

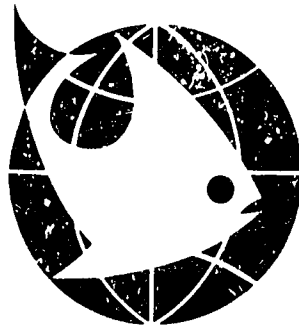
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**FISHERIES STOCK ASSESSMENT**

**TITLE XII**

**Collaborative Research Support Program**



**Fisheries Stock Assessment CRSP Management Office  
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**The University of Maryland—Center for Environmental and Estuarine Studies  
The University of Rhode Island—International Center for Marine Resource Development  
The University of Washington—Center for Quantitative Sciences  
The University of Costa Rica—Centro de Investigación en Ciencias del Mar y Limnología  
The University of the Philippines—Marine Science Institute (Diliman)—College of Fisheries (Visayas)**

**In collaboration with The University of Delaware; The University of Maryland—College of Business and Management; The University of Miami; and The International Center for Living Aquatic Resources Management (ICLARM).**

**WORKING PAPER SERIES**

Working Paper No. 33

"The Tropical Fishery System Model  
CORECS - Continuous REcritument  
Simulation"

by  
Jerald S. Ault  
University of Miami

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**Fisheries Stock Assessment CRSP**

**The Tropical Fishery System Model  
CORECS - COntinuous RECRuitment Simulation**

by

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## Introduction

Tropical fishery systems (TFS) are based on complex suites of interactions and dependencies making assessments difficult. Fishery assessment techniques (FATs) were traditionally developed for technologically sophisticated industrial fisheries based in cold-water seas exploiting single-species stocks which exhibit seasonal (discrete) rates. Along with the advanced fishing technology infused into the TFS, now too have followed the traditional stock assessment methodologies. Traditional models are important but have limited utility (Rothschild, 1986). They are important because their simplifying assumptions allow use of aggregate quantities, deterministic variables and equilibrium conditions. They are limited because they may be inadequate for assessing the highly dynamic multispecies tropical warm-water fisheries. The rationale for constructing oversimplified mathematical caricatures of reality has been that one hopes to capture the essence of observed patterns and processes without becoming enmeshed in the details (May & Oster, 1976). However, failure to comply with the basic assumptions of even the simplest genre of the traditional models when they are applied to tropical situations may have insidious effects on derived policy. A general crisis of confidence has emerged concerning the fundamental validity of the scientific basis for fisheries worldwide (Beverton, 1983) because of the gross simplifications of dynamical systems. Thus it is critical to determine of what validity are assessments that are made on the TFS.

The fundamental differences inferred by the development of the first hypothesis in Ault (1988) and Ault and Fox (1988a) led to testing of the *hypothesis* that the TFS can be accurately portrayed by developing a suite of analytical and numerical methods which sufficiently mimic tropical fish stock dynamics and system responses to exploitation and can directly aid decision making. The objective of this paper was to develop a continuous-time probabilistic simulation model which depicts salient features of the TFS. Simulation has been defined by Minsky (1986) as a situation in which one system mimics the behavior of another. In principle, a modern computer can be used to simulate any other kind of

machine, physical or biological. The ability to ever know the true underlying answers about fish populations in the tropical fishery system are extremely limited or nonexistent. Thus it is critical to have simulations as "*known systems*" against which to test methodologies. This approach represents the most logical avenue to system validation.

One technique for formulating optimal policy is the use of mathematical models (Wagner, 1975; Bradley et al., 1977). Most mathematical models encountered in the fishery literature which were developed specifically for temperate-based fisheries consider recruitments as periodic discrete-pulsed events occurring at single fixed reference points once each year. The approach may be inappropriate for tropical marine fisheries. For continuously-breeding life histories the population's instantaneous probability density structure taken at any finite interval of time will be substantially different than that for the discrete-pulsed approach. Most real-world problems of this kind confronting the analyst, being neither linear nor even nearly linear, fall outside the domain of traditional closed-form analysis, and must be tackled in the first instance on a computer which make possible the use of numerical models and simulation methods (Thompson and Stewart, 1986).

### **Simulation Modeling**

Simulation modeling is defined as a numerical technique for conducting experiments with certain types of mathematical models which describe the behavior of a complex system on a computer over extended periods of time (Naylor et al., 1966; Law and Kelten, 1982). Simulation is helpful in resolving questions posed by the DM. It is one of the most powerful quantitative decision analysis tools available to fisheries science (Hilborn & Walters, 1987). Simulation allows the inclusion of multiple objectives in the planning process as opposed to a single objective in past practice which broadens and enhances the decision making framework (Ault & Fox, in press). Numerical simulation offers the most flexible and realistic representation for complex problems of any quantitative technique (Van Horn, 1971). Numerical methods have made possible

examination of large dynamic systems of differential equations with coupling and feedbacks both from deterministic and stochastic perspectives. The essence of simulation is to provide the DM with: (i) a detailed and realistic representation of the problem under study, and (ii) the ability to test and examine various alternatives he may want to consider (Bradley et al., 1977). Simulation models are characterized by: (i) many variables and their functions, (ii) stochastic variables and their distributions, (iii) many parameters, (iv) many linkages between elements of the model, (v) nonlinearities, (vi) assorted constraints, and (vii) a response (or responses) that may or may not have a time path. A simulation model is constructed in the hope that it will successfully mimic a real world system so that its behavior can be anticipated or changed. The model may, as a consequence, become very complicated and involved.

Frequently it is impractical, or even impossible to perform controlled experiments with business, economic or fishery systems. Nonetheless, it may be possible to perform a type of quasi-experiment with a mathematical model of the perceived system through the use of computer simulation techniques (Naylor et al., 1966; Law and Kelton, 1982; Hertz and Thomas, 1983). The attractive feature for the development of simulations is that they force explicit statements of assumptions and hypotheses, and encourage exploration of alternative hypotheses. Much is learned from simulation and mathematical programming because of the understanding provided from examining tradeoffs. Since a computer simulation study is indeed an experiment, one should pay close attention to experimental design questions prior to conducting a simulation experiment (Hunter and Naylor, 1970; Ignall, 1972). Purposeful designs are not only appreciated for their economic benefits in terms of experimental trials required, but also because they provide a structure for the investigator's learning process. Well-conceived experimental designs serve to: (i) to provide a framework for investigating the relationship of the response to the factors to determine the underlying mechanisms governing the process under study, and (ii) to find the combination of factor levels at which the response variable is optimized. For the

pragmatic experimentalist, these can be viewed as ideal experiments, and show what could be achieved in perfectly controlled noise-free laboratories. Perhaps more importantly, in for example the case of chaotic motions, they show what *cannot* be achieved even under such ideal conditions (Thompson and Stewart, 1986). Simulation models can be important in complicated systems analysis for establishing heuristics for policy making by facilitating selection of the most effective optimum sustained benefits strategy. Clearly, simulation models DO NOT generate optimum solutions, but simply permit the evaluation of an alternative relative to the inputs supplied externally by the DM.

### **CORECS (Continuous Recruitment Simulation) Model**

Of the large number of fishery simulation models presently available there are at least three which were designed to be generally applicable to most exploited fish populations and which utilize discrete mathematics (Walters, 1969; Fox, 1973; Ault & Fox, 1985, 1986a). These three models use closed-form simulation equations. None of them allows for continuous dynamics, nor probabilistic growth or mortality. The aforementioned programs also lack an exact accounting of the probability density distribution of individuals for any finite point in time. To their credit even very simple simulations can help to better appreciate how fish stocks will respond to exploitation (Hilborn & Walters, 1987). The tropical fishery system is complex. This section's work is intentionally trying to be eclectic rather than reductive in order to maximize what has been learned from our experiments with early implementations (Ault & Fox, 1986a,b, in press). *Cohorts* in tropical latitudes are produced more or less in a continuum relative to the discrete, retracted recruitments of temperate and boreal fishes. To appropriately address the problem development in the area of continuous-time population modeling was required. This study adopted an alternative approach utilizing continuous mathematics and discrete dynamical mathematics described by ordinary differential and finite difference equations, respectively. Continuous variables are the principle means of looking more deeply into



demographic matters (Keyfitz, 1968, 1977).

The dynamical continuous model CORECS (COntinuous-time RECrutment Simulation) was developed. Continuous simulations model a system using state variables which change continuously with respect to time to understand the complex relationships of the TFS and to anticipate future situations. Continuous simulation models involve one or more differential equations which give relationships for the rates of change over time evolution (Law and Kelton, 1982). Some of the CORECS model specialized features include the experimenters ability to divide the time stream up into as many finite-infinite increments as desired, allowing the introduction of cohorts among any and/or every time step with any probability density distribution required. Using this scaling feature probability density functions unique to specific classes of continuous demographic relationships may be introduced into simulations. Population structure is simulated numerically in CORECS by introducing multiple production of cohorts by species group within any one year. These are allowed to be static or dynamic among years. Thus, simulated tropical populations with varying lengths of protracted spawning and variable, density-dependent recruitment rates, but with known catches at age (or size) can be parameterized in the algorithm. These events can also be stochastic. A stochastic process  $\{\chi(t), t \in T\}$  is a family of random variables indexed on a continuous parameter  $t$  that takes on all values of the set  $T$ . Letting the set  $T$  comprise all points on the real line permits us to describe the stochastic process as  $\{\chi(t), -\infty < t < \infty\}$ . The observed behavior of a stochastic process during some arbitrary time interval forms a time series (Fishman and Kiviat, 1967). The structure of the model CORECS was optimized following the methods in Metcalf (1982). CORECS allows simulations which facilitate comparisons and contrasts of interpretations derived from populations modeled with either the discrete-event versus the new continuous-event approaches.

### **Description of the TFS Model**

The CORECS model is intrinsically age-structured having its roots in determinism; its superstructure is length-structured and stochastic. The stochastic model is based on the nonlinear Leslie matrix (1945, 1948). The simulator has been developed very generally to admit a series of classes of situations found in each sector of tropical and subtropical fisheries. As such, the model provides the level of detail necessary to incorporate known parameters, those that may be developed in other projects, and alternate hypotheses for those which do not and will not exist or be available within a reasonable time frame. The foundation of the model is developed below.

### **Timing and Accounting**

CORECS utilizes a dynamical difference time ordination. The ordination is dependent upon the user's choice of the finite time-step ( $\Delta t$ ) incrementation. The numerical forward and centered calculations performed within CORECS were facilitated by derivation of an algorithm that allowed substantial flexibility with regard to the generation and maturation of population abundance and density particles within the population mass field. For the numerical solution of the continuous forward and centered difference equations a simplified quasi-continuous cohort algorithm is substituted to move cell values in the continuous-time simulations (Figure 1b). Logical units of time are chosen for reasons of desired periodicity and system stability. All statistics are accumulated on the  $\Delta t$  basis.  $P(\gamma, j, t)$  is either the number of viable fertilized ova cast, or the number of larvae born in period  $\gamma$  and are in their  $j$ th time unit of life during time step  $t$ . For example, if the time-step chosen is months, then  $P(13, 12, t)$  is the number of individuals recruited in month 13 of the time stream that are in the 12th month of life during the  $t$ -th period of the simulated time stream (Figure 1a). Output is time-integral specific and is summed for all intervals.

Continuous numerical simulation allows more flexibility in terms of the component relationships and interactions that may be added to the time derivatives with only a minor

increase in computational difficulty. It also provides the means to simulate any sized  $\Delta t$  desired. The general relations for the first-order forward and centered differenced simulation equations can be stated if we let  $\dot{P}(t) \equiv$  population derivative (where a dot and it's further use indicates a derivative with respect to time). Now assume that  $t = 0$ , and the boundary condition  $P(0)$  is specified; then the forward difference of  $P(t)$  can be generally stated as:

$$\dot{P}(t) = \frac{P(t + \Delta t) - P(t)}{\Delta t} \quad (1)$$

so that, 
$$P(t + \Delta t) = P(t) + \Delta t \dot{P}(t) \quad (2)$$

Given the initial states from the forward equations then the linear first-order centered difference equations are generally written as:

$$\dot{P}(t) = \frac{P(t + \Delta t) - P(t - \Delta t)}{2\Delta t} \quad (3)$$

with some rearrangement:

$$P(t + \Delta t) = P(t - \Delta t) + 2\Delta t \dot{P}(t) \quad (4)$$

A component of random variability is introduced into the model by adding an error term to the time derivative so that the stochastic centered equation becomes:

$$P(t + \Delta t) = P(t - \Delta t) + (2\Delta t \dot{P}(t))(1 + \mu(t)) \quad (5)$$

$\mu(t) \equiv$  a random variable from a predesignated statistical distribution.

In this example the error term has been applied to the first-order derivative following Southward (1968). The error term can assume any functional probability distribution in that the stochastic element included is additive. However, we might assume here, primarily based on the lack of the appropriate statistical observations, that the error term is normally distributed, with a mean zero and a standard deviation which is specified. Typically tropical fish stocks may experience a number of population and environmental

pressures whose effect(s) may not be well enough understood to be explicitly represented as terms in the coupled differential equations but can be simply represented, as a first approximation, in a single stochastic term. State variables are computed as follows:

### Mortality

Mortality rates applications are time-step and age-specific and are assumed to be representable by following the forward and centered dynamic difference equations for stock abundance dynamics:

#### *Forward System*

$$\begin{aligned}
 N(\gamma,0,t+\Delta t) &= f[\Psi(t)] \\
 N(\gamma-1,1,t+\Delta t) &= N(\gamma-1,0,t) + [\Delta t \cdot \dot{N}(\gamma-1,0,t)] \\
 &\vdots \\
 &\vdots \\
 N(\gamma-k,k,t+\Delta t) &= N(\gamma+k-1,k-1,t) + [\Delta t \cdot \dot{N}(\gamma-k-1,k-1,t)] \quad (6) \\
 &\vdots \\
 &\vdots \\
 N(\gamma-n,n,t+\Delta t) &= N(\gamma-n-1,n-1,t) + [\Delta t \cdot \dot{N}(\gamma-n-1,n-1,t)]
 \end{aligned}$$

where,  $N(\gamma,j,t) \equiv$  ensemble abundance in cohort  $j$  born in period  $\gamma$  present during time period  $t$ .

so that  $\gamma$ ,  $j$ , and  $t$  are birthdate, age, and time-step, respectively; and  $\Psi(t)$  is equal to the potential of the spawning stock to produce recruits in some period  $t$ . In this system of equations dependencies may be incorporated on all three factors. Given initial values from the forward equations the centered system is:

#### *Centered System:*

$$\begin{aligned}
 N(\gamma+2,0,t+3\Delta t) &= f[\Psi(t + 2\Delta t)] \quad (7) \\
 f[\Psi(t + 2\Delta t)] &\equiv \text{some function of the spawning stocks' potential to produce} \\
 &\quad \text{recruits in period } t + 2\Delta t.
 \end{aligned}$$

The second age strata is computed by forward difference to generate the appropriate vector of observations for the centered system shown as:

$$\begin{array}{l}
 N(\gamma, 2, t+3\Delta t) = N(\gamma, 0, t+\Delta t) + [2\Delta t \cdot \dot{N}(\gamma, 1, t+2\Delta t)] \\
 \vdots \\
 \vdots \\
 \vdots
 \end{array} \quad (8)$$

$$N(\gamma+3-n, n, t+3\Delta t) = N(\gamma+3-n, n-2, t+\Delta t) + [2\Delta t \cdot \dot{N}(\gamma+3-n, n-1, t+2\Delta t)]$$

where,

$N(\gamma, j, t) \equiv$  number of fish in cohort  $\gamma$  aged  $j$  at the beginning of period  $t$  where  $j$  and  $t$  are integers.

$$Z(j, t) = M(j, t) + A(j, t) \cdot F(j, t) \quad (9)$$

$F(j, t) \equiv$  instantaneous rate of fishing mortality of a fully available cohort,  $j = 0, \dots, t_\lambda - 1$ , in period  $t$ . The total life span is then  $t_\lambda = n \cdot m$ , where  $n$  is equal to the number of discrete integer age groups and  $m$  is equal to the number of annual divisions of the time stream.

$$F(j, t) = \begin{cases} 0 & \text{if } j < t_p \\ > 0 & \text{if } j \geq t_p \end{cases} \quad (10)$$

$A(j, t) \equiv$  size- or age-specific selectivity or availability factor for the  $j$ th cohort in period  $t$ . If partial selection is required then the availability multiplier is  $A(j, t) \cdot Q(j) \cdot F(j, t)$ , where  $F(j, t)$  is the level of effective fishing effort on cohort  $j$  in period  $t$ , and  $Q(j)$  is the catchability coefficient for the  $j$ th cohort.

$M(j, t) \equiv$  instantaneous rate of natural mortality for cohort  $j$  in period  $t$ .

$$M(j, t) = \begin{cases} 0 & \text{if } j < t_p \\ > 0 & \text{if } j \geq t_p \end{cases} \quad (11)$$

With the natural and fishing mortality stated so generally it is possible to evaluate the effects of seasonal mortality and size-specific selectivity patterns. Since  $F(j, t)$  is assumed to be proportional to the fishing effort it has close parallel with effective effort

coupled by some scaling fraction. Hence it follows that  $F(j,t)$  is the *control variable*. The coefficient  $A(j,t)$  allows various patterns of selectivity to be incorporated. The stochastic version of the simulation model allows  $A(j,t)$  and  $M(j,t)$  to become randomly distributed from specified probability density functions with known means and variances. The system of equations can be reformulated in vector notation form as:

$$\vec{N}(t+\Delta t) = e^{-(M+F(t))\Delta t} \vec{N}(t) + \vec{b} \approx f[\vec{N}(t), F(t)] \quad (12)$$

### Population Sizes

The ensemble number in cohort  $j$  born in period  $\gamma$  present during time period  $t$  is given by :

$$\bar{N}(\gamma,j,t) = N(\gamma,j,t)(1-e^{-Z(j,t)})/Z(j,t) \quad dt \quad (13)$$

The fishable average abundance for a cohort with birthdate  $\gamma$  and aged  $j$  at  $t$  is:

$$\bar{N}(\gamma,j,t) = \int_t^{t+\Delta t} N(\gamma,j,t)(1-e^{-(M(j,t)+A(j,t)F(j,t))})/(M(j,t)+A(j,t)F(j,t)) dt \quad \forall \gamma \quad (14)$$

so that the total fishable average population in period  $t$  is:

$$\bar{N}(t) = \int_t^{t+\Delta t} \int_{t_p}^{t_\lambda} \bar{N}(\gamma,j,t) dj dt \quad \forall \gamma \quad (15)$$

### Growth Relationships

A number of models have been applied to describe weight as a function of age and Richards (1959) has shown that these models are related. Although any growth relationship can be used, the ensemble length of an individual within each cohort  $j$  during any time period  $t$  is described in this example by a form of the von Bertalanffy (1938) equation, primarily because it seems to fit growth data well. The limiting form of the equation is:

$$\dot{L}(j) = K(L_\infty - L(j)) \quad (16)$$

where  $L_\infty$  and  $K$  are parameters. One initial boundary condition was required to satisfy the equation specified at  $t = 0$ , such as  $L(0) = L_{t_p}$  (where  $t_p \equiv$  age of first recruitment). The forward simulation of the length is then calculated as:

$$L(\gamma,j+1,t+\Delta t) = L(\gamma,j,t) + [\Delta t \cdot \dot{L}(\gamma,j,t)] \quad (17)$$

and the function centered in time is:

$$L(\gamma, j+1, t+\Delta t) = L(\gamma, j-1, t-\Delta t) + [2\Delta t \cdot \dot{L}(\gamma, j, t)] \quad (18)$$

The von Bertalanffy model may be inappropriate for organisms whose growth is seasonally variable because it assumes that the growth rate is time invariant. Seasonal variations in the growth of fishes, are at least in part, related to temporal changes in air and water temperature and seasonal variations in the abundance and quality of food (Cloern and Nichols, 1978). A seasonal relationship of growth was added to the length model by incorporating a simple periodic function into the time derivative written in the centered system as:

$$L(\gamma, j+1, t+\Delta t) = L(\gamma, j-1, t-\Delta t) + \left\{ [2\Delta t \cdot \dot{L}(\gamma, j, t)] \cdot \left(1 + \text{SIN}\left(\frac{2\pi}{\rho}\right)\right) \right\} \quad (19)$$

where  $\rho \equiv$  period. This may be shown to increase its seasonal variance in time by introducing an amplitude function,  $\theta$ , to the right-hand side:

$$\theta(t) \text{SIN}\left(\frac{2\pi}{\rho}\right) \quad (20)$$

where,  $\theta(t) = \alpha(t)^\beta$ , and  $\alpha$  and  $\beta$  are parameters of the power curve  $\theta$ .

To generate a stochastic seasonal growth function the centered relation is written:

$$L(\gamma, j+1, t+\Delta t) = L(\gamma, j-1, t-\Delta t) + \left\{ [2\Delta t \cdot \dot{L}(\gamma, j, t)] \cdot \left[1 + \theta(t) \text{SIN}\left(\frac{2\pi}{\rho}\right)\right] \right\} (1 + \mu(t)) \quad (21)$$

A density-dependent growth relationship was also programmed into the model with respect to the parameters  $K$  and  $L_\infty$  being a  $f(\vec{N})$ . Although unless exceptionally detailed data are available, growth is generally assumed to be independent of population density. Since the simulator can be specified to produce small, finite intervals  $\Delta t$ , any shape growth curve can be approximated. Note that the scale of the rate parameters are completely arbitrary in these sets of equations. The time step should be adjusted in terms of the fastest evolving rate to maintain stability, in perhaps a nonlinear system of equations.

The average length for an ensemble individual from cohort  $\gamma$  aged  $j$  was calculated by specifying the aforementioned differenced boundary conditions and using the dynamical

equations so that the average ensemble weight for an individual of that same cohort is:

$$W(\gamma, j, t) = \alpha [L(\gamma, j, t)]^\beta \quad \forall \gamma \quad (22)$$

where,  $\alpha$  and  $\beta$  are parameters of the power curve  $W$ .  
and  $W(\gamma, j, t) \equiv$  average weight of an individual in cohort  $\gamma$  aged  $j$  at the beginning of interval  $\Delta t$ .

The average biomass of cohort  $\gamma$  aged  $j$  during the finite interval  $\Delta t$  may be expressed as:

$$B(\gamma, j, t) = N(\gamma, j, t) \cdot W(\gamma, j) \quad (23)$$

The deterministic nature of the growth equation suggests that for any given length there is a determined age. In reality, there can be a number of possible ages for any given length (Bartoo & Parker, 1983). The variance of size at a given age increases with increasing age (size) in fishes (Schnute & Fournier, 1980; Rosenberg & Beddington, 1986). To incorporate the dimensionality of a probabilistic representation of sizes distributed stochastically at a given age, a power function was fit to observed data on the progression of the standard error of the mean average length in the catch on ages of fish as determined by direct methods of aging such as by reading otoliths or scales. The estimation of length at age is typically reported in the form of discrete units (i.e. annual age classes). As a result, the observed data for the standard error of length at age for given ages, which are typically distributed nonlinearly, were fit to a generalized continuous power function of the form:

$$\sigma(j, t) = \alpha (A(j, t))^\beta \quad (24)$$

where,  $\sigma(j, t) \equiv$  standard error of length for fish aged  $j$  at some time  $t$ .  
 $A(j, t) \equiv$  the continuous age  $j$  of a fish at time  $t$ .  
 $\alpha$  &  $\beta \equiv$  coefficients of the power curve model  $\sigma$ .

With estimated standard error of length at age a stochastic model was developed for the intrinsically deterministic von Bertalanffy equation. A description of the ensemble numbers at a given length  $L$  may be written generally as:

$$\tilde{N}(L) = \int_0^L R(\tau - j) S(j) p(L; j) dj \quad (25)$$



where,  $R(\tau - j) \equiv$  Recruitment at  $(\tau - j)$  periods ago.  
 $S(j) \equiv$  Survivorship to at least age  $j$ .  
 $p(L ; j) \equiv$  Probability of being a length  $L$  at an age  $j$ .

Now assume that  $p(L ; j)$  comes from a designated probability distribution (Figure 2a); such that a description of the probability that given a fixed age  $j$  the probability distribution of lengths can be generalized, where  $b$  and  $a$  are the upper and lower limits of the prediction interval, respectively as:

$$P(a \leq L(j) \leq b) = \Phi \left( \frac{b - \bar{L}(j)}{\sigma(j)} \right) - \Phi \left( \frac{a - \bar{L}(j)}{\sigma(j)} \right) \quad (26)$$

and the description of the population numbers can be written discretely as:

$$N(L ; t) = \sum p(L ; j) N(j ; t) \quad (27)$$

Now note that expressions (26) and (27) represent the expectation of the numbers at a given length at a specific time and are as such completely independent of age (Figure 2b). Using the stochastic model it is shown that overlappings in lengths at a given age are weighted between ages, the degree of weighting is proportional to the length probabilities at the given ages. A continuous Markov chain transition probability model for both growth and survivorship can be incorporated into the model. The model can be generalized by calculating transition probabilities for each specific lattice point in the  $p(L ; j)$  matrix. This feature represents a quasi-continuous time analog of the Markov chains and as such are characterized by the Markovian property that given the present state, the future is independent of the past. All Markov chains considered are assumed to have stationary transition probabilities.

### Yields and Catches

A generalized approach following Fox (1973) applied to discrete systems was modified and adopted in CORECS for simulating the yield in weight ( $Y_w$ ) and the catch in numbers ( $Y_n$ ) since the mortality rates may be cohort and time-step specific and  $j$  and  $t$  are continuous

variables. The values were calculated as:

$$Y_w(t) = \int_t^{t+\Delta t} \int_{l_p}^{l_\lambda} A(j,t) F(j,t) N(\gamma,j,t) W(\gamma,j) dj dt \quad (28)$$

$$Y_n(t) = \int_t^{t+\Delta t} \int_{l_p}^{l_\lambda} A(j,t) F(j,t) N(\gamma,j,t) dj dt \quad (29)$$

and thus the mean weight in the total catch for interval  $\Delta t$  was:

$$\bar{W}_c(t) = \frac{Y_w(t)}{Y_n(t)} \quad (30)$$

The mean length in the total catch for interval  $\Delta t$  irrespective of the functional representations was:

$$\bar{L}(t) = \frac{\int_t^{t+\Delta t} \int_{l_p}^{l_\lambda} A(j,t) F(j,t) N(\gamma,j,t) L(\gamma,j) dj dt}{Y_n(t)} \quad (31)$$

### Quantitative Processes Mapping Spawning to Recruitment

Distinction of the spawning stock instantaneous probability density distribution is of paramount importance for developing an understanding of the nature of the true SRR for commercially exploitable stocks in tropical environments. Two primary difficulties in studying SRR problems were defined by Paulik (1973) as: (i) the basic variables defy measurement, and (ii) the time scales are lengthy. To this effect then the spawning potential of the stock of interest may be defined in the simulation model by the following representations:

$$\text{Let, } N_0 = R(t+\tau) = f[\Psi(t)] \quad (32)$$

$$\Psi(t) = \int_{\alpha}^{\beta} g(j,t) N(\gamma,j,t) dj \quad (33)$$

where,

$R(t+\tau) \equiv$  number of recruits produced at the instantaneous slice of time  $(t+\tau)$ , where  $\tau \equiv$  time lag between spawning and subsequent recruitment.

$g(j,t)$   $\equiv$  fecundity index for age  $j$  fish.  
 $\Psi(t)$   $\equiv$  potential of the spawning stock to produce recruits in some period  $t$ .

Now define,

$\alpha$   $\equiv$  age of recruitment to the reproductive portion of the stock for animals following the equations specified.  
 $\zeta(j,t)$   $\equiv$  average measure of egg production for fish age  $j$  during the period  $t$ .  
 $\Theta_f(j,t)$   $\equiv$  proportion of females in the  $j$ -th age group during the period  $t$ .  
 $N(\gamma,j,t)$   $\equiv$  total number of fish age  $j$  alive during the period  $t$ .  
 $\omega(j,t)$   $\equiv$  proportion of females in the  $j$ -th age group that are mature during the period  $t$ .  
 $C(j,t)$   $\equiv$  proportion of females aged  $j$  that are mature and are in spawning condition in period  $t$  ( $t \in [0,1]$ ).

The size of adult stock can be measured in a number of ways, the most direct way is the total egg production. The total fecundity index ( $g$ ) for the stock is:

$$g = f(\zeta, \Theta, \omega, C) \quad (34)$$

Such that one plausible representation for the spawning potential in the manner of Paulik (1973) was:

$$\Psi(t) \equiv \int_t^{t+\Delta t} \left\{ \int_{\alpha}^{\beta} N(\gamma,j,t) \zeta(j,t) \Theta_f(j,t) \omega(j,t) C(j,t) dj \right\} dt \quad (35)$$

Another representation of the available stock spawning biomass for the finite interval  $\Delta t$  was calculated as:

$$\Psi(t) \equiv \int_t^{t+\Delta t} \left\{ \int_{\alpha}^{\beta} B(\gamma,j,t) dj \right\} dt \quad (36)$$

Parrish et al. (1986) concluded that age-specific fecundity in serial spawning fishes is of greater significance for management than previously thought. They stated that much of the observed variance in the SRR for multiple-spawning fishes may be due to the fact that the

spawning biomass is a poor index of the egg production and reproductive potential of a given stock. Nonetheless, the recruitment to the stock at the time  $(t+\tau)$  can be generally stated as:

$$R(t+\tau) = f[\Psi(t), \Gamma(t), \Gamma(t+1), \dots, \Gamma(\tau)] \quad (37)$$

where,  $\Gamma(\tau) \equiv$  environmental forcing factors for the  $\tau$  periods between spawning and recruitment.

The environmental forcing factors represent generally the physical environment including the man induced effects and natural variability like climatological events. All the terms except  $N(\gamma, j, t)$  will be, in general, independent of fishing.

### Fecundity on Weight

A continuous function for fecundity (in terms of viable ova produced) dependent upon a given weight was derived from information on fecundity at discrete ages, and average body weight at discrete ages. These two relationships were incorporated into one generalized continuous power function following Ault (1985):

$$\zeta(j, t) = a(W(j, t))^b \quad (38)$$

where  $\zeta(j, t) \equiv$  production of viable ova of a female fish aged  $j$  at time  $t$ .  
 $W(j, t) \equiv$  ensemble weight for an animal aged  $j$  at time  $t$ .  
 $a$  &  $b \equiv$  coefficients of the model.

### Maturation

A maturity schedule of the sexes necessary to compute several fundamental relationships associated with the reproductive sector of CORECS was developed within the simulator by generation of two vectors of age-specific values following Fox (1973). One vector denoted the average fraction of males in a cohort during the breeding season,  $\Theta_m(j, t)$ , and the other denoted the average female fractions  $\Theta_f(j, t)$ .

The ensemble number of males in strata  $j$ ,  $\bar{N}_m$ , during period  $t$  is (let  $t_m = \alpha$ ):

$$\bar{N}_m(j,t) = \int_{t_m}^{t\lambda} \Theta_m(j,t) N(\gamma,j,t) (1-e^{-Z(j,t)})/Z(j,t) dj \quad (39)$$

The ensemble number of females in strata  $j$ ,  $\bar{N}_f$ , during period  $t$  is:

$$\bar{N}_f(j,t) = \int_{t_m}^{t\lambda} \Theta_f(j,t) N(\gamma,j,t) (1-e^{-Z(j,t)})/Z(j,t) dj \quad (40)$$

The simple sex ratio in terms of males to females in in age strata  $j$  during period  $t$  is:

$$S_j(j,t) = \frac{[\bar{N}_m(j,t)]}{[\bar{N}_f(j,t)]} \quad (41)$$

### Stock Recruitment Functions

The stock recruitment model uses a value for the stock's reproductive potential which can be defined variously by equations (35) or (36) and can be either of the form proposed by Ricker (1954):

$$N(\gamma,0,t+\tau) = \int_t^{t+\Delta t} \alpha \Psi(t) e^{-\beta\Psi(t)} dt \quad (42)$$

or Beverton and Holt (1957):

$$N(\gamma,0,t+\tau) = \int_t^{t+\Delta t} 1 / (\alpha + \beta\Psi(t)) dt \quad (43)$$

where  $\alpha$  and  $\beta$  are the specific parameters for either the Ricker or the Beverton and Holt functions.

### Linkage of Autonomous Ensemble Growth and Reproduction

Many theories utilized in fishery science have assumed steady state conditions, giving yield and other characteristics of the population in terms of four primary factors: (i) recruitment, (ii) natural mortality, (iii) fishing mortality, and (iv) growth. It is clear from the preceding sections that reproductive mechanisms should be studied more intensively,

particularly the link between population spawning and the subsequent distribution of recruitments at the seasonal level in tropical marine waters. A deterministic, constant recruiting population is a persistent population that replaces the biomass of its parents during each generation on the average. Perhaps then it seems productive to pursue a model of age-specific reproduction that incorporates life history features specific to birth which includes the population fraction of mature females in an unbiased index of population reproductive contribution. The basic tenant of the analytical approach is that the model should retain the essential features of a population's dynamics. The following approach attempts to incorporate some salient features of a population's birth, growth, and survivorship processes and examines those features impact on population stabilities. The index must be combined with an index of survivorship to age/size, weight at age, and adult abundance data to provide any meaningful input in terms of true population phenomena. We desire to have an expression which relates the properties of the life table into a birth rate at age/size relationship such that:

$$\mathfrak{R}(j,t) = \Xi(j+1,t+1) \cdot l(j,t) \quad (44)$$

where,

- $\mathfrak{R}(j,t)$        $\equiv$       the number of progeny born in the interval  $t$  to  $t+1$  per female aged  $j$  to  $j+1$  at time  $t$ , who will be alive in the age group  $0-1$  at time  $t+1$ .
- $\Xi(j+1,t+1)$     $\equiv$       net number of births per individual from age category  $j+1$  at the beginning of period  $t$ .
- $l(j,t)$             $\equiv$       fraction of individuals from age category  $j$  which survive to age  $j+1$  in in period  $t$ .
- $l(0,\tau)$           $\equiv$       called the radix is an arbitrary constant such as unity.

$$l(k,t) = l(0,\tau) \cdot l(k-1,t) = l(0,t) \prod S_j \quad (45)$$

and

$$S(j) = e^{-Z_j} \quad (46)$$

$S(j)$   $\equiv$  the probability that an individual age  $j$  to  $j+1$  at time  $t$  will be alive in the group  $j+1$  to  $j+2$  at time  $t+1$ .

Stating (44) assumed that the survival fractions,  $l(j,t)$ , were approximately identical over the reproductive span of the adults, i.e.,  $l(j,t) \approx l(t)$ , for the reproductive life span of adults. Allowance could be made such that all age-specific density-independent adult survival could be moderated by a density-dependent factor, and we can also incorporate functional relationships that allow for variations in age-specific fecundity and weight. Deriso (1978) originally suggested a method that partitioned the total weight of the fecund population into categories that correspond to age-partitioning. However, his age-partitioning was formalized as annual discrete increments for which Deriso solved annual difference equations. Here, we show that it is possible to generalize the age-specific weights of the sexually mature in a continuous-time population in the form of a first-order differential equation. This is done by assuming that the change in ensemble weight per period is a function of two distinct, but not mutually exclusive, physiological processes. These are: (i) diversion of assimilated resource energy to meet present somatic and future reproductive needs, and (ii) diversion of a portion of energy to meet the present period metabolic and gonadal growth requirements during the present period. The equation is generalized in continuous-time dynamics for the present and one-lagged period by:

$$\dot{W}_j(t) = \lambda \rho W_j(t) - (1 - \rho) W_j(t) + \rho [\lambda \rho W_j(t - \Delta t)] - (1 - \rho) [\lambda \rho W_j(t - \Delta t)] \quad (47)$$

where,

$W_j(t)$   $\equiv$  the ensemble weight for age strata  $j$  at the start of period  $t$ .

$\rho$   $\equiv$  fraction of body weight allocated to somatic growth and future reproduction per period  $\Delta t$ .

$(1 - \rho)$   $\equiv$  fraction of body weight diverted to present period gonadal growth and metabolism per period  $\Delta t$ .

$\lambda$   $\equiv$  growth proportionality factor ( $0 \leq \lambda \leq 1$ ).

$\alpha$   $\equiv$  minimum age of reproduction.

All adults aged  $\alpha$  and greater are assumed to be reproductively mature. Individuals may lose or gain reproductive ability as they age. The term,  $\rho$ , contains a loss or gain term which represents the per period fraction of weight that becomes either reproductive or somatic. In this case,  $\lambda$ , is the growth proportionality constant defined above, except that it applies only to reproductive weight. With a little rearrangement of (47):

$$\dot{W}_j(t) = W_j(t)[\lambda\rho - 1 + \rho] - W_j(t - \Delta t)[(\lambda\rho)^2 - \lambda\rho - \lambda\rho^2] \quad (48)$$

The dynamic centered first difference can be written:

$$W_j(t + \Delta t) = W_j(t - \Delta t) + 2\Delta t[ W_j(t)(\lambda\rho - 1 + \rho) - W_j(t - \Delta t)((\lambda\rho)^2 - \lambda\rho - \lambda\rho^2)] \quad (49)$$

and is simulated by specifying two boundary conditions  $W_j(0)$  and  $W_j(1)$ . The parameters  $\lambda$  and  $\rho$  can be adjusted based on information specific to the genera. Regardless of the definition of the coefficients equation (49) provides a flexible relationship to simulate continuous-time age-specific reproductive potential. To incorporate the aspect of alternating sex ratios and hermaphroditism a separate factor is added.

$$\mathfrak{R}(x,t) = \zeta(j,t) \cdot \Theta_f(j,t) \cdot l(j,t) \quad (50)$$

Equation (50) embodies an index that is combined with survivorship to age, weight at age, and the production of ova at size to provide a functional birth equation.

### Model Components for Incorporating Seasonal Recruitments

A summarization of the spawning and recruitment patterns for marine fishes distributed circumtropically was given in Table 1 of Ault and Fox (1988a). The results of 67 studies comprised 28 families. Walsh (1987) presented the results of 54 studies for 48 species of Hawaiian fishes. From all of the aforementioned information it is clear that reproductive activity in the tropical environments has a duration that may last from three to twelve months, the average is about 7.0 months. These results are incongruent with the assumption of continuously uniform recruitment because the average larval period may



only be 0.5 to 3.0 months (Brothers et al., 1983; Brothers & Thresher, 1985; Ralston, 1987). The conclusions for seasonal recruitments are confirmed by the results shown in Figure 2 of Ault and Fox (1988a) and by those for Hawaiian fishes (Walsh, 1987, Figure 2). Reproduction and recruitment for most families of tropical and subtropical fishes occurs over a large portion of the year (*protracted*) and appears to be cyclical, thus as a first approximation these processes may conceivably be modeled as a variety of periodic and distributional functions.

### Trigonometric Recruitment Function

Recruitment distributions shown in Ault (1988) and Ault & Fox (1988) appear to be cyclical or periodic over a given year and thus it seems reasonable for one class of functions to ascribe these time distributions to simple sine or cosine relationships. The choice is arbitrary since the sine and cosine curves are the same in the sense that they can be made to coincide by shifting one of them along the abscissa. The graph of the cosine function is merely a sine curve with a phase shift of  $-1/2 \pi$  units; that is, a sine curve shifted  $1/2 \pi$  units to the left. It is a fairly straightforward matter to expand the basic dynamic pool model (Beverton & Holt, 1957) and develop an analytical population model that incorporates periodic protracted seasonal recruitments. Consider the continuous variable time measured in real units and define:

$N(j,t)$       $\equiv$      as the number of individuals aged  $j$  alive at time (note that  $j$  is also continuous).

Now consider a cohort (generation time sequence unspecified) that has entered the fishable population where it undergoes a total instantaneous mortality rate  $Z$ , such that :

$$N(j+1, t+\Delta t) = N(j,t)e^{-Z\Delta t} \quad (51)$$

If we define the age of recruitment to be zero, then the number of recruits at a given time  $t$  can be generalized for a periodic recruiting population in terms of a cosine function following Ralston (1987):

$$N(0,t) = N_0' (1 - \cos 2\pi t) \quad (52)$$

The number of individuals aged  $j$  alive at time  $t$  in a stationary population can be expressed as:

$$N(j,t) = N_0' [1 - \cos 2\pi(t-j)]e^{-Zj} \quad (53)$$

so that the total population of individuals alive at any time  $t$  assuming an infinite life span is:

$$\begin{aligned} N(t) &= \int_0^{\infty} N(j,t) dt \\ &= N_0' \int_0^{\infty} (1 - \cos 2\pi(t-j))e^{-Zj} dj \end{aligned} \quad (54)$$

Integrating by parts the right-hand side of the integrand of (57) yields:

$$\int_0^{\infty} \cos 2\pi(t-j)e^{-Zj} dj = \left( \frac{2\pi \sin 2\pi t + Z \cos 2\pi t}{4\pi^2 + Z^2} \right) \quad (55)$$

Now by substituting the right-hand side of (55) into the partially integrated solution of (54) gives the analytical solution of Ralston (1987):

$$N(t) = N_0' \left[ \frac{1}{Z} - \left[ \frac{2\pi \sin 2\pi t + Z \cos 2\pi t}{4\pi^2 + Z^2} \right] \right] \quad (56)$$

The analytical solution is only useful to demonstrate that the population abundance at any time  $t$  is dependent only on the total instantaneous mortality rate and the time; the population will now undergo oscillations inter-annually prescribed by the parameters of the sine and cosine functions. Clearly (54) can be solved for any of the class of trigonometric functions by substitution of the periodic relationship within the brackets of the integrand. To compute changes in biomass at any time  $t$  under the seasonally oscillating recruiting pattern when one desires to establish the simple autonomous biomass relation one simply replace a solution like (56) into an equation like (23) and adjusts the limits of integration to calculate various features of the populations recruited biomass. These calculations are performed numerically in CORECS.

### Trigonometric Recruitment Distributions

The magnitude of the periodic recruitment functions are generally not known and are inferred from catch rates, although seasonal catch rates may also be affected by the seasonal availability of the stock. At equilibrium, the population's probability densities are indeterminate to a scale factor. The functional form of the annual recruitment relationship is desired to determine its effects on the probability density distribution of the stable population fraction at size. Three such plausible annual recruitment distribution cases were simulated, viz.: (i) a uniform time-step continuous recruitment, (ii) a unimodal-annual recruitment, and (iii) a bimodal-annual recruitment (Figure 3a). The value of total annual recruitment was equivalent in all three cases and was fit for cases (ii) and (iii) by the following general formulation:

$$R(\gamma, t) = \varphi | \text{SIN}(\alpha t + \beta) | \quad 0 \leq t \leq 1 \quad (57)$$

which is a sine curve with an amplitude of  $\varphi$  and a period of  $2\pi/\alpha$ .

where,  $\varphi \equiv$  amplitude scalar (i.e. maximum displacement from the horizontal axis).  
 $\alpha \equiv$  scaling frequency. If the period of the recruitments were 6 months (i.e. bimodal annually), then  $\alpha = 12$  and the period is  $\pi/6$ .  
 $\beta \equiv$  horizontal translation (i.e. shift is to the left when  $\beta$  is positive and to the right when  $\beta$  is negative).

### Beta Distribution Recruitment Function

As shown in Figure 2 of Ault and Fox (1988a) and discussed in Pauly and Navaluna (1983) and Walsh (1987) the recruitment frequency distributions are not strictly smoothly periodic as would be modeled in the previous section. Another plausible distribution sufficient to recover the observed forms of spawning and recruitment is the beta distribution. The beta distribution (Law and Kelton, 1982; Ross, 1985) was used as a rough model of the recruitment behavior within a year because of the variety of data

empirically confirming several functional distributions for the marine fish family types examined (see Ault and Fox, 1988a). The distribution offers considerable statistical modeling flexibility because of the variety of shapes the beta density can assume. A density function is placed on a given interval [a,b] by assuming that the random variable  $\chi$  has a beta distribution on this interval with shape parameters of  $\alpha_1$ , and  $\alpha_2$ .

Thus, a continuous random variable whose probability density is given by:

$$f(t) = \begin{cases} \frac{t^{\alpha_1-1}(1-t)^{\alpha_2-1}}{\beta(\alpha_1, \alpha_2)} & \text{if } 0 < t < 1 \\ 0 & \text{otherwise} \end{cases} \quad (58)$$

where

$$\beta(\alpha_1, \alpha_2) = \frac{\Gamma(\alpha_1) \Gamma(\alpha_2)}{\Gamma(\alpha_1 + \alpha_2)} \quad (59)$$

and the quantity  $\Gamma(\alpha)$  is called the gamma function (Ross, 1985). The time variable  $t$  is of any specified duration and is partitioned in units of  $\Delta t$ . For example, consider a cohort that has entered the fishable population where it undergoes a constant mortality rate for a given age strata. Defining the age of recruitment to be zero and by truncating at some arbitrary age  $t_\lambda$ , the total number of individuals alive at any time which is composed of  $\chi$  cohorts can be calculated directly by numerical solution of the integral:

$$N(t) = N_0' \int_{t_p}^{t_\lambda} \left[ \frac{t^{\alpha_1-1}(1-t)^{\alpha_2-1} \Gamma(\alpha_1 + \alpha_2)}{\Gamma(\alpha_1) \Gamma(\alpha_2)} \right] e^{-Zj} dj \quad (60)$$

The beta distribution allows definition of a variety of annual recruitment structures (Figure 3b), hence allowing for a spectrum of potential population density distribution arrangements.

### Beta Recruitment Distributions

The analytical description of protracted recruitments in tropical marine fishes populations can be simulated by variously parameterizing equation (60). Generation of the beta function:

$$\beta(\alpha_1, \alpha_2) = \frac{\Gamma(\alpha_1) \Gamma(\alpha_2)}{\Gamma(\alpha_1 + \alpha_2)} = \frac{(\alpha_1 - 1)! (\alpha_2 - 1)!}{((\alpha_1 + \alpha_2) - 1)!} \quad (61)$$

was accomplished by generalizing equation (58) by generating the continuous random variable values of the gamma function by application of Stirling's formula (Beyer, 1979) which states:

$$n! = e^{-n} n^n (2\pi n)^{1/2} \quad (62)$$

A general method for simulating the beta distribution is given by Law and Kelton (1982).

### Random Processes Affecting Recruitment

Environmental variability may have a substantial influence on marine fish stocks, primarily by affecting survival to the time of recruitment (Hightower & Grossman, 1985). One attempt to model the gamma process terms indicated in equation (37) has been a multiplicative lognormal error used in recent studies of stock-recruitment functions (Walters & Hilborn, 1976; Laurec & Champagnat, 1980; Peterman, 1981; Walters & Ludwig, 1981; Archibald et al., 1983; Swartzman et al., 1983; Huang & Walters, 1983; Hightower & Grossman, 1985, 1987) of the general form:

$$R = f[\Psi(t)]e^{\nu} \quad (63)$$

- $R(t + \tau)$   $\equiv$  recruitment.
- $f[\Psi(t)]$   $\equiv$  unspecified function of parent stock, most often represented by the spawning biomass (Doubleday, 1975; Deriso, 1980; Shepherd, 1982).
- $\nu$   $\equiv$  normally distributed random variable with mean  $\emptyset$  and variance  $\sigma^2$

The favored SRR (possibly with the random element to represent environmental effects) can be used to determine the subsequent recruitment for simulation studies. The

multiplicative lognormal error term has been used both for mathematical convenience as well as for assumed biological realism. The model was developed along the following lines. Assume that the loss of eggs, larvae, or juveniles can be accommodated by:

$$\frac{1}{N} \dot{N} = -M(t) \quad \Rightarrow \quad N(t) = N(t_0)e^{-M(t-t_0)} \quad (64)$$

If  $M(t)$  is approximately normally distributed as a random variable with any kind of probability density function then:

$$N(t) = N(t_0)e^{-\int_{t_0}^t M(x)dx} \quad (65)$$

According to the Central Limit Theorem a large sum of random variables (i.e.  $\int_{t_0}^t Mdt$  is  $\sim N(M, \sigma^2)$ ), and thus  $\xi \sim N(0, \sigma^2)$ . Therefore we have:

$$N(t) = N(t_0)e^{-(M + \xi)(t-t_0)} \quad (66)$$

which is distributed lognormally. Instead of computing deterministic yield and stock level, the model then computes expected values and variances for each of these variables. Theoretically justification for error term,  $e^{\nu}$ , is that it can be viewed as a random survival term resulting from several independent and multiplicative environmental factors. Stochastic models of the SRR can be used for risk analysis; they can be used to estimate the probability that the stock biomass, measured in whatever arbitrary units desired, will fall below a given level. Two possible models given earlier and now written with a lognormal error term are the Ricker function:

$$N(\gamma, 0, t+\tau) = \alpha \Psi(t) e^{-\beta \Psi(t)} e^{\nu} \quad (67)$$

or the Beverton and Holt:

$$N(\gamma, 0, t+\tau) = 1/(\alpha + \beta/\Psi(t)) e^{\nu} \quad (68)$$

### Nonlinear Probabilistic Distribution Search

Stochastic representations of growth and survivorship dictated that a nonlinear search routine was employed in order to represent age-independent length frequency distributions abstracted from age-length information. The method was required because the

probabilistic representation of growth allowed animals of several different ages to assume the same length for any finite interval of time (Figure 2b). The search was accomplished by developing a nonlinear routine that scanned the continuous probability surface and reorganized observations by the desired level of discretization. To eliminate searching of void probability space Chebyshev's nonparametric inequality was employed (Ross, 1985). In essence if  $X$  is a random variable with a mean  $\mu$  and a variance  $\sigma^2$ , then Chebyshev's inequality allows the derivation of bounds on searching probabilities when only the mean, or both the mean and the variance of the probability distribution are known. Since the actual distributions are generally known in the simulated cases, then the desired probabilities are exactly computed, allowing full knowledge of the probability bounds.

### **The Discrete to Continuous Transition**

CORECS functionally differs from the traditional fish population simulation models by the representation of the time domain, and the probabilistic way in which the birth, growth, and survivorship processes are accounted. Traditional exploited fish population models (e.g., POPSIM (Walters, 1969), GXPOPS (Fox, 1973)) discretize the distribution of cohorts in time by the introduction, once annually, of a single pulse of recruits dependent on the populations aggregate age-discrete spawning potential at the immediate beginning of the year. These singular cohorts are then pushed through the year deterministically (in the form of one cohort per yearclass) by forward difference equations. At the completion of each simulated year singular cell values (e.g., one value per yearclass per month) are then summed back through the year to represent annual averaged stock dynamics. This approach is shown graphically for a Grouperoid stock with a uniform-discrete recruitment pattern during an arbitrary slice of time (Figure 4a). For a population with  $n$ -discrete age classes, only  $n$  distinct cells of animals are present at any one instant of time. As long as recruitment is constant (i.e. uniform), the cohort's distribution in time (or age distribution) is the reflection of the age-specific survival rates applied against the  $n$ -

individual annual cohorts since their issue into the population. This class of numerical methodology approaches the problem somewhat holistically and may be unrealistically artificial. Under the caveat that all the population rates applied remain absolutely constant through time, then the discrete procedure may not necessarily be prone to significant error. However, if there are partial or periodic trends in recruitment which show strong dependence on population structure, seasonal survivorships, etc., then the discrete-time approach may deleteriously influence the anticipated results.

The quasi-continuous time algorithm embodied in the simulation model CORECS fundamentally varies from the discrete class of simulation models in that it allows cohorts to be introduced singularly and independently/dependently along a time stream of any desired finite division. Assume that a year ( $n$ ) can be divided into  $m$  arbitrary time-steps (i.e., months, days, minutes, etc.). Then for any instant  $t$  in time there exists  $m \times n$  elements of a probability density distribution of individuals. For example, if constant recruitment per interval is assumed, then the net effect would be to increase the individual birthing sequence along the time stream from  $n$ -elements to an introduction of  $m$  cohorts within any annual  $n$  interval. The number of cells occupied by population members at any instant  $t$  in the case of the deterministic model is a function of the number of distinct annual age classes in the population ( $n = t\lambda$ ), times the number of population birth event steps ( $m$ ) within a given annual increment. The resultant deterministic structure is a fully representative, quasi-continuous probability distribution of the population's  $m \times n$  dimensioned stable age distribution (Figure 4b). The distribution approaches a fully continuous function as the limit of the time increment approaches an infinitesimally small unit. This condition presents no problems numerically, however, depending upon the division of the time stream the procedure may tax the specific computing resources central processing unit. For microcomputers to adequately simulate the dynamics of a tropical fish stock, the logical time-steps might be monthly, or if data were of higher quality, every two weeks. Utilizing the continuous algorithmic approach,  $m \times n$  points of any probability



density distribution can be included for any instantaneous moment of time. Thus it is possible to describe nearly any type of probability density function for a population (e.g. reproductive value at age) that we may actually be encountered in the natural tropical or temperate marine environment. The continuous approach also allows one to account for more sources of the variability that might otherwise be occluded by adopting a discrete approach.

By allowing for various distributional forms of instantaneous cohort introduction into the population a spectrum of potential population distributions are possible. Each of these specific distributions are dependent upon the life history characteristics, the form of the birth function, and any exogenous forms of perturbation that might influence the population structure. When recruitment is protracted and the distribution of the issue of recruits is normally distributed through a given year, the resultant stable age distribution for a finite increment of time is seen in the case of the grouperoids (Figure 4c). Now note that there are peaks and troughs associated with the stable age distribution. There may be reproductive windows that a particular population passes through to optimize its reproductive value for a given spawning period  $t$  with recruitment characteristics of this class. When the sex ratio approaches 1:1 the majority of the grouperoids reproductive potential can be shown to rest on the older age/size segment of the population, and that segment's ability to produce reproductive input is tied to the season and the instantaneous population distribution at that finite instant of time (Bannerot, 1984). Six possible recruitment function forms were introduced for each of the genera examined in this section under unexploited, deterministic conditions. When the number in the population is plotted on length, the results are seen in Figure (5a,b,c) for the grouperoid, scombroid, and engrauloid life histories, respectively. The modes of the distributions are increasingly compacted with increased length.

Probabilistic length at age presents another dimension to the concept of the population distribution problem which has rarely been addressed specifically in the fisheries literature.

In this case the number of elements occupied by population members expands to  $m \times n \times p$  cells for any instantaneous moment of time, where  $p$  is equal to the number of specific probability points estimated at each level of age. In particular, when the discrete distribution of population cohorts for grouperoids shown in Figure 4a is distributed probabilistically with respect to length at age in accordance with the stochastic growth function delineated in Ault and Fox (1988c), we note that in the older age classes six annual age groups can with probability be of exactly the same length (Figure 6a). When the CORECS model generates cohorts according to a normal recruitment distribution with a period of one year, and the growth of these cohorts is probabilistically distributed, the result is a complex bivariate normal population distribution of overlapping cohorts for any given instantaneous moment of time (Figure 6b). It should be noted that the distribution of discrete-pulsed, probabilistically distributed cohorts for the engrauloids, because of the intrinsically high natural mortality rate, has proportionally few population members found in the older age/size groups. Similar to the situation with scombroids, because of the higher growth rates the cohorts spread out fairly well in the first couple of years of life, however the older ages can overlap extensively with a probabilistic representation of marginally increasing standard error of age at length. This may suggest that indirect aging methods for anything but the fastest growing, youngest age groups could be subject to some amount of bias when developing age-length keys. Scombroids grow to a larger size and die faster than the grouperoids, in that they attain >75% of their maximum size in about 1/3 of the time required for grouperoids. However, they do so under a significantly higher level of mortality. Engrauloids on the other hand have a growth rate which is intermediate to scombroids and grouperoids, however engrauloids have much lower intrinsic survival rates. Both scombroids and engrauloids reach >75% of their maximum size after 2-3 years of life, grouperoids do not attain this length until >10 years of life.

## **Summary**

A dynamical numerical model of the tropical fishery system (CORECS) was developed which mimics tropical fish stock dynamics. The approach was designed to examine the deficiencies of fishery assessment techniques when applied in a tropical context through the use of continuous rather than discrete variables. CORECS is a generalized, continuous-time, multicohort simulator that incorporates a set of probability relationships for recruitment, growth and mortality. CORECS computes population and catch length-frequency data according to a variety of hypotheses that were formulated from empirical data on tropical fish populations.

A copy of the program is available upon request from the senior author (J. Ault).

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## List of Figures

- Figure 1:** Structure of the continuous time numerical model CORECS showing: (A) upper triangular form for generation of initial conditions, followed by centered in time sequences for the n-cohort population matrix ( $N \equiv$  [oldest annual integer age in the catch]  $\times$  [division of time stream within annual increment],  $t \equiv$  time stream,  $j \equiv$  length (or time) class,  $\gamma \equiv$  birthdate,  $R(\gamma,j,t) \equiv$  recruitment date  $\gamma$  in time stream  $t$  for length class  $j = 1, \dots, n$ ,  $t=1, \dots, \infty$ ;  $P(\gamma,j,t) \equiv$  population abundance for cohort  $\gamma$  in time stream  $t$  for length class  $j$ ,  $\xi \equiv$  last period of planning horizon), and (B) the simplified quasi-continuous cohort algorithm (NM  $\equiv$  number of periods of the generation,  $P(I,J) \equiv$  population cell value for those born in period  $i$  of simulation and presently in their  $j$ th period of life,  $R(K) \equiv$  cohort strength in period  $k$ ).
- Figure 2** Graphical description of the stochastic growth function of the CORECS model showing: (A) the probability that at a fixed age  $x$  the normal probability distribution of lengths is defined by a mean and variance relationship, and (B) the expectation of some arbitrary set of numbers of individuals at given lengths at some specific instant in time.
- Figure 3:** Annual recruitment structures for tropical and subtropical marine fishes derived from: (A) the trigonometric population equation (56): (i) continuous uniform, (ii) protracted unimodal ( $\pi/12$ ), and (iii) protracted bimodal ( $\pi/6$ ); and (B) the beta distribution population equation (61): (i)  $\alpha_1 = 1.5, \alpha_2 = 5$ ; (ii)  $\alpha_1 = 1.5, \alpha_2 = 3$ ; (iii)  $\alpha_1 = 5, \alpha_2 = 5$ ; and (iv)  $\alpha_1 = 5, \alpha_2 = 1.5$ .
- Figure 4** The discrete to continuous transition for a deterministic grouperoid life history under various recruitment hypotheses: (A) discrete uniform, (B) continuous uniform, and (C) protracted normal.
- Figure 5** Deterministic probability density distributions resulting from the specific life history parameterizations and six (by panel) recruitment hypotheses (rows) (i) continuous uniform, (ii) normal, (iii) beta skewed right, (iv) beta skewed left, (v) trigonometric unimodal, and (vi) trigonometric bimodal; for the genera (columns) (A) grouperoids, (B) scombroids, and (C) engrauloids.
- Figure 6:** Probabilistic representation of population structure for the grouperoid (A) uniform discrete-pulsed, and (B) protracted normal recruitment hypotheses.

(A) Cohort Matrix Structure.

		Time (t)						
		Birthdates ( $\gamma$ )						
Age(j)	1	2	3	4	• • •	N	• • •	$\xi$
1 ↓	R(1,1,1)	R(2,1,2)	R(3,1,3)	R(4,1,4)	• • •	R(N,1,N)		R( $\xi$ ,1, $\xi$ )
2	0	P(1,2,2)	P(2,2,3)	P(3,2,4)	• • •	P(N-1,2,N)		P( $\xi$ -1,2, $\xi$ )
3	•	•	P(1,3,3)	P(2,3,4)	• • •	P(N-2,3,N)		P( $\xi$ -2,3, $\xi$ )
4	•		•	P(1,4,4)	• • •	P(N-3,4,N)		P( $\xi$ -3,4, $\xi$ )
•	•			•	• • •	•		•
•	•				•	•		•
•	•					•		•
N	0	•	•	•	• • •	0 P(1,N,N)	•	P(N+ $\xi$ +1,N, $\xi$ )

(B) Simplified Quasi-Continuous Cohort Algorithm

```

DO 1000 K = 1,NM
X = K
J = 1
DO 100 I = X,1,-1
IF (I.EQ.X) GOTO 10
IF (I.NE.X) GOTO 20
10 P(I,J) = R(K)
GOTO 50
20 P(I,J) = P(I,J-1)
50 J = J+1
100 CONTINUE
1000 CONTINUE

```

Figure 1

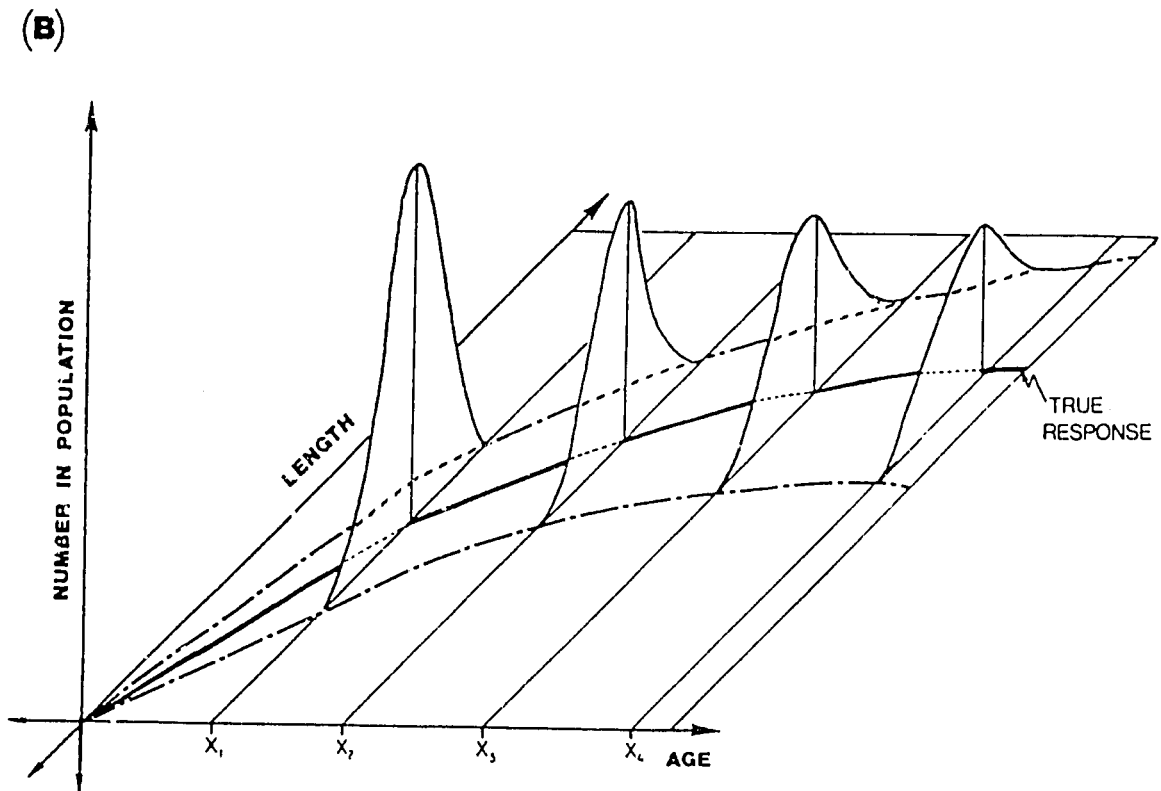
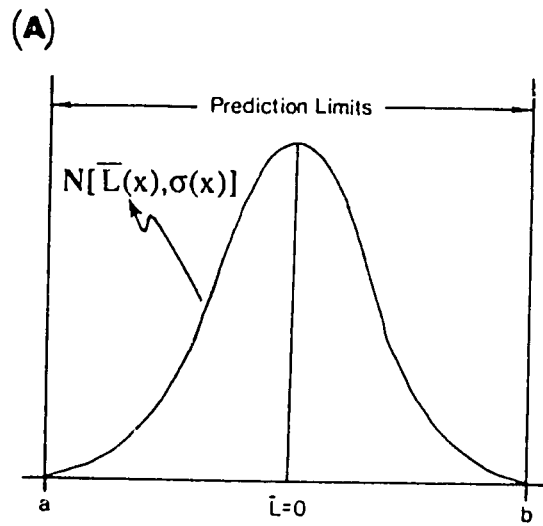
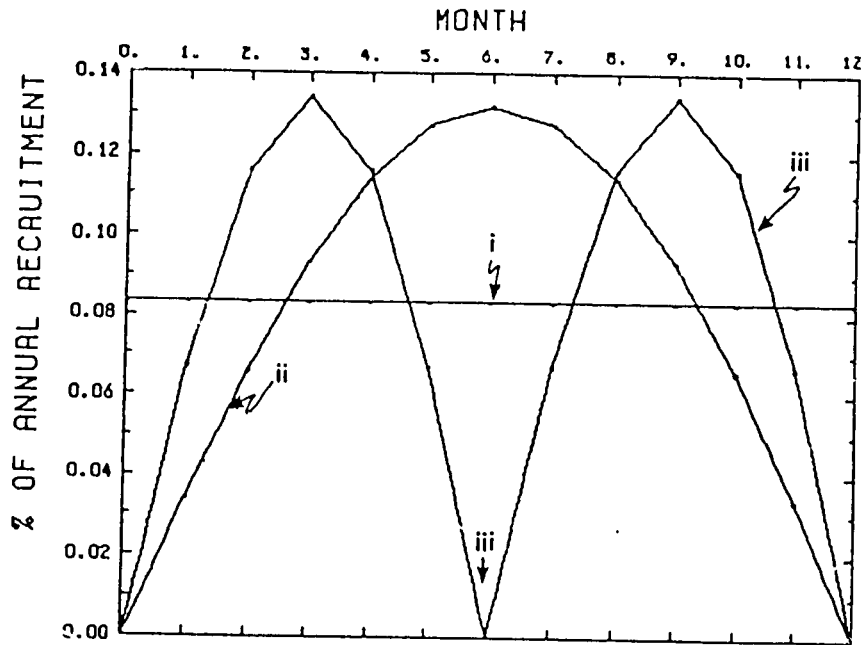


Figure 2

(A) Trigonometric Recruitment



(B) Beta Recruitment Function

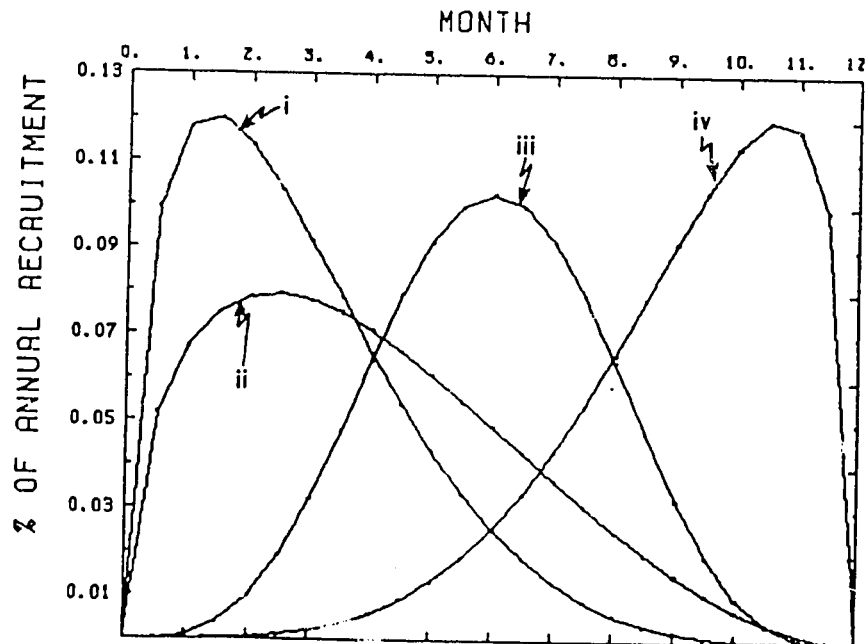


Figure 3

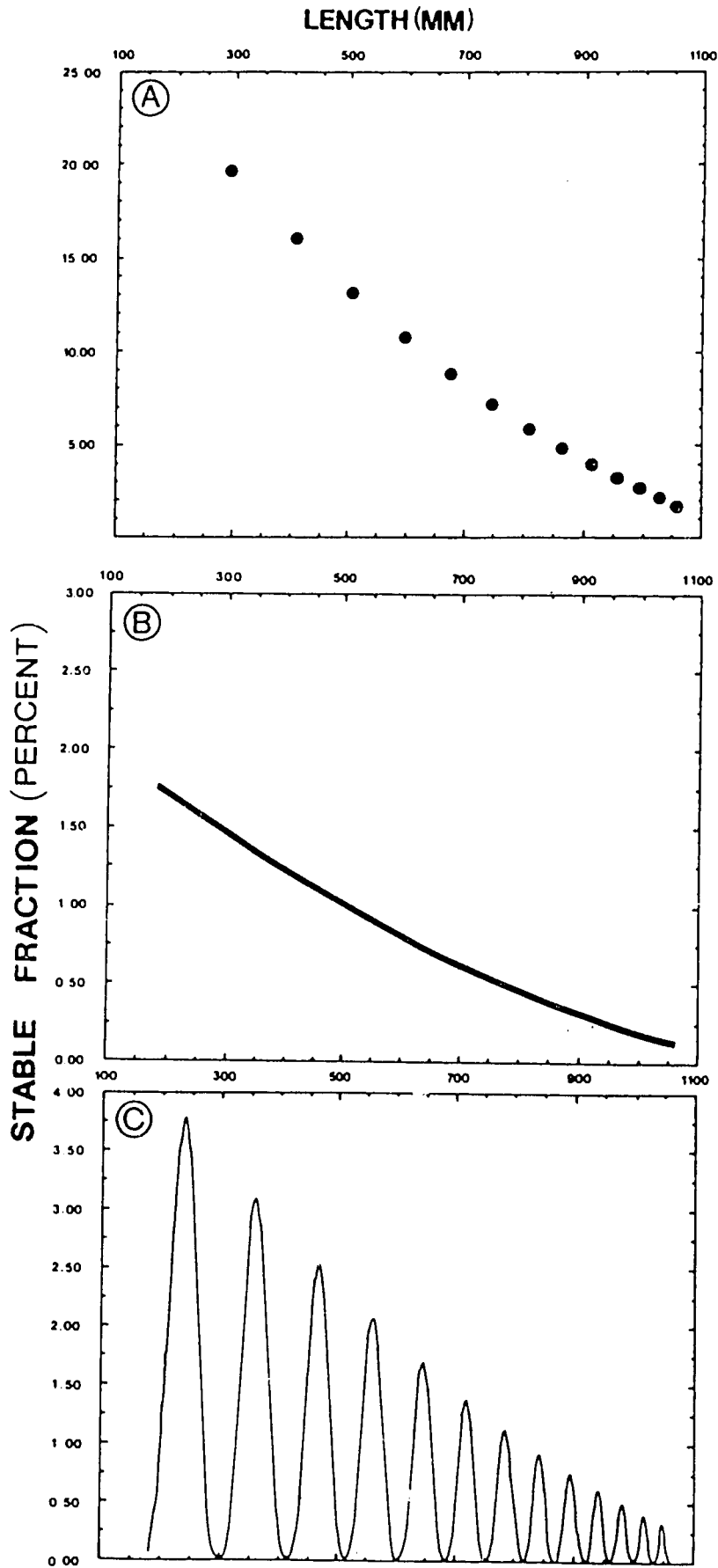
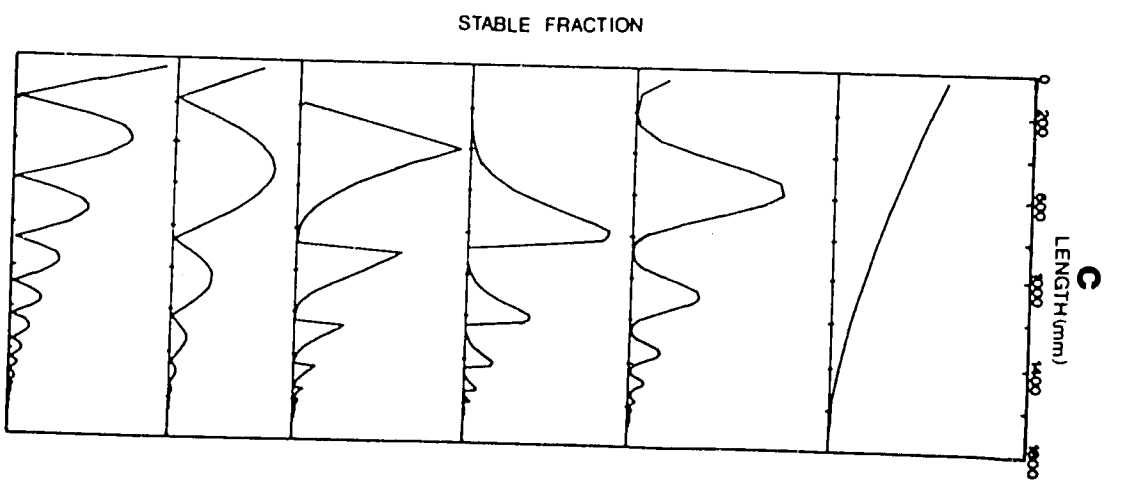
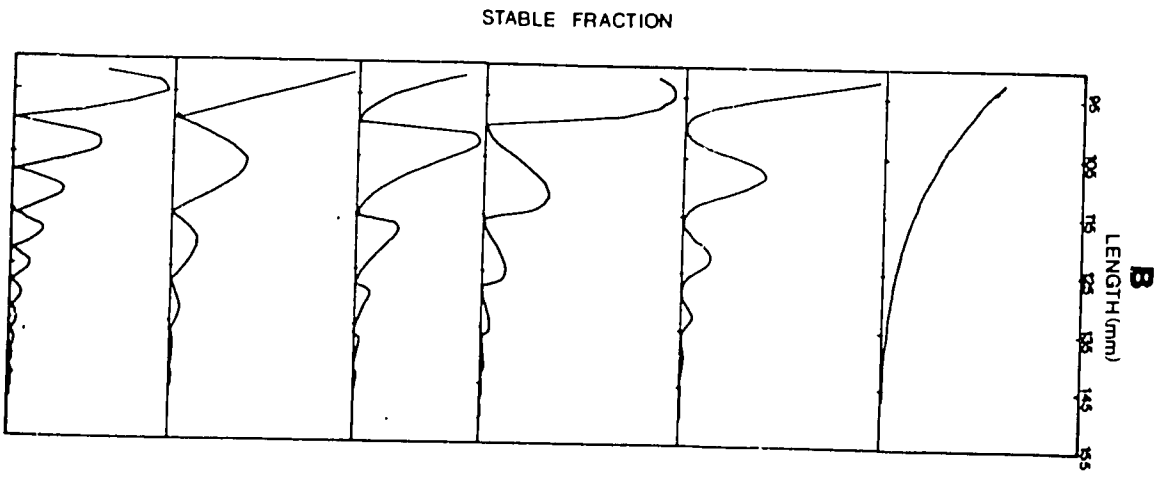
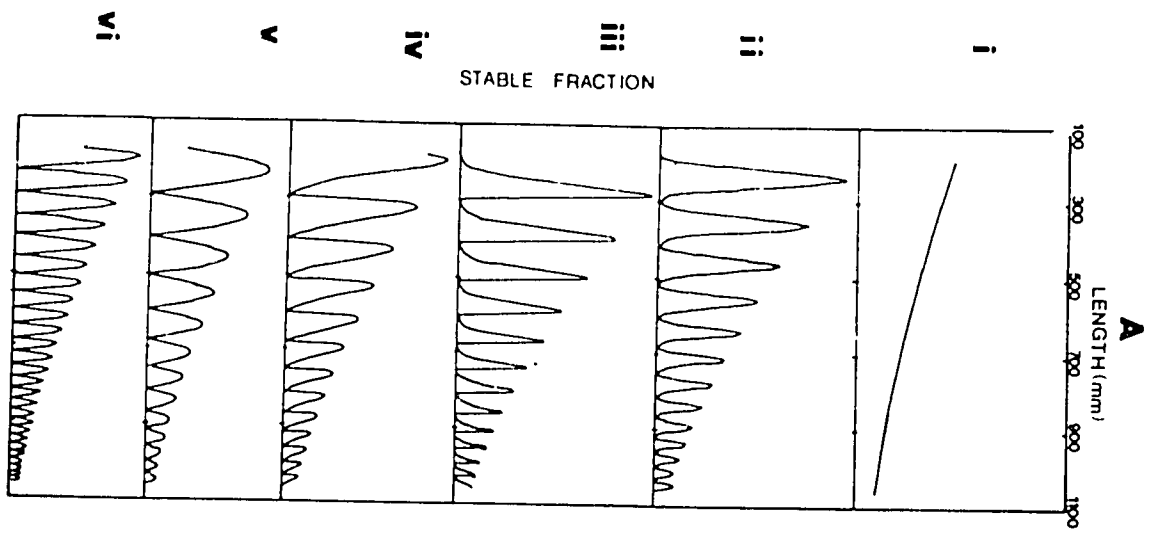


Figure 4

42

Figure 5



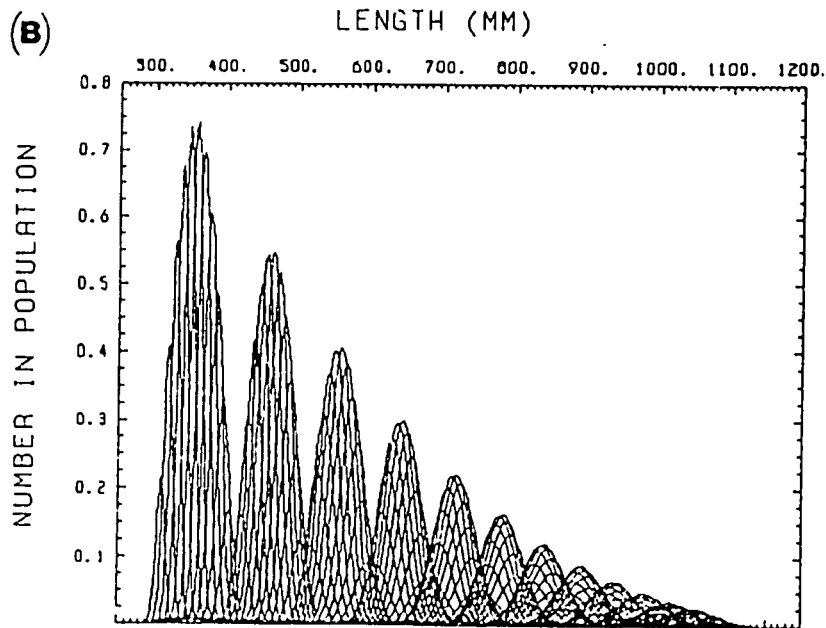
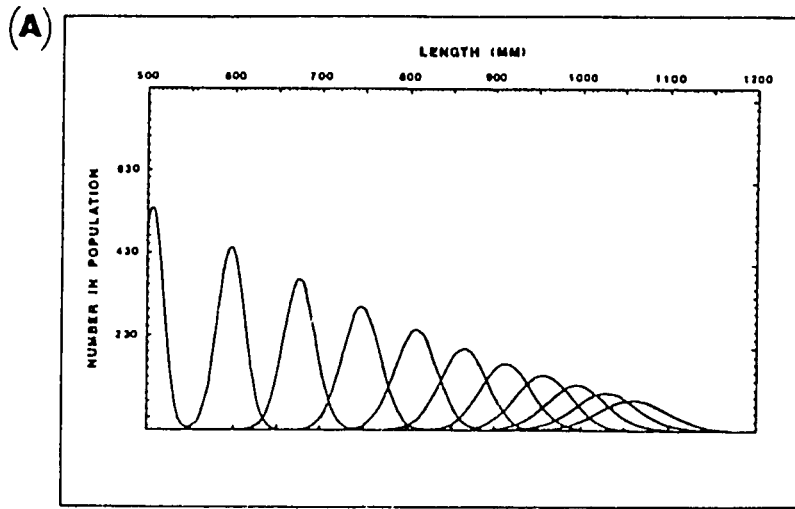


Figure 6