). The recruitment term provides the interrelation between age (size) groups. Eq(8) as written then allows for partial selection and partial recruitment, which includes density- and time-dependency. Rearranging the population derivative Eq(8) in terms of age-specific ensemble weight

$$W_i = W_i^\infty + \frac{W_i^\infty}{M_i}\left[\frac{1}{N_i}(\dot{N}_i - R_{ij}) + F_i\right].$$ (9)

Solving Eq(9) for the ensemble weight at age, taking the derivative with respect to time and calling M_i time and age constant and expressing everything else a function of time leads to

$$\dot{W}_i = \frac{W^\infty_i}{M_i}\left[\frac{1}{N_i}\left\{(\ddot{N}_i - \dot{R}_{ij}) - (\dot{N}_i - R_{ij})\left(\frac{\dot{N}_i}{N_i} + \frac{\dot{M}_i}{M_i}\right)\right\} + \dot{F}_i - \frac{\dot{M}_i F_i}{M_i}\right].$$ (10)

now substituting Eq(9) into Eq(4) gives

$$\dot{W}_i = \frac{r_i}{k_i}\left(W_i^\infty + \frac{W_i^\infty}{M_i}\left[\frac{1}{N_i}(\dot{N}_i - R_i) + F_i\right]\right)\{K_i - N_i - B_i N_j\} - \alpha_i\left(W_i^\infty + \frac{W_i^\infty}{M_i}\left[\frac{1}{N_i}(\dot{N}_i - R_i) + F_i\right]\right),$$ (11)

and the derivative of weight Eq(10) into the right-hand side of Eq(11) leads to the full equation for population density yields

$$\frac{W^\infty_i}{M_i}\left[\frac{1}{N_i}\left\{(\ddot{N}_i - \dot{R}_{ij}) - (\dot{N}_i - R_{ij})\left(\frac{\dot{N}_i}{N_i} + \frac{\dot{M}_i}{M_i}\right)\right\} + \dot{F}_i - \frac{\dot{M}_i F_i}{M_i}\right] =$$

$$\frac{r_i}{k_i}\left(W_i^\infty + \frac{W_i^\infty}{M_i}\left[\frac{1}{N_i}(\dot{N}_i - R_i) + F_i\right]\right)\{K_i - N_i - B_i N_j\} - \alpha_i\left(W_i^\infty + \frac{W_i^\infty}{M_i}\left[\frac{1}{N_i}(\dot{N}_i - R_i) + F_i\right]\right).$$ (12)

With some reorganization of Eq(13) let the forcing term, f, be represented as

$$f = \frac{W_i^\infty}{M_i}\left[F_i\left(r_i\left(1 - \frac{B_i N_j}{K_i}\right) - \alpha_i\right) + \frac{r_i R_i}{K_i} + \frac{\dot{M}_i F_i}{M_i} - \dot{F}_i\right] + W_i^\infty\left[r_i + r_i\left(1 - \frac{B_i N_j}{K_i}\right) - \alpha_i\right].$$ (13)

Terms will be by definition independent of N_i, but contain forcing by the deterministic parameters and the specific densities of the competing N_j cohorts. Finally, the j-dimensional differential equation is written as

Substituting for the constant terms within age strata and replacing B_i by Eq(5) and K_i by r_i/a_i then

With substitution of the intra-strata constants and some

$$\ddot{N}_i\left[\frac{W_i^{\infty}}{M_i}\left(\frac{1}{N_i}\right)\right]$$

$$+\dot{N}_i\left[\frac{W_i^{\infty}}{M_i}\left(\frac{1}{N_i}\right)\left\{\frac{1}{N_i}(R_i-\dot{N}_i)-\frac{\dot{M}_i}{M_i}-r_i\left(1-\frac{B_iN_j}{K_i}\right)-\alpha+\frac{r_i}{K_i}\right\}\right]$$ (14)

$$+N_i\left[\frac{W_i^{\infty}r_i}{K_i}\left(1+\frac{F_i}{M_i}\right)\right]$$

$$+\frac{1}{N_i}\left[\frac{W_i^{\infty}}{M_i}\left(\frac{\dot{M}_iR_i}{M_i}-\dot{R}+R_i\left(r_i\left(1-\frac{B_iN_j}{K_i}\right)-\alpha_i\right)\right)\right]=f$$

$$A_1=\frac{W_i^{\infty}}{M_i}$$

$$A_2=r_i\left(1-\frac{B_iN_j}{K_i}\right)-\alpha_i$$

$$A_3=R_i$$

$$A_4=\dot{M}_i/M_i$$

$$A_5=A_4+A_2$$

$$A_6=A_1*\frac{r_i}{K_i}$$

$$A_7=W_i^{\infty}*\frac{r_i}{K_i}*\left(1+\frac{F_i}{M_i}\right)$$

$$A_8=A_1*(A_4*A_3)-\dot{R}+(A_3*A_2)$$

rearrangement of Eq(15)

$$\ddot{N}_i\left[A_1\left(\frac{1}{N_i}\right)\right]+\dot{N}_i\left[A_1\left(\frac{1}{N_i}\right)\left\{\frac{1}{N_i}(A_3-\dot{N}_i)-A_5\right\}+\frac{A_6}{N_i}\right]+N_i[A_7]+\frac{1}{N_i}[A_8]=f.$$ (15)

and further recognizing that Eq(16) is in the general form of the
2nd order nonlinear differential equation

$$\ddot{N}+B_1\dot{N}(aN+N)+B_2N=f.$$ (16)

Eq(17) can be recast as a second-order differential equation for a
specific ensemble individual i as

$$\ddot{N}_i=\frac{\dot{N}_i^2}{N_i}-\dot{N}_i\left[\frac{A_3}{N_i}-A_5+\frac{A_6}{A_1}\right]-N_i^2\left(\frac{A_7}{A_1}\right)+\frac{N_if}{A_1}-\frac{A_8}{A_1}.$$ (17)

Solution Schemes

As written above, the coefficients, r_i, K_i,..., etc., are all functions of the age of an organism. Therefore, if we choose the index i to follow the year class of the organism, the problem becomes a fairly complicated time integration for each year class. This can be viewed as a close parallel to the _Lagrangian_ problem of following the evolution of a particle's momentum in fluid dynamics given the forcing as a function of space-time. Although the analog is not exact, like the momentum equation for fluid flows, it is a simpler task to consider the evolution at a fixed point in "age" space. In the latter case the coefficients are fixed and the problem can be solved as single levels in age given the history of the other age classes. This can be done in three models:

(1)   A locally approximate solution given the N_j's from a "reasonable" selection of the overall solution space and then solve for a given N_j; or...

(2)   Specify the coefficients for all age classes and then integrate the entire set using an interactive approach; or...

(3)   Linearize and abstract the system (Schaffer, 1981).

Numerical Analysis in the Lagrangian Dynamics

For most continuous models analytic solutions are not possible, this is particularly true for highly complex sets of nonlinear equations. However, numerical analysis techniques are used to integrate the differential equations numerically, given specific values for the state variables at time zero (Carnahan and Wilkes, 1973). The evolutions must normally be modeled by nonlinear equations for which closed-form solutions are unobtainable. They may be readily integrated by computer algorithms, so that the response from given starting boundary conditions can be easily established. For any time step, $\Delta t = t \rightarrow (t + \Delta)$. we desire to calculate trajectory for any cell i in region j

$$N_i'(t+\Delta t) = N(t) + \zeta N. \tag{18}$$

Once we calculate the N_i's, we use the specific values to compute the vector of the ensemble weights, W_i, such that we can calculate specific ensemble abundances, which can then be computed directly in terms of density. The approach chosen to integrate the continuous second order nonlinear system of coupled equations was by rewriting specific dynamic difference equations for the numerical simulations. A numerical running scheme was designed to conduct the analysis and its development is outlined below.

Numerical Running Schemes

Two classes of processes motivate the numerical simulation approach. One process, moving the coupled system forward in time using the single time-step approach averages the particles position forward as a point between the present and the next time step. This system of equations can be unstable, particularly when using

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complex second-order equations. As a result, forward simulations are used to generate a vector of initial state values, given boundary conditions for the system. The vector of initial state values are then passed to the second process, a centered system of equations which averages the particles position over three time steps. Centered systems are intrinsically more stable in the evolution of time.

Given boundary conditions for a series of state values, the initial population state vector utilizing the state equations are generated in numerical simulation by the following system of forward difference equations. Let the <u>second-order forward difference</u> be generally represented by

$$\ddot{N}(t) = \frac{\dot{N}(t+\Delta t) - \dot{N}(t)}{\Delta t}, \tag{19}$$

and the <u>first-order</u> forward difference is

$$\dot{N}(t) = \frac{N(t+\Delta t) - N(t)}{\Delta t}. \tag{20}$$

Substituting the properly time-stepped Eq(21) into Eq(20) leads to the dynamic forward second difference equation:

$$\ddot{N}(t) = \frac{N(t+2\Delta t) - 2N(t+\Delta t) + N(t)}{\Delta t^2}, \tag{21}$$

$$N(t+2\Delta t) = \ddot{N}(t)\Delta t^2 + 2N(t+\Delta t) - N(t). \tag{22}$$

The form of the general second-order nonlinear differential equation can be rearranged to the second-order forward difference:

$$\ddot{N}(t) = f - B_1 \dot{N}(t)(a+N(t)) - B_2 N(t). \tag{23}$$

Substituting Eq(24) into Eq(23) gives

$$N(t+2\Delta t) = \Delta t^2 f - \Delta t^2 B_1 \dot{N}(t)(a+N(t)) - \Delta t^2 B_2 N(t) \\ + 2N(t+\Delta t) - N(t). \tag{24}$$

Now substituting for the first-order forward difference term on the right-hand side of Eq(25) results in the dynamic forward difference for simulation of the general form of the second-order nonlinear differential equations

$$N(t+2\Delta t) = \Delta t^2 f - \Delta t B_1 [N(t+\Delta t) - N(t)](a+N(t)) - \Delta t^2 B_2 N(t) \\ + 2N(t+\Delta t) - N(t). \tag{25}$$

Eq(26) and its variants can generate the initial population state vector utilizing the state equations, but due to the inherently unstable properties of Eq(26) in time evolution we now need to develop the centered relationships.

Given the initial population state vector utilizing the state equations cast as a forward difference we now desire to compute the

population state vector centered with respect to evolution in time, which are generally calculated as follows. Let the <u>second-order centered difference</u> be generally represented as

$$\ddot{N}(t) = \frac{\dot{N}(t+\Delta t) - \dot{N}(t-\Delta t)}{2\Delta t},$$ (26)

and the first-order centered difference

$$\dot{N}(t) = \frac{N(t+\Delta t) - N(t-\Delta t)}{2\Delta t}.$$ (27)

Substituting the appropriate representation of Eq(28) into Eq(27) leads to the general form of the dynamic centered second-order difference equation

$$\ddot{N}(t) = \frac{N(t-2\Delta t) - 2N(t) + N(t+2\Delta t)}{4\Delta t^2},$$ (28)

$$N(t+2\Delta t) = \ddot{N}(t)4\Delta t^2 + 2N(t) - N(t-2\Delta t).$$ (29)

If we now proceed similarly to the fashion we did in the previous section by substituting Eq(24) into Eq(30) we get

$$N(t+2\Delta t) = 4\Delta t^2 f - 4\Delta t^2 B_1 \dot{N}(t)(a+N(t)) - 4\Delta t^2 B_2 N(t)$$
$$+ 2N(t) - N(t-2\Delta t).$$ (30)

Substitution of Eq(28) into the right-hand side of Eq(31) leads to the dynamic centered difference solution for simulation of the general form of second-order nonlinear differential equations

$$N(t+2\Delta t) = 4\Delta t^2 f - 2\Delta t B_1 [N(t+\Delta t) - N(t-\Delta t)](a+N(t))$$
$$- 4\Delta t^2 B_2 N(t) - 2N(t) - N(t-2\Delta t).$$ (31)

Eq(32) allows centered time evolution of the second-order state equations. To compute each specific N(t+1) you require four previous time-stepped values: N(t), N(t-1), N(t-2), and N(t-3).

The Multicohort Numerical Simulation System of Equations

As evidenced by the development of the forward and centered systems of equations in the two previous sections we are now in a position to specifically write down the non-general coupled system of second-order nonlinear population density/abundance equations for multicohort-multispecies systems with age structure. Recasting Eq(18) as a second-order dynamical differential equation we have:

Building upon the arguments presented above Eq(33) can be written

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$$\dot{N}(t) = N(t)\left(\frac{f}{A_2}\right) - \frac{\dot{N}(t)}{N(t)}(A_7) + \frac{\dot{N}(t)^2}{N(t)} + \dot{N}(t)\left(A_3 - \left(\frac{A_4}{A_2}\right)N(t)\right) - N(t)^2\left(\frac{A_5}{A_2}\right) - A_6 \quad (32)$$

as a forward difference equation

$$N(t+2\Delta t) = \Delta t^2 N(t)\left(\frac{f}{A_2}\right) - \Delta t^2 \dot{N}(t)\left(\frac{A_7}{N(t)}\right) + \Delta t^2 \dot{N}(t)^2\left(\frac{1}{N(t)}\right) + \Delta t^2 \dot{N}(t)(A_3$$
$$- \left(\frac{A_4}{A_2}\right)N(t)) - \Delta t^2 N(t)^2\left(\frac{A_5}{A_2}\right) - \Delta t^2 A_6 + 2N(t+\Delta t) - N(t) \quad (33)$$

Thus, with the appropriate substitutions of Eq(21) into the right-hand side of Eq(34), the <u>forward in time</u> evolution simulations for each specific cohort can be calculated by:

$$N(t+2\Delta t) = \Delta t[N(t+\Delta t) - N(t)]^2\left(\frac{1}{N(t)}\right) - \Delta t[N(t+\Delta t) - N(t)]\left[\frac{A_3}{N(t)} - A_5 + \frac{A_6}{A_1}\right] -$$
$$\Delta t^2 (N(t))^2\left(\frac{A_7}{A_1}\right) + \Delta t^2 \frac{N(t)f}{A_1} - \Delta t^2\left(\frac{A^8}{A_1}\right) +$$
$$2N(t+\Delta t) - N(t) \quad (34)$$

Clearly, the potential instabilities associated with an equation as complex as Eq(35) which contains several squared first-order terms, in addition to its intrinsic second-order form, required development of the centered form of the set of coupled second-order nonlinear equations. Again, recalling the arguments presented above, Eq(33) can now be transformed into a <u>second-order nonlinear centered dynamical difference</u> equation:

$$N(t+2\Delta t) = 4\Delta t^2 N(t)\left(\frac{f}{A_2}\right) - 4\Delta t^2 \dot{N}(t)\left(\frac{A_7}{N(t)}\right) + 4\Delta t^2 \dot{N}(t)^2\left(\frac{1}{N(t)}\right)$$
$$+ 4\Delta t^2 \dot{N}(t)(A_3 - \left(\frac{A_4}{A_2}\right)N(t)) - 4\Delta t^2 N(t)^2\left(\frac{A_5}{A_2}\right) - 4\Delta t^2 A_6 + 2N(t) - N(t-2\Delta t) \quad (35)$$

With the appropriate substitutions of Eq(28) into the right-hand side of Eq(36) the centered equations with respect to time for the simulated time evolutions for each specific cohort can be calculated as:

$$N(t+2\Delta t) = 2\Delta t[N(t+\Delta t) - N(t-\Delta t)]^2\left(\frac{1}{N(t)}\right) - 2\Delta t[N(t+\Delta t) - N(t-\Delta t)]\left[\frac{A_3}{N(t)} - A_5 + \frac{A_6}{A_1}\right] -$$
$$4\Delta t^2 (N(t))^2\left(\frac{A_7}{A_1}\right) + 4\Delta t^2 \frac{N(t)f}{A_1} - 4\Delta t^2\left(\frac{A_8}{A_1}\right) +$$
$$2N(t) - N(t-2\Delta t) \quad (36)$$

The reader should note that there is one centered difference equation like Eq(37) for every jth cohort in the multicohort population (j = 1,...,n). Thus the coupled system of multicohort equations consists of a centered vector of state equations, one equation for each cohort.

Simulation of Second Order Nonlinear Differential Equations

The requirement remains for gaining insight into what can transpire in the evolution of a fisher system. Furthermore, in the possible ways the system can be influenced by the initial

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conditions set and ensuing levels of perturbations introduced over time. To understand the dynamical behavior of the coupled equation system specified herein, simulations were conducted to examine regions of stability or instability. The simulation system was parameterized for depiction of a fast growing, high mortality life history (Tables 1 and 2). Up to seven cohorts were followed in time evolution; however, the number could have arbitrarily been n-dimensional.

Simulation results here demonstrated classic limit cycles similar to those produced by the Lotka-Volterra family of equations which are referenced extensively in the non linear dynamics literature (Garrido, 1983; Webb, 1985; Thompson & Stewart, 1986; Briggs, 1987; Grebogi et al., 1987). Limit cycles were pronounced when an approximate form of Eq(2) was simulation utilizing an insignificant metabolic costs term. For a given parameterization, the cohorts increased in abundance and biomass relative to the magnitude of their intrinsic growth term. Dampening was introduced through density-dependence and was exacerbated by the interactions of local cohorts (Figure 2). IN all cases, the population approached long term equilibrium states; then experienced increasing oscillations which eventually settled into stable limit cycles. The population(s) then fluctuating regularly between capacity and zero states (Figure 2a). This condition was as characteristic of two cohorts as it was of five ore more cohorts (Figure 2b).

Several interesting features were exemplified by the stable sets of second order coupled nonlinear equations when they were modeled as a problem of Lagrangian dynamics. First, appropriate control cf the metabolic costs term induced the equivalent of the standard fishery exponential population mortality curves. No allowance was made in the time domain for recruit leakage from outside the cohort cell (Figure 3a). The general condition is intuitively appealing to the traditional oriented fishery demographer because of its semblance to the familiar frame of reference. Secondly, when recruitment communication between cohorts occurs both: (i) in the r_j term, and (ii) pulsed with respect to the $R(i,j)$ term, there is a shifting of dominance between cohorts in time evolution (Figure 3b). These "moving" cohorts are fully dynamic and can be affected locally by (i) their ability to capture available environmental resources; (iii) cohort carrying capacities, (iii) competition between other cohorts (iv) population densities within and among age strata, (v) age-specific continuous recruitments from the local population, and (vi) potential recruitments from sources extrinsic to the local population which are typical for many tropical fishery systems. Thirdly, older age groups may damp recruitments because of their predatory effect on the younger age strata. Numerically strong population age strata can completely dominate or cause catastrophic collapse of other age strata for specific ranges of time evolution (Figure 3 c, d). Non-equilibrium population dynamics are prevalent. Numerically strong cohort classes can completely

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dominate other age strata if the competition between the groups is intense enough. Thus, the parochial fishery manager attitude that a strong year class or cohort is productive for the fishery may be only marginally true from a current period yield perspective, but is completely inaccurate and fatuous when the effect of this strong cohort is to damp out other local cohorts as it passes through the fishery, negatively impacting the reproductive ability of the population to support itself. Subsequent cohorts are damped by a big cohort. The system is a complicated one with switching between states. Strong competition between cohorts can cause the ensemble weight at age to fluctuate significantly through time (Figure 4c). Exploitation reduces competition by decreasing specific cohort abundances, and further serves to stabilize the competition induced effects by increasing the ensemble weight per individual and the fecundity per age-specific unit of biomass. These findings contrast with Parris et al.'s (1986) conclusions which state that the reduction in age composition caused by heavy exploitation will greatly reduce the average fecundity per unit of biomass. Increased number of cohorts caused the total biomass to remain relatively stable and suggest a rationale for continuous cohort production in tropical regions.

The requirement for any fishery development or management program is to develop information as to what portion of the biomass is available for exploitation, and to allow a level of exploitation such that the population is steady-state or increasing. Utilizing the coupled set of equations developed here and a small enough parameter space it may be possible to develop an understanding where bifurcations and catastrophes exist. A population with the kinds of interaction terms addressed here when evaluated cohort by cohort appears as a bumpy ride. Looking at the aggregate population biomass (i.e. total biomass when you sum across cohorts) gives the appearance of being significantly damper than the individual cohorts. Formally some equilibrium may exists; however, pushing up and down on the system produces oscillations which indicate an unstable equilibrium. In dissipative systems where no interactions between cohorts exists you obtain the stable equilibrium as suggested by the traditional models discussed elsewhere (Ault, 1988; Ault & Fox, 1988 a, b, c). No matter what the initial distribution, without nonlinearities the population will contract to a fixed stationary distribution. However, stochastic dynamics apparently arise from simple and rigidly deterministic density-dependent mechanisms. This suggests that apparently chaotic dynamics may be ubiquitous, and that they can arise more readily in systems of higher dimensionality. The complicated behavior of simple deterministic models can have disturbing implications for the analysis and interpretation of biological data. Implications for ecological and fishery theory of high-order prior and aperiodic orbits are most unsettling (May & Oster, 1976). Many systems have shown a tendency to shift from many species to a few with increased exploitation over time. The limit cycles viewed in the Poincare sections here suggest that the cycles exist because of the interactions (Figure 5). The limit

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cycles shown by the present system of equations also suggests that the system has an unstable equilibrium,and that possibly bifurcations exist. In other words, the traditional assumptions regarding stable-point equilibrium point may be unrealistic, and formal equilibrium does not exist. Causes of cyclical fluctuations are of considerable theoretical interest (Botsford & Wickham, 1979), and when the species concerned are of economic importance they are of practical value as well. Knowledge of the specific mechanism causing cyclical fluctuations is necessary in formulation of effective fishery policy.

The differential equations presented herein can provide important rare insights into the study of realistic population dynamics and can assist determination of the effects of competition in harvested tropical multicohort - multispecies systems. The model included some of the simplest assumptions for the complex processes that tropical multispecies populations undergo. However, while the attempt was to model the system more appropriately, the assumptions utilized are clearly an extension of traditional methods which are consistent, justifiable and follow thermodynamic laws. The model was developed in an attempt to ask relevant questions of the parameters. Clearly this approach cannot be any less robust than the state of the present traditional models when applied to the tropical domain.

Future Scope of the Multicohort - Multispecies Model

While the analysis is not complete, its purpose has been to describe the process steps for multicohort nonlinear dynamic system modeling as a technique to study marine fish stock(s) population dynamics. A unique feature of the study is that it represents the first time an n-cohort, n-species relations have been coupled and solved as a system of equations. Beyond its intrinsic mathematical interest, the method may have considerable significance for advancing the study and understanding of structured populations under exploitation and their interaction with other fluctuating environmental variables. The model may be considered as depicting respectively the mode of action of: (i) density-independent, and (ii) density-dependent factors. Accepting these parallels, the model may demonstrate some widely discussed properties of population regulation mechanics. Models as complex as the one presented here are generally not used in fisher analysis because the amount of data needed to completely specify a complex model of a specific population is seldom available for a real fishery. Nonetheless, the intent here was to expose aspects of population behavior that may otherwise be occluded by the simplifications inherent in many traditional fishery models. Recognition that density-dependent mechanisms can produce cyclical and sometimes chaotic behavior in fish populations does have important implications for the way that certain kinds of data are analyzed. Not even in the most exact of the physical sciences are the coefficients of any model ever known with absolute precision. As such, the model of this section may then suggest a new tact for

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strategies based on current data, or new kinds of data that may be of paramount importance to truly resolve tropical multicohort-multispecies dynamics. Clearly, the model will provide more accurate views and predictions of system behavior as real data become available. Data specific to a particular system will be necessary to provide a more cogent understanding of the underlying nature and behavior of the system.

Multiple equilibria and strange attractor states appear to become prevalent features of biological systems when interactions such as competition and density-dependencies are explicitly modeled (May 1981, 1987). A logical extension of the multicohort model would be (i) to work out a principal components analysis that would estimate the most likely position of the system subjected to perturbations, (ii) to develop exact probabilities of system outcomes by performing a sensitivity analysis to parameter scalings and controlled perturbations in the deterministic model, and (iii) extend these to a Markov model for predicting behavior of the multicohort - multispecies system. In conclusion, the present formulation of intraspecific competition, together with an expanded version which incorporates interspecific competition, should be applied to a laboratory and/or a natural situation to test its usefulness for prediction. This approach may indicate the framework necessary for moving expert systems for fishery management from diagnostic analysis to optimal decision making.

Conclusions

Nonlinear model's principal value is that they allow consideration of the effects of crowding, resource limitation and interactions. While inclusion of nonlinearities in age-dependent population models increases their mathematical difficulty, it is also thought to enhance their reliability for physical description and behavior prediction (Webb 1985). The mathematical underpinnings of the subject discussed here are still rather esoteric by current standards in population dynamics; nonetheless, the central notions are elementary. Development of the model is pursued on the basis of the belief that more useful results are obtain from models that include essential, biologically realistic nonlinearities than those obtained from archaic linear models with arbitrary auxiliary constraints.

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List of Figures

A

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PARAMETER

(A) **Multicohort Population Equations**
TIME EVOLUTION

(B) **Multicohort Population Equations**
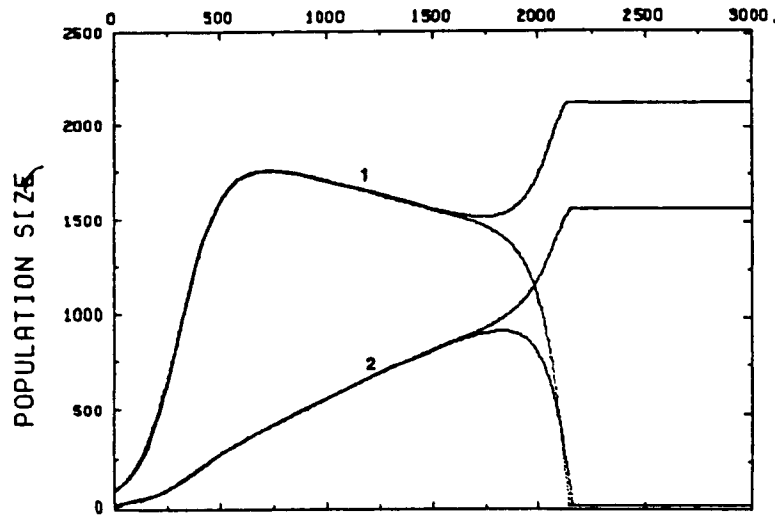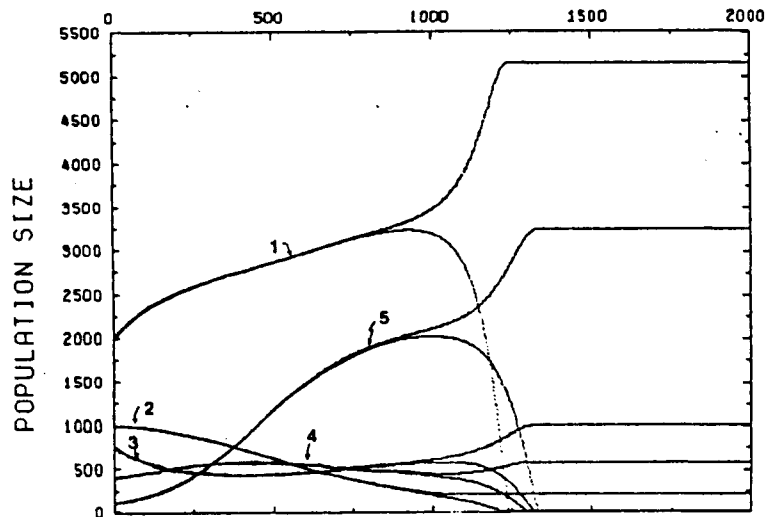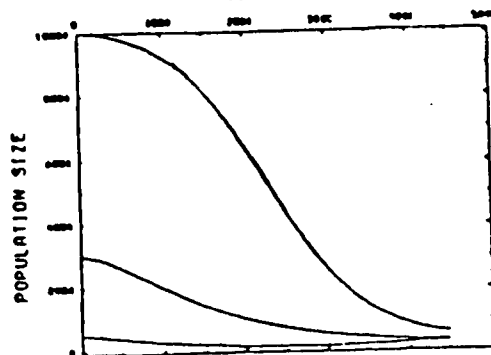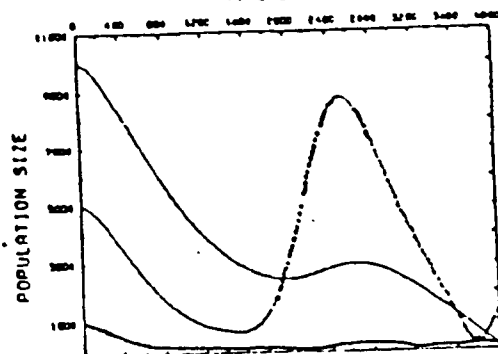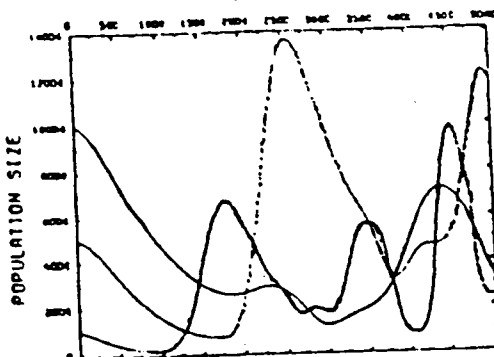TIME EVOLUTION

Figure #2

A. Multicohort Population Equations
TIME EVOLUTION

B. Multicohort Population Equations
TIME EVOLUTION

C. Multicohort Population Equations
TIME EVOLUTION

D. Multicohort Population Equations
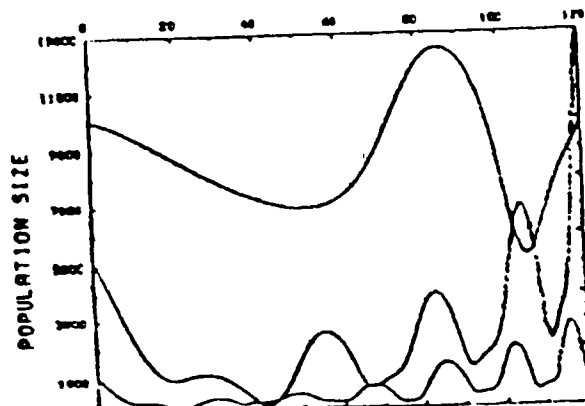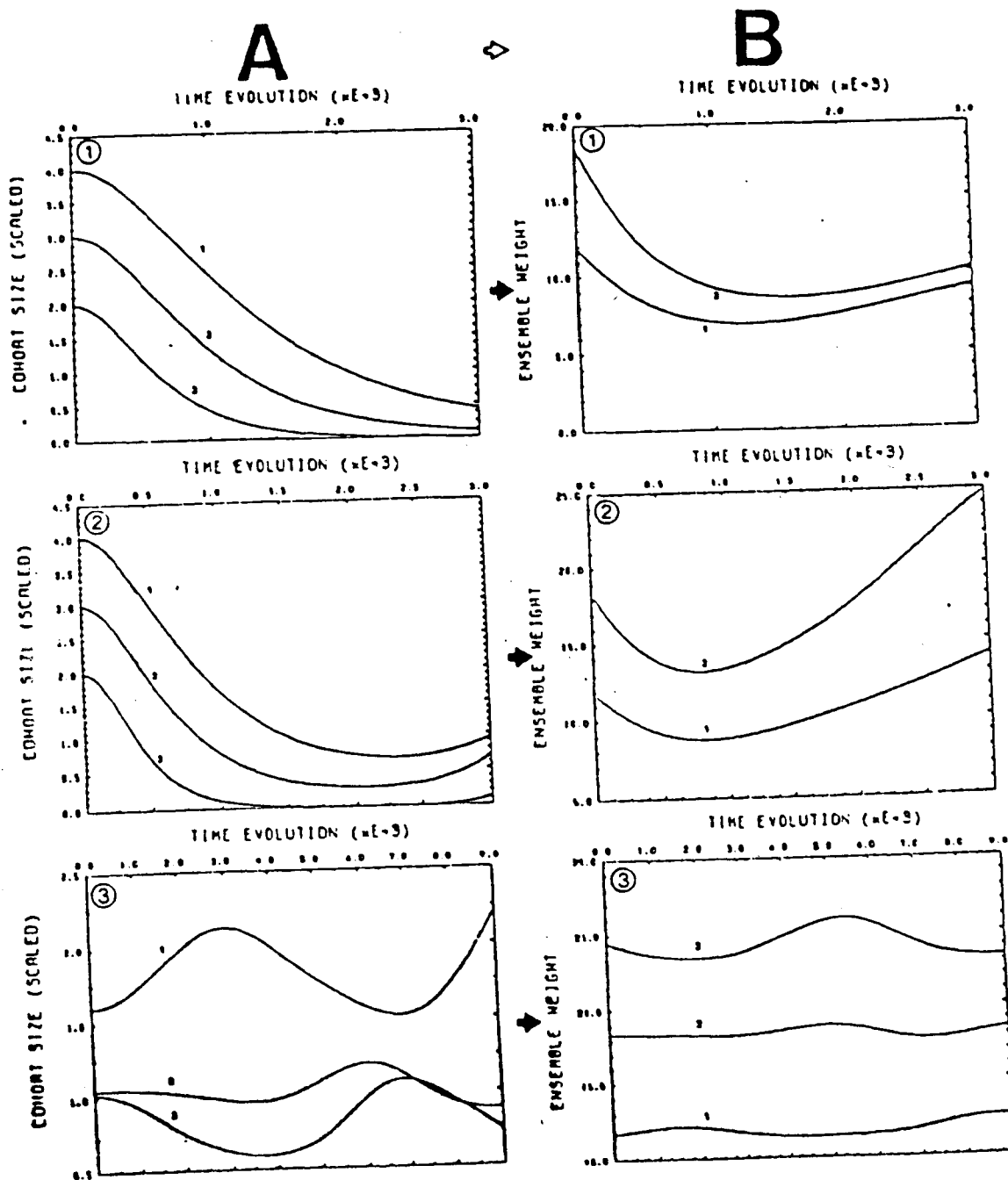TIME EVOLUTION (×100)
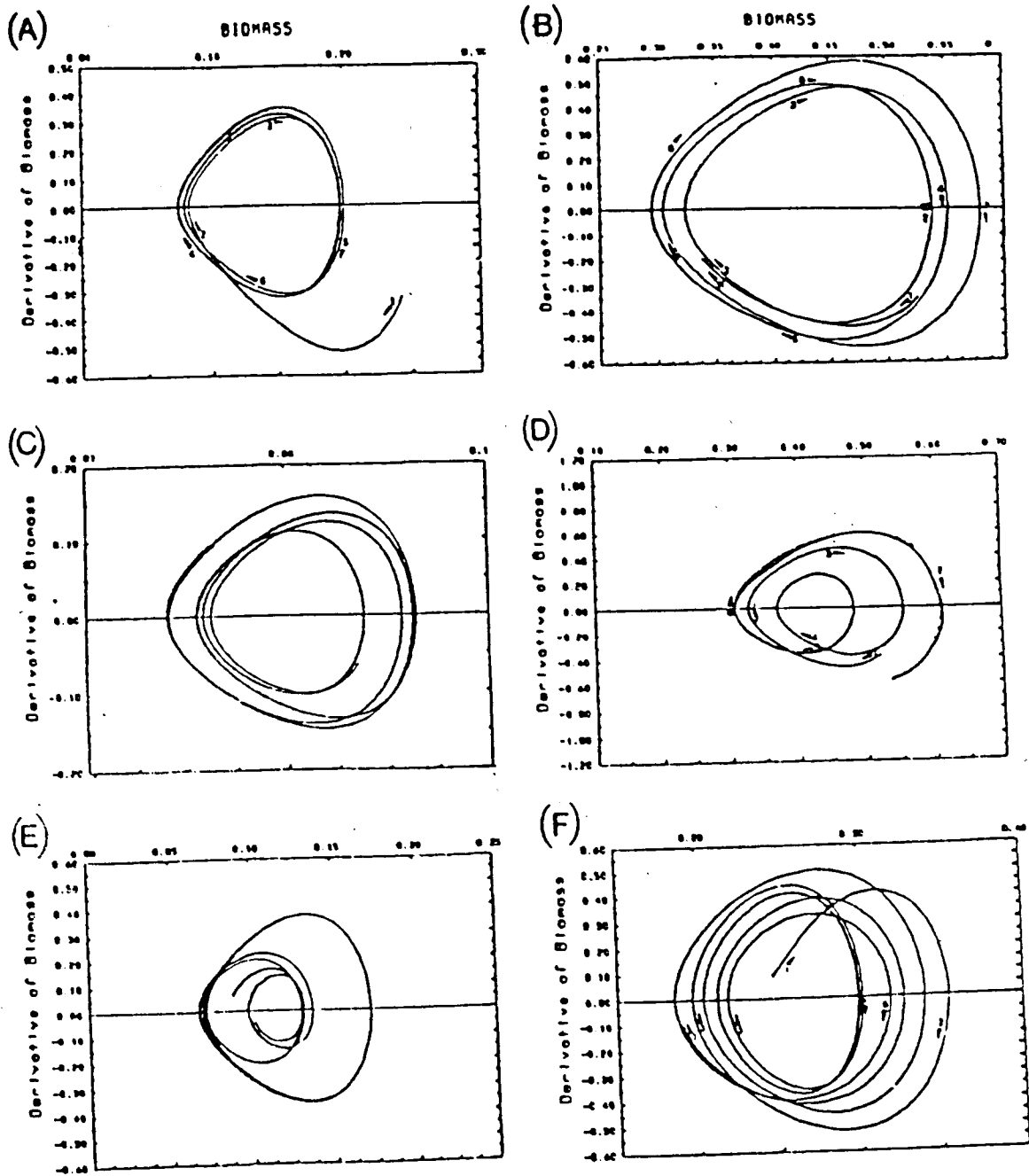
Figure 3

Figure 4

Figure 5

Table 1: Engrauloid annual rate parameters used in the continuous simulations of the second order nonlinear multicohort population model. Data from Tillman & Stadelman (1976), Hunter & Goldberg (1980), Hunter & Leong (1981), Parrish et al. (1986), Caddy & Sharp (1986).

Cohort	r(i)	a(i)	m(i)	$W_\infty(i)$	f(j)	a(i)
I	1.023	.0003500	1.1	11.81	1.00	0.077
II	1.012	.0007500	1.1	18.41	1.93	0.088
III	1.001	.0003913	1.1	24.50	2.93	0.099
IV	0.990	.0004444	1.1	29.68	3.88	0.110
V	0.985	.0004667	1.1	33.86	4.72	0.116
VI	0.979	.0005455	1.1	37.14	5.42	0.121
VII	0.974	.0006250	1.1	39.46	5.98	0.127

Table 2: Matrix of interaction b(i,j) coefficients. Rows are the cohorts affected while the columns are the cohorts who are causing the interaction.

AFFECTS

	1	2	3	4	5	6	7
1	XXX	.00025	.000005	.000001	.000001	.0000001	1.0E-8
2	.000125	XXX	.000125	.000125	.000125	1.0E-6	1.0E-7
3	.000225	.00035	XXX	.000125	.000025	1.0E-5	1.0E-6
4	.000	.00001	.001	XXX	.0001	.00005	1.0E-7
5.	.0001	.001	.001	.001	XXX	.00001	1.0E-5
6	.000	.000001	.00001	.0001	.0005	XXX	1.0E-4
7	.000	.000001	.00001	.0001	.0002	.00001	XXX