

Age-Structured Abundance/Density Equations for Tropical Multicohort Populations

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ABSTRACT

Traditional fishery management models may be inappropriate for assessing the highly dynamic tropical seas environment. The high dimensionality of intraspecies interaction and interdependencies suggests that the structure typical of many tropical multicohort populations have deleterious consequences on results obtained when constant parameterization and density-independent state interactions are assumed. Tropical multicohort populations may vitiate the simple traditional management models. To examine this phenomenon, the dynamics of any arbitrary number of n -interacting cohorts were modeled by coupled second-order nonlinear differential equations and a supporting numerical simulation scheme was developed. In the study even rigidly deterministic systems showed dynamic limit cycles. Certain populations showed little or no tendency to converge to expected equilibrium states. These features suggest that the traditionally assumed "asymptotic stable-point equilibria," may be unrealistic for some system states. Implications for assessments derived from traditional management models are discussed. Determinations of system state space probabilities are explored. This approach may indicate the framework necessary for moving expert systems for tropical fishery management from diagnostic analysis to optimal decision making.

INTRODUCTION

Traditional yield models have gained general recognition as being reliable for the description of population demographics over a spectrum of classes of temperate marine fishes. Embedded within these mathematical models are implicit assumptions requiring constant life history parameterization, low to nonexistent population interactions, and equilibrium states. Ault (1988) demonstrated that both the logistic assessment and dynamic pool classes of autonomous density-independent models may be inadequate for expressing the dynamics of tropical fishery stocks because they neglect or condense the age-structured interactions and feedbacks that structured populations actually exhibit (Murdoch *et al.*, 1975; Guckenheimer *et al.*, 1977; Botsford & Wickham, 1979). Because of the paucity of suitable data, very simple single-species models with minimal data requirements have been touted for providing policy support to fishery institution management in tropical regions (Munro, 1982; Pauly, 1982; 1983). This presents a major paradox because virtually no exploited fish population is ever in a steady state. Furthermore, the expected yield from a given single-species fishery cannot be entirely dissociated from the impact of the same stock on the abundance of its predators or food resources

(Caddy & Sharp, 1986). Concepts like yield-per-recruit may also be of dubious validity when recruitment is continuous, periodic and variable in time. In the development of a model for a continuously-breeding population, differences in the scales of events acting on the population should be reconciled. Gross misinterpretations of stock abundance and productivity may occur when cohort production is on a time scale significantly smaller than a year. Populations in these cases may show little or no tendency to converge to expected equilibrium state(s).

Although the probability that interspecific and intraspecific competition influences the productivity of fish stocks has been widely recognized, the difficulty has been in determining how to assess it. There are a paucity of theoretical or research models on which to base expectations of population productivity where intraspecific competition is involved. Mathematical models are typically of interspecific competition and have been based largely on the Lotka-Volterra equation (Lotka 1925, 1932; Volterra 1928, 1938). In these, but two species — of population sizes N_1 , N_2 — are considered to compete according to an extended Verhulst-Pearl scheme:

$$\frac{dN_1}{dt} = \rho_1 - \mu_1 (aN_1 + bN_2) \quad (1)$$

This ordinarily leads to the extinction of one species and dominance of the other at some static population level (Kerner, 1961; Haimovici, 1979a, 1979b). The most serious deficiency of this approach is that no recognition of age classes, nor any other vital statistic that may be pertinent, including time-lagged behavior, is made (Larkin, 1963).

This paper focuses on the observations that the demographic characteristics of tropical marine fish stocks are interrelated, strongly density-dependent, and evolve continuously with respect to time. The study's objectives are:

1. To mathematically model multiple cohort interactions and dependencies.
2. To understand the evolution of tropical multicohort fishery systems by developing a dynamic-systems numerical model that incorporates salient population features through attention to continuous, deterministic nonlinear age-structured methods.
3. To elucidate the properties of the model as a first step towards understanding what is going on and how multicohort populations evolve with respect to perturbations and time.

Background to Study

There is a tendency among many population dynamicists, and even the 'muddy boots' ecologists to interpret apparently erratic data as either stochastic "noise" or random experimental error. Another possibility is that some deterministic models can give rise to apparently chaotic dynamics (May & Oster, 1976; Thompson & Stewart, 1986; May, 1987) (Figure1).

Population interactions among age-strata may be important determinants of fish stock abundance in tropical multispecies environments. 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 and Holt, 1957; Paulik, 1972; Pielou, 1977; Keyfitz, 1977). Traditional management models may not be suitable for tropical environments because the interactions and dependencies among multicohort populations suggest that these populations may not have asymptotic, stable-point equilibria, and as such may vitiate the simple 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).

The principal value of nonlinear models is that they allow consideration for the effects of crowding, resource limitation, and interactions. While inclusion of nonlinearities in age-dependent population equation models increases their mathematical difficulty, it also enhances 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. The model is pursued based on the belief that more useful results are obtained from models that include essential, biologically realistic nonlinearities than those obtained from archaic linear models with arbitrary auxiliary constraints. The mathematical details of such a 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 mean characteristics of weight and density of each age strata and the entire population as a function of time. For continuously-breeding populations the intrinsic population dynamics consist of j cohort life stages which exhibit dependence upon the periodicity of their entrance into the population. Each cohort life stage is affected by certain exogenous mechanisms:

1. The resource assimilation rate
2. The size-or age-specific metabolic requirements

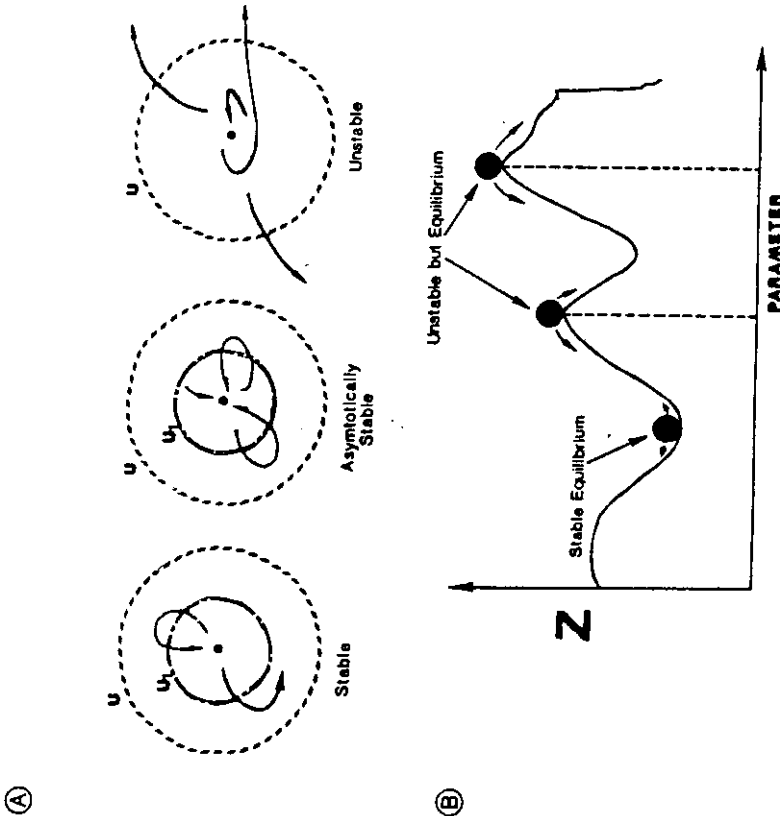


Figure 1. Depiction of stability and bifurcations of equilibria and cycles for n -dimensional system of differential equations. Panel (A) shows three phase portraits illustrating the character of Liapunov stability for an equilibrium state (following Thompson & Stewart, 1986): (i) *stable equilibrium* point where every nearby solution stays nearby for all future time, (ii) *asymptotically stable equilibrium* because all solutions tend to equilibrium as $t \rightarrow \infty$, and (iii) *unstable equilibrium* because perturbation may lead to multiple equilibria or chaos. Panel (B) characterizes the states of equilibrium portrayed in Panel (A) as a basketball on a mountain side. As the parameter spin increases, the system has an increasing propensity for becoming unstable.

3. Environmental carrying capacities for each age strata
4. Competition between cohorts
5. And population densities within and among cohorts, all of which contribute to composite populations increases or decreases.

Let's assume that the mean individual weight, W_i , of an individual in the i^{th} age (= size) class is governed by the balance between the competition for available environmental resources and the age-specific based metabolic rate. With these constraints, we start with the general governing equation from the classic energy balance, which can be written:

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

where a dot denotes differentiation with respect to time, and

r_i = resource assimilation or growth rate.
 α_i = 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 i^{th} individual can be influenced by its local cohort density and the individual abundances of the other j cohort life stages, then equation (2) can be transformed to:

$$\dot{W}_i = W_i r_i - a_i W_i N_i - \sum_{i \neq j} b_{ij} W_i N_j - \alpha_i W_i \quad (3)$$

If we set $K_i = r_i/a_i$, we find that after a little rearranging:

$$\dot{W}_i = r_i W_i \left\{ K_i - N_i - \left(\sum b_{ij} / a_i \right) \cdot N_j \right\} / K_i - \alpha_i W_i \quad (4)$$

Now define:

- a_i = environmental carrying capacities (*i.e.*, intraspecific checks on the rate of increase) for the cohort in lifestage i .
- $\sum b_{ij}$ = competition coefficient between ensemble individual 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_j = population abundance for the i^{th} individual in cohort j .

N_j = population abundance for the j^{th} cohort.

where $B_i = \sum b_{ij}/a_i; i \neq j$ (5)

The term B_i represents the ration of how much damping is generated by competing cohorts relative to the damping effect which cohort strength has on itself. The values of the interaction parameters, b_{ij} , represent fixed coefficients between cohorts, although changes in this parameter may be represented as a quasi-simulation of habitat modification, or perhaps population genetic changes (Larkin, 1963). Equation (4) has competition in a form reminiscent of the Lotka-Volterra family of equations. 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 intraspecific competition feature can be accomplished by adding an averaged term, $-\sum C_{ijk}(t)$, with the brackets to account for the j -cohort, k -species interactions. Note that a basal metabolic costs term has been added which increases the equation's ability to model physiological mechanisms and addresses the growing acceptance that physiological processes play important roles in regulating fish growth, survivorship, and recruitment (Hoar *et al.*, 1979, 1983; Caddy & Sharp, 1986).

We now endeavor to develop a fairly 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

$$\dot{N}_i = R_{ij} - Z_i N_i \tag{6}$$

Equation (6) varies from standard fishery representation of the change in cohort abundance with respect to time because of the added 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.*:

$$Z_i = M_i (W_i^* - W_i) + F_i \tag{7}$$

M_i = instantaneous natural mortality for the cohort in lifestage i
(here assumed time constant, *i.e.* $M = M_i$)

- W_i^∞ = optimal weight (biomass) for an individual of the i^{th} cohort.
 F_i = fishing and/or predatory pressure for the cohort in lifestage i .
 A tradeoff here may be seen: whereas bigger fish at a given age may be less susceptible to natural mortality or predation, they are more susceptible to fishing predation.
 R_{ij} = instantaneous rate of recruitment from j^{th} to the i^{th} lifestage cell, which in the case for recruitment to the initial age becomes,

$$R_{i=0} = \sum_{j=1}^n \left(\sum_{i=1}^m f_{ij} (W_j - W_j^\infty) \right) \quad (8)$$

with f_j = fecundity of the j^{th} 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). This would imply that the ensemble weight of a specific j^{th} 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 (6) for the populations of all the various stages in the life history of the species concerned.

$$\dot{N}_i = R_{ij} - [M_i (W_i^\infty - W_i) + F_i] N_i \quad (9)$$

The natural mortality then reflects the degree of metabolic stress the population undergoes reflecting endogenous constraints and provides coupling 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. Equation (9) as written then allows for partial selection and partial recruitment, which includes density – and time-dependency. Rearranging the population derivative (9) in terms of age-specific ensemble weight:

$$W_i = W_i^\infty + \frac{1}{M_i} [F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij})] \quad (10)$$

Solving (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:

$$\dot{W}_i = \frac{1}{M} [\dot{F}_i + \frac{1}{N_i} \{ (\ddot{N}_i - \dot{R}_{ij}) - \frac{\dot{N}_i}{N_i} (\dot{N}_i - R_{ij}) \}] \quad (11)$$

substituting (10) into equation (4):

$$\begin{aligned} \dot{W}_i = & \{ r_i (W_i^\infty + \frac{1}{M} [F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) - \dot{F}_i]) [K_i - N_i - B_i N_j] \} / K_i \\ & - \alpha_i (W_i^\infty + \frac{1}{M} [F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij})]) \end{aligned} \quad (12)$$

and substituting for the derivative of weight (11) into (12) the full equation is:

$$\begin{aligned} \dot{W}_i = & \frac{1}{M} [F_i + \frac{1}{N_i} \{ (\ddot{N}_i - \dot{R}_{ij}) - \frac{\dot{N}_i}{N_i} (\dot{N}_i - R_{ij}) \}] \\ = & \{ r_i (W_i^\infty + \frac{1}{M} [F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) - \dot{F}_i]) [K_i - N_i - B_i N_j] \} / K_i \\ & - \alpha_i (W_i^\infty + \frac{1}{M} [F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij})]) \end{aligned} \quad (13)$$

and with some reorganization now let the forcing term, F , be represented as:

$$\begin{aligned} F = & \frac{1}{M} [F_i \{ r_i (1 - (B_i N_j / K_i)) - \alpha_i \} + (r_i R_{ij} / K_i) - \dot{F}_i] \\ & + W_i^\infty [r_i (1 - (B_i N_j / K_i)) - \alpha_i] \end{aligned} \quad (14)$$

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. Then the j -dimensional differential equation is written as:

$$\begin{aligned}
 F = & \ddot{N}_i (1/MN_i) \\
 & + \dot{N}_i \left[(1/MN_i) \{ (R_{ij}/N_i) - (\dot{N}_i/N_i) + r_i (B_i N_j/K_i) - 1 \} + \alpha_i \right] + r_i/MK_i \\
 & + N_i \left[(r_i/K_i) \{ W_i^\infty + F_i/M \} \right] \\
 & + (1/MN_i) [R_{ij} \{ r_i (1 - (B_i N_j/K_i)) - \alpha_i \} - \dot{R}_{ij}] \quad (15)
 \end{aligned}$$

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

$$A_2 = 1/M$$

$$A_3 = r_i (1 - (B_i N_j/K_i)) - \alpha_i = r_i - \sum b_{ij} N_j - \alpha_i$$

$$A_4 = \frac{r_i}{MK_i} = \frac{a_i}{M}$$

$$A_5 = \frac{r_i}{K_i} \left[W_i^\infty + \frac{F_i}{M} \right] = a_i \left[W_i^\infty + \frac{F_i}{M} \right]$$

$$A_6 = R_{ij} (A_3) - \dot{R}_{ij}$$

$$A_7 = R_{ij}$$

With substitution of the intra-strata constants and some rearrangement of (15):

$$\begin{aligned}
 F = & \ddot{N}_i \left(\frac{A_2}{N_i} \right) \\
 & + \dot{N}_i \left(\left(\frac{A_3}{N_i} \right) \left[\frac{1}{N_i} (A_7 - \dot{N}_i) - A_3 \right] \right) + A_4 + N_i A_5 + \frac{A_6}{N_i} \quad (16)
 \end{aligned}$$

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

$$F = \ddot{N} + B_1 \dot{N}(aN + N) + B_2 N \quad (17)$$

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

$$\ddot{N}_i = (\dot{N}_i^2/N_i) + \dot{N}_i (A_3 - (A_4/A_2)N_i) - (\dot{N}_i/N_i)A_7 - N_i^2 (A_5/A_2) + N_i (F/A_2) - A_6 \quad (18)$$

Solution Schemes

As written above, the coefficients r_j , 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_i ; 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 Technique

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, 5 $(t+\Delta t)$, we desire to calculate the populations trajectory for any cell i in region j :

$$N_i'(t+\Delta t) = N(t) + \zeta N \quad (19)$$

Once we calculate the N_j 's, we use the specific values to compute the vector of the ensemble weights, W_j , 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 Scheme

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 complex second-order and higher equations are used. 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.

The Forward in Time System

Given boundary conditions for a series of state values, the initial populations state vector utilizing the state equations are generated in numerical simulation by the following system of forward difference equations:

Let the second-order forward difference be generally represented by:

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

and the first-order forward difference:

$$\dot{N}(t) = \frac{N(t + \Delta t) - N(t)}{\Delta t} \tag{21}$$

Then substituting the properly time-stepped equations (21) into (20) leads to the dynamic forward second difference equation:

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

$$N(t + 2\Delta t) = \ddot{N}(t) \Delta t^2 + 2N(t + \Delta t) - N(t) \tag{23}$$

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

$$N(t) = F - B_1 \dot{N}(t) (a + N(t)) - B_2 N(t) \tag{24}$$

Substituting equation (24) into equation (23) gives:

$$N(t + 2\Delta t) = \Delta t^2 F - \Delta t^2 B_1 \dot{N}(t) (a + N(t)) - \Delta t^2 B_2 N(t) + 2N(t + \Delta t) - N(t) \quad (25)$$

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

$$N(t + 2\Delta t) = \Delta t^2 F - \Delta t B_1 [N(t + \Delta t) - N(t)] (a + N(t)) - \Delta t^2 B_2 N(t) + 2N(t + \Delta t) - N(t) \quad (26)$$

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

The Centered in Time System

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 second-order centered difference be generally represented as:

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

and the first-order centered difference:

$$\dot{N}(t) = \frac{N(t + \Delta t) - N(t - \Delta t)}{2\Delta t} \quad (28)$$

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

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

and

$$N(t + 2\Delta t) = N(t)4\Delta t^2 + 2N(t) - N(t - 2\Delta t) \quad (30)$$

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

$$N(t + 2\Delta t) = 4\Delta t^2 F - 4\Delta t^2 B_1 \dot{N}(t) (a + N(t)) - 4\Delta t^2 B_2 N(t) + 2N(t) - N(t - 2\Delta t) \quad (31)$$

With substitution of (28) into the right-hand side of (31) we obtain the dynamic centered difference solution for simulation of the general form of second-order nonlinear differential equations:

$$N(t + 2\Delta t) = 4\Delta t^2 F - 2\Delta t B_1 [N(t + \Delta t) - N(t - \Delta t)](a + N(t)) - 4\Delta t^2 B_2 N(t) - 2N(t) - N(t - 2\Delta t) \quad (32)$$

Equation (32) allows centered time evolution of the second-order state equations: To compute each specific $N(t+1)$ you require $N(t)$, $N(t-1)$, $N(t-2)$, and $N(t-3)$, *vis a vis*, four previous population cohort time-step values.

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 (17) as a second-order dynamical differential equation we have:

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

Building upon the arguments presented above, (33) can be written as a forward difference equation:

$$N(t + 2\Delta t) = \Delta t^2 N(t) \frac{(\dot{F})}{A_2} - \Delta t^2 \frac{\dot{N}(t)}{N(t)} (A_7) + \Delta t^2 \frac{\dot{N}(t)^2}{N(t)} (1) + \Delta t^2 \dot{N}(t) \left(A_3 - \frac{(A_4)N(t)}{A_2} \right) - \Delta t^2 N(t)^2 \frac{(A_5)}{A_2} - \Delta t^2 A_6 + 2N(t + \Delta t) - N(t) \quad (34)$$

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

$$\begin{aligned}
 N(t + 2\Delta t) = & \frac{\Delta t^2 N(t) \overline{F}}{A_2} - \frac{\Delta t (N(t + \Delta t) - N(t)) (A_7)}{N(t)} + \frac{(N(t + \Delta t) - N(t))^2 (1)}{N(t)} \\
 & + \Delta t \frac{(N(t + \Delta t) - N(t)) (A_3 - \frac{A_4}{A_2} N(t))}{A_2} - \frac{N(t)^2 (A_5 \Delta t^2)}{A_2} \\
 & - \Delta t^2 A_6 + 2N(t + \Delta t) - N(t) \quad \nabla_j \quad (35)
 \end{aligned}$$

Clearly, the potential instabilities associated with an equation as complex as (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, equation (33) can now be transformed into a second-order nonlinear centered dynamical difference equation:

$$\begin{aligned}
 N(t + 2\Delta t) = & \frac{4\Delta t^2 N(t) \overline{F}}{A_2} - \frac{4\Delta t^2 \dot{N}(t) (A_7)}{N(t)} + \frac{4\Delta t^2 \dot{N}(t)^2 (1)}{N(t)} \\
 & + \frac{4\Delta t^2 \dot{N}(t) (A_3 - \frac{A_4}{A_2} N(t))}{A_2} - \frac{4\Delta t^2 N(t)^2 (A_5)}{A_2} - 4\Delta t^2 A_6 + 2N(t) - N(t - 2\Delta t) \quad (36)
 \end{aligned}$$

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

$$\begin{aligned}
 N(t + 2\Delta t) = & \frac{4\Delta t^2 N(t) \overline{F}}{A_2} - \frac{2\Delta t (N(t - \Delta t) - N(t - \Delta t)) (A_7)}{N(t)} \\
 & + \frac{(N(t + \Delta t) - N(t - \Delta t))^2 (1)}{N(t)} \\
 & + 2\Delta t \frac{(N(t + \Delta t) - N(t - \Delta t)) (A_3 - \frac{A_4}{A_2} N(t))}{A_2}
 \end{aligned}$$

$$- 4\Delta t^2 N(t)^2(A_2) - 4\Delta t^2 A_6 + 2N(t) - N(t - 2\Delta t) \quad \bar{V}_j \quad (37)$$

$$\frac{A_2}{A_2}$$

The reader should note that there is one centered difference equation like (37) for each j^{th} cohort in the multicohort population ($j+1, \dots, n$). 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

Clearly there remains a requirement for gaining insight into what can transpire in the evolution of a fishery system, and in the possible ways the system can be influenced by the set of initial conditions and ensuing levels of perturbations introduced over time. To understand the dynamical behavior of the coupled equation system specified, simulations were conducted to examine regions of stability or instability. The simulation system was set with appropriate parameters for depiction of an engrauloid life history (Table 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 nonlinear dynamics literature (Garrido, 1983; Webb, 1985; Thompson & Stewart, 1986; Briggs, 1987; Grebogi *et al.*, 1987). Limit cycles were pronounced when an approximate form of equation (3) was simulated 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, and the overall population ceiling established by the carrying capacity of the cohort (Figure 2). In all cases, the population approached long term equilibrium states; but then experienced accelerating oscillations which finally settled into stable limit cycles where the population(s) oscillated regularly between capacity and zero states (Figure 2a). This condition was as characteristic of two cohorts as it was of five or 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 of 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. Second, when recruitment communication between

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), and Caddy & Sharp (1986).

Cohort	$r(i)$	$a(i)$	$m(i)$	$\dot{W}(i)$	$f(j)$	$\alpha(i)$
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 coefficients $b(ij)$. Rows are the cohorts affected while the columns are the cohorts who are causing the interaction.

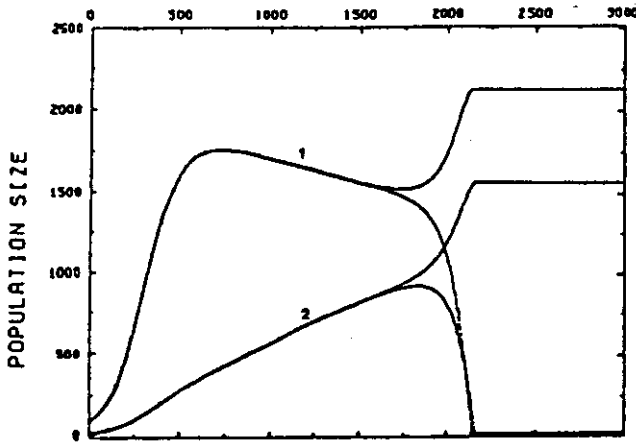
		EFFECTS						
		1	2	3	4	5	6	7
1	XXX	.00025	.000005	.000001	.000001	.0000001	.0000001	1.0E-8
2	.000125	XXX	.000125	.000125	.0000125	1.0E-6	1.0E-7	
3	.000225	.00035	XXX	.000125	.000025	1.0E-5	1.0E-6	
4	.000	.00001	.001	XXX	.0001	.00005	1.0E-7	
5	.000	.001	.001	.001	XXX	.00001	1.0E-5	
6	.000	.00000	.00001	.0001	.0005	XXX	1.0E-4	
7	.000	.00000	.00001	.0001	.0002	.00001	XXX	

cohorts occurs both in the r_j term, and pulsed with respect to the $R(ij)$ 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:

1. their ability to capture available environmental resources,
2. cohort carrying capacities,
3. competition between other cohorts,
4. population densities within and among age strata,
5. age-specific continuous recruitments from the local population and
6. potential recruitments from sources extrinsic to the local population which are typical for many tropical fishery systems.

Third, older age groups may damp recruitments because of their predatory effect on the younger age strata. Numerically strong population age strata can

(A) Multicohort Population Equations
TIME EVOLUTION



(B) Multicohort Population Equations
TIME EVOLUTION

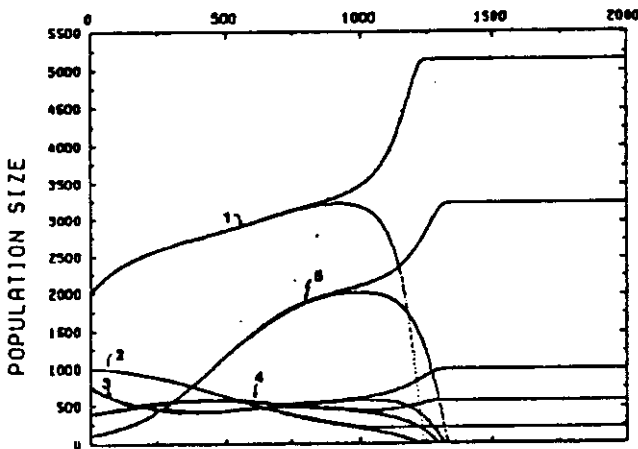


Figure 2. Time evolution of the nonlinear multicohort population equations showing limit cycles for: (A) two cohorts, and (B) five cohorts.

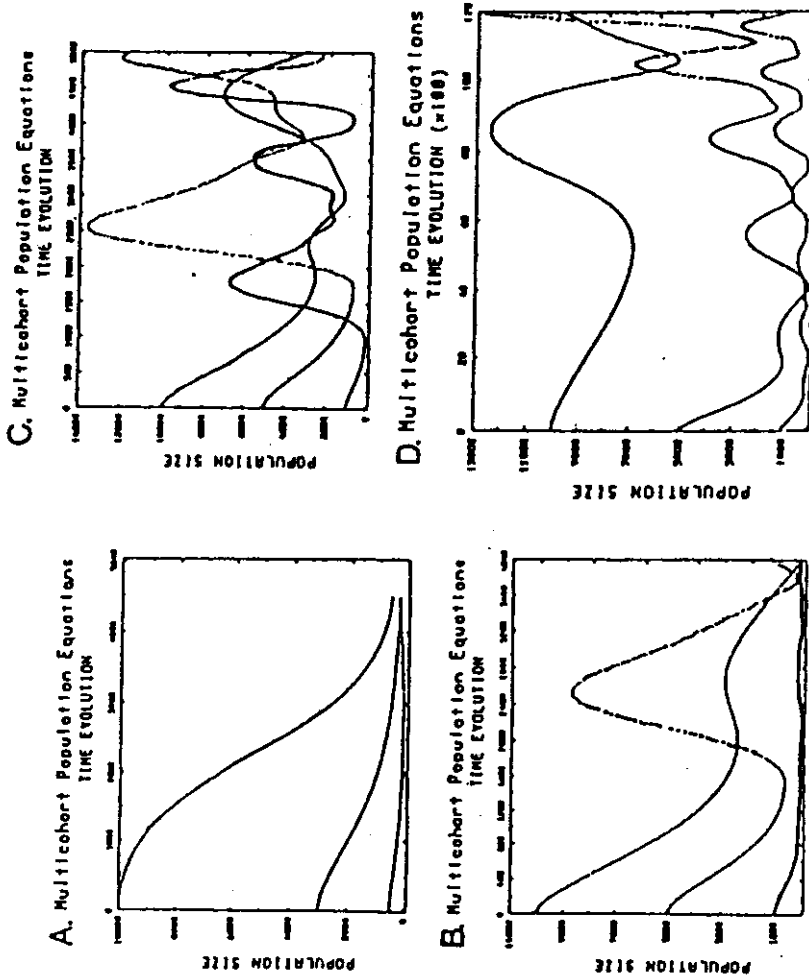


Figure 3. Time evolution of the nonlinear population equations showing: (A) a large metabolic term and no recruitment communication between age strata, and (B, C, D) temporal communication between cohorts.

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 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 Parrish *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 numbers 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 more damped than the individual cohorts. Formally some equilibrium may exist; 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, 1988a, 1988b, 1989). No matter what the initial distribution, without nonlinearities the population will contract to a fixed stationary distribution. However, apparently stochastic dynamics 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

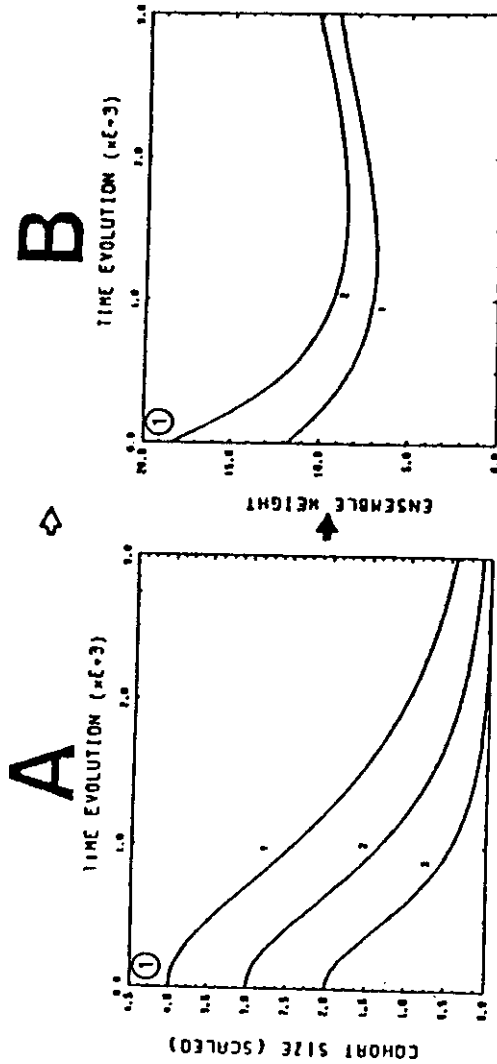


Figure 4a. Simulated population cohort abundance (A) and associated ensemble weights (B) modeled by equations (35) and (37) for cases where the optimal weights at age strata are identical.

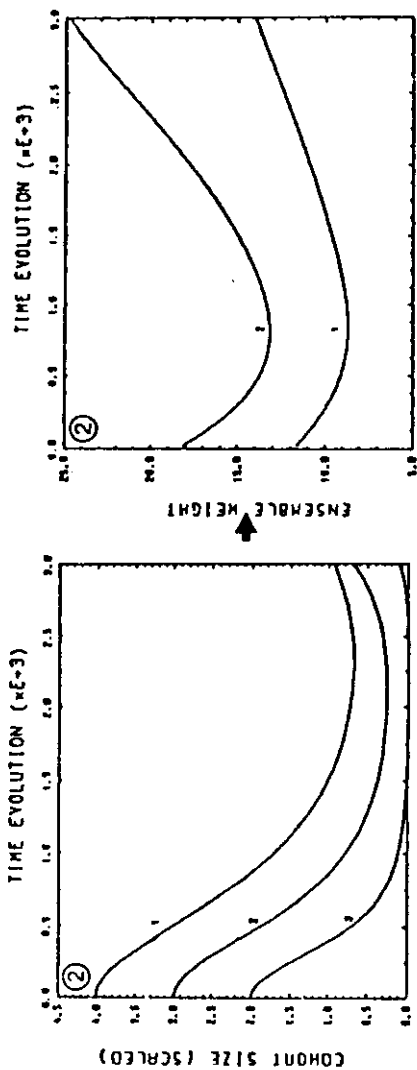


Figure 4b. Simulated population cohort abundance (A) and associated ensemble weights (B) modeled by equations (35) and (37) for cases where optimal weights increase with increasing age.

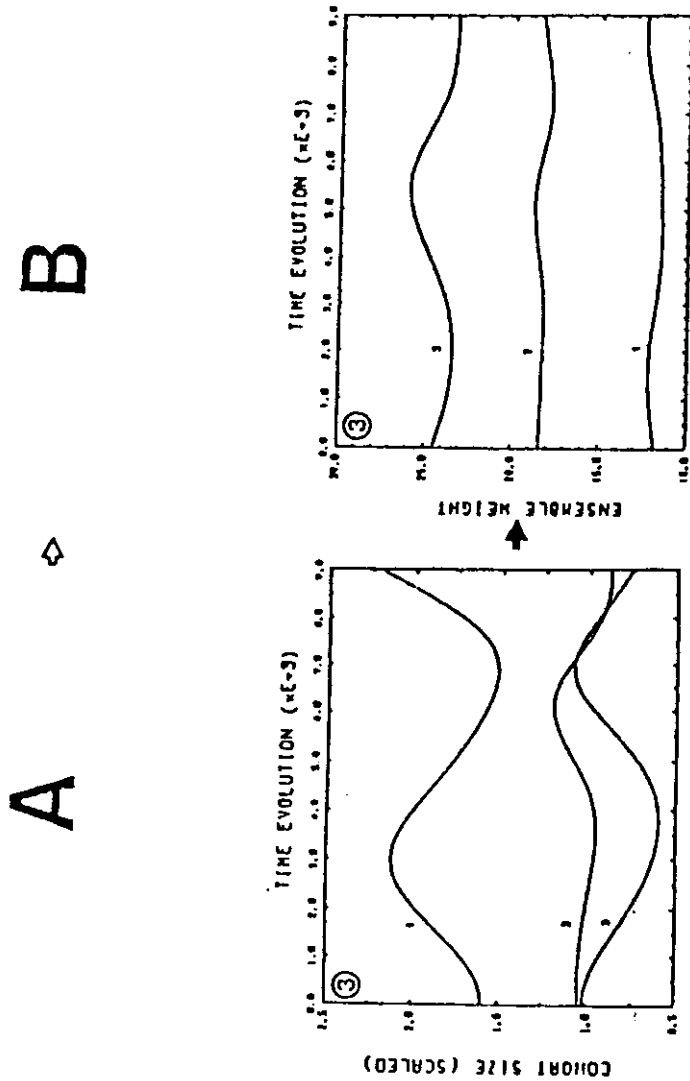


Figure 4c. Simulated population cohort abundance (A) and associated ensemble weights (B) modeled by equations (35) and (37) for cases where optimal weights increase with increasing age and increased interaction between cohorts.

of high-order period 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 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 coupled nonlinear 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 multicohort model made 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 can not 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, the purpose has been to describe the multicohort nonlinear dynamic system modeling as a technique to study tropical marine fish stock(s) population dynamics processes. The unique feature of the equations presented in this section is that it represents the first time anyone has coupled an n-cohort, n-species relation and solved the system of equations. Beyond its intrinsic mathematical interest, it may have considerable significance for advancing the study and understanding of structured populations under exploitation. 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 that presented here are generally not used in fishery 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 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

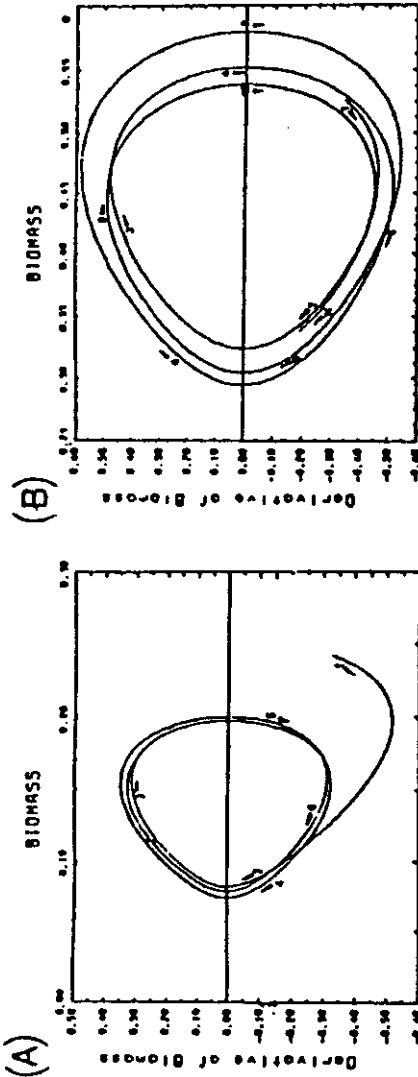


Figure 5. Domains of attraction for the phase-space trajectories showing a spectrum of limit cycles for various initial conditions and continuous recruitment: (A) system approaching a dynamic limit cycle, (B) increasing optimal weights at age increasing age strata, (C) conditions in (B) with low fishing mortality, (D-E) conditions in (B) with moderate growth term, and (F) large growth term.

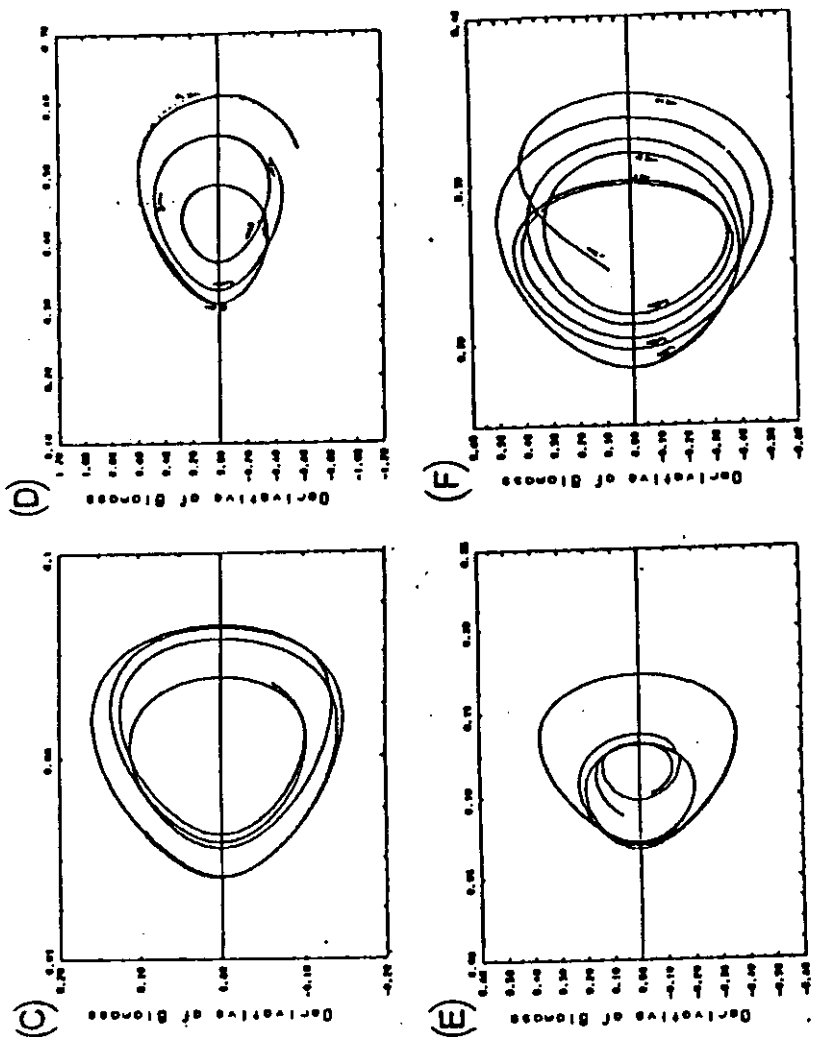


Figure 5. continued.

mechanisms can produce cyclical and sometime 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 every known with absolute precision. As such, the model of this section may then suggest a new tact for 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.

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