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A Length-Based Numerical Model for Simulating Resource Decision Dynamics

by

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Abstract

A length-based n-cohort population-dynamics age-independent simulation model is described. The model is based upon probability distributions of growth, mortality and recruitment. We simulated population and catch length-frequency distributions according to hypotheses formulated from empirical data and biological processes. The model is used to evaluate traditional stock assessment methods.

Introduction

Methods for improved stock assessment and analysis of marine fisheries are becoming increasingly important because of general resource declines in most fished areas of the world. Of particular importance is the need to assess the status of stocks over specified time-horizons under various management policies to determine the most effective strategy. The difficulty has been in designing an effective dynamic systems model that can be used to examine management policy.

Concise management strategy is typically difficult to articulate because it encompasses several objectives 1) biological - conserve resources while building infrastructure and maximizing physical yield, 2) economic -provide short-term and long-term capital needs while maximizing profits; and 3) socio-political - create employment opportunities, promote development, and equitably distribute resources.

Optimal time-bound policy can be facilitated by using mathematical models (Wagner 1975; Bradley et al. 1977). Time-bound policy has been investigated with several types of dynamic system simulation models (Walters, 1969; Fox, 1975; Getz et al. 1985; Ault and Fox, 1989; Hightower, 1989). Simulation models have advantages over other analytic approaches because the chance of "real" resource failure is minimized by simulating "known systems" against which to test various hypotheses. However, most models have used discrete age-structure, and generally model recruitment as a fixed pulse in time. Discrete models have not proven highly useful for prediction. Given that growth and mortality are continuous processes, and that recruitment to the stock can occur over broad ranges during the year (esp. tropical fishery stocks Ault & Fox (1989)) suggests the need to develop different models. In particular, models that account for the stochastic nature of growth and mortality, and that pattern recruitment so that stock length frequency distributions recapitulate empirical observations.

The objectives of this paper were: (i) to develop a continuous-time probabilistic model for simulating fishery population resource dynamics and to parameterize the model for the three stocks, and (ii) to conduct experiments on system behavior and determine the efficacy of certain stock assessment techniques.

Methods

COREX (COntinuous REcruitment eXperimental simulation) is a mathematical model developed along generalized lines to admit various classes of situations characteristic of fisheries worldwide. COREX is stochastic and length-structured. The stochastic model is based on the nonlinear Leslie matrix (1945, 1948). COREX is configured to simulate any sized time-step. State variables are time-step and age-step specific in the model. For example, population abundance (number) is described by the rate equations

$$\dot{N}(\gamma, j, t) = -Z(j, t) N(\gamma, j, t),$$

$$Z(j, t) = M(j, t) + A(j, t) * SL(j, t) * F(j, t),$$

(1)

where $Z(j,t)$ is the total instantaneous mortality rate with γ, j, and t are denoted as birthrate, age, and time-step, respectively. Total instantaneous mortality is stated generally to facilitate evaluation of seasonal and size-specific patterns of mortality. Since $F(j,t)$ is proportional to the fishing effort, the scaling factor $A(j,t)$ determines the availability of the cohort to the fishing gear(s). The coefficient $SL(j,t)$ allows incorporation of any selectivity pattern.

Stock abundance is modeled using the population abundance and first-order forward equations assuming that time t equals zero after specifying boundary condition N(0). The general forward

2

finite difference of N(t) is

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

Further use of a dot indicates a first-order derivative taken with respect to time. The initial three time-steps from the forward equations are then passed to the centered difference equations generally written as

$$\dot{N}(t) = \frac{N(t+\Delta t) - N(t-\Delta t)}{2\Delta t}.$$ (3)

Typically, fishery stocks may experience a number of population and/or environmental pressures whose effect(s) may not be well understood. However, as a first approximation these effects can be included into the model in a single stochastic term (v) with rearrangement of (2) as

$$N(t+\Delta t) = N(t-\Delta t) + [(2\Delta t\dot{N}(t))(1+v)].$$ (4)

The centered vector of simultaneous nonlinear equations for population abundance, whose first term is defined as some function of the stock, is written

$$N(\gamma+2,0,t+3\Delta t) = f[\Psi(t+2\Delta t)]$$

$$N(\gamma,2,t+3\Delta t) = N(\gamma,0,t+\Delta t) + [2\Delta t\dot{N}(\gamma,1,t+2\Delta t)]$$

$$\vdots$$

$$N(\gamma+3-n,n,t+3\Delta t) = N(\gamma+3-n,n-2,t+\Delta t) + [2\Delta t\dot{N}(\gamma+3-n,n-1,t+2\Delta t)]$$ (5)

The fishable average abundance of cohort j, born with birthdate γ, present during time period t is:

$$\overline{N}(\gamma,j,t) = \int_{t}^{t+\Delta t} N(\gamma,j,t)(1-e^{-Z(j,t)})/Z(j,t)\ dt \quad \forall \gamma.$$ (6)

The total fishable average population in t is given by (6) and integrated with respect to age. A sex-specific maturity schedule was developed by generating two vectors whose elements are the sex fractions per cohort; one vector denoted the average fraction of the cohort that are males during the breeding season $(\Theta_m(j,t))$, and the other the average female fraction $(\Theta_f(j,t))$. The average number of females is then written

$$\overline{N}_f(\lambda,\bullet,t) = \int_{t_m}^{t_\lambda} \Theta_f(j,t)\overline{N}(\gamma,j,t)\ dj \quad \forall \gamma.$$ (7)

3

Ensemble individual length was described by the von Bertalanffy equation (1938) because it seems to fit abalone growth data reasonably well. The equation's limiting form is

$$\dot{L}(j,t) = K(L_\infty - L(j,t)),\tag{8}$$

where L_∞ and K are model parameters. The ensemble allometric weight for an abalone from cohort λ aged j at t was calculated by the power curve

$$W(\gamma, j, t) = \alpha_1 [L(\gamma, j, t)]^{\beta_1} \qquad \forall\, \gamma.\tag{9}$$

The average biomass of the cohort aged j during the finite interval t was expressed by the product of equations (6) and (9). The growth curve presented so far suggests that for any given length there is a determined age, while in reality any given length considered can be composed of a number of possible ages. Since the variance in size at any given age may remain constant or increase with increasing age a continuous power function was used to generalize the pattern of progression of the standard error of the mean average length

$$\sigma(j,t) = \alpha_2 [AGE]^{\beta_2}.\tag{10}$$

Assuming that $P(L|j)$ (read: the probability that given an age j the abalone is length L) comes from a normal probability density distribution (Figure 1a), then the probability distribution of lengths given an age j is (i.e., where **b** and **a** are the constrained upper and lower limits of the prediction interval, respectively)

$$P(a \le L(j,t) \le b) = \phi\left(\frac{b - \overline{L}(j,t)}{\sigma(j,t)}\right) - \phi\left(\frac{a - \overline{L}(j,t)}{\sigma(j,t)}\right).\tag{11}$$

Expression (11) represents the expectation of the numbers of abalone at a given length for a specific time interval. The stochastic age-independent model for ensemble number at a given length for the entire population is

$$\tilde{N}(L) = \int_{t_p}^{t_\lambda} R(\tau - j)\, S(j)\, P(L|j)\, dj.\tag{12}$$

The function for fecundity dependent upon a given weight was derived from information on the production of viable ova at

4

discrete ages and incorporated into a continuous power function following Ault (1985):

$$\zeta(j,t) = \alpha_3 [W(\bullet, j, t)]^{\beta_3}.$$ (13)

There are two fundamental spawning strategies. Spawning in temperate zones is characterized by discrete-pulses periodicity, while tropical zone spawning is characterized by quasi-continuous pulses of variable magnitude (Ault & Fox 1989b). Others may lie somewhere between because the spawning period is protracted over a specified period of the year and cohorts appear to be produced in a continuum. We defined a "cohort" as a set of larvae from the same stock which are issued (i.e. spawned) at the same event and which subsequently enter (i.e. recruit to) the population at the same instant in time.

Spawning is the precursor to recruitment. Ault and Fox (1989) showed seasonal peaks over protracted spawning seasons for many tropical and subtropical marine species. We used the beta distribution as a rough approximation of the seasonal spawning behavior within a year because of the variety of shapes the flexible statistical model can assume (Law & Kelton, 1982; Ross, 1985) (Figure 1b)

$$C(t) = \frac{t^{\alpha_1-1}(1-t)^{\alpha_2-1}}{\beta(\alpha_1,\alpha_2)} \quad if \ 0 < t < 1,$$

$$where \ \beta(\alpha_1,\alpha_2) = \frac{\Gamma(\alpha_1)\Gamma(\alpha_2)}{\Gamma(\alpha_1+\alpha_2)}.$$ (14)

This allowed for a spectrum of population density distributions. The most direct measurement of the adult stock may be total egg production (Parrish et al. 1986; Rothschild & Fogarty 1989). Mature fecund potential which becomes input to a density-dependent nonlinear recruitment function at some time interval Δt was modeled as

$$\psi(t) = \int_{t_m}^{t_\lambda} \overline{N}_f(\gamma, j, t) \ \zeta(j, t) \ \omega(j, t) \ C(j, t) \ dj.$$ (15)

Cohort production is defined on the stock level and is proportional to the interval of integration, the annual distribution of spawning, and some annual recruitment scalar. The intensity of a cohort's recruitment at some time τ is a function of the stock's spawning potential at some earlier time $\tau-t$. What remains is the necessary connection of Paulik's (1973) diagram to translate the stock's fecund potential to recruits via the pathway of eggs to larvae to recruits.

Environmental variability is thought to have a substantial

influence on abalone stocks, primarily affecting survival from spawning to the time of recruitment (i.e. $t+\tau$). Several recent SRR studies have modelled environmental variability with multiplicative error terms applied to a Ricker (Walters & Hilborn 1976; Walters & Ludwig 1981), Beverton & Holt (Hightower & Grossman 1985, 1987; Hightower & Lenarz, 1989), or the Getz functions (Swartzman et al. 1983; Koslow, 1989; Getz & Haight, 1989) to estimate the probability that the stock biomass will fall below a given level (Getz & Haight, 1989).

A continuous systems generalization of Fox's (1973) discrete approach was incorporated for simulating density and abundance in the catch. Yield in weight and yield in numbers are:

$$Y_w(\bullet, t) = \int_{t_{\rho'}}^{t_\lambda} A(j, t)\, SL(j, t)\, F(j, t)\, \bar{N}(\gamma, j, t)\, \bar{W}(\gamma, j, t)\ dj, \qquad (16)$$

$$Y_n(\bullet, t) = \int_{t_{\rho'}}^{t_\lambda} A(j, t)\, SL(j, t)\, F(j, t)\, \bar{N}(\gamma, j, t)\ dj. \qquad (17)$$

Mean weight in the total catch is the ratio of equation (13) over (14). Mean length in the total catch for the interval is

$$\bar{L}(\bullet, t) = \frac{\displaystyle\int_{t_{\rho'}}^{t_\lambda} A(j, t)\, SL(j, t)\, F(j, t)\, N(\gamma, j, t)\, L(j, t)\ dj}{Y_n(\bullet, t)}. \qquad (18)$$

Simulation experiments for three stock-types were conducted from life history parameters developed from the literature (Table 1). The factorial design of the simulation investigation used 72 possible combinations of input classes of spawning-recruitment, growth, and catch data aggregation patterns (Table 2). The selected range of recruitments, growth coefficients and catch aggregation were designed to encompass the degree of variability encountered.

Equilibrium yield-per-recruit (YPR) surface lattice points were generated for several ranges of the base parameters. Life history features included 1:1 sex ratios, age-constant and time-invariant growth and survivorship, and continuous uniform recruitment (Figure 4).

Timing and Accounting

COREX allows substantial flexibility in modeling the component

relationships and interactions added to the derivatives. All population statistics are accumulated on the time-step specific basis. $N(\gamma,j,t)$ is either the number of viable fertilized ova cast, or the number of larvae hatched in period γ which are in their j-th period of life during a given time-step t. For example, for a monthly time-step, then $N(13,12,t)$ 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. These conditions dictated that a nonlinear search routine be employed to extract age-independent length frequency distributions from age-length information. The search was accomplished by scanning the probability surface and reorganizing observations by specified levels of discretization. To eliminate searching of void probability space, Chebyshev's nonparametric inequality was employed to allow full knowledge of the probability bounds (Ross 1985). To contrast the COREX algorithm with the traditional discrete-class simulation models, assume that a year (n) can be divided into quasi-continuous time-steps of any width (m) (i.e., months, days, minutes, etc.). Thus, for any width time interval (Δt) there will exist (m x n) elements of a probability density distribution of individuals. Deterministically, the net effect would be to increase the number of recruitments along the time line from the traditional n-cohort approach (i.e. where n≡ the number of annual age groups in the stock), to a resultant m x n dimensioned distribution (Figure 2b). COREX can produce populations conforming to any type of probability density distribution. For example, a beta normal distribution of annual recruitments produces a series of age-related modes (Figure 2c), and with probability, at least ten or more older annual age groups can be of exactly the same length.

Results

When recruits are generated with a normal distribution with period one year, and grow according to a probabilistic function, the result is a complex distribution of overlapping cohorts at lengths at any given moment of time (Figure 3).

Traditional modeling assumes that individuals are discretely distributed in time. Each annual cohort is separated by a time-bound increment which is a functional response to the growth and recruitment processes. Pooling the yield distribution by increasing increments of length embeds several ages among one another in the length frequency diagram. Simulations with a fast growing life history type (i.e. high growth coefficient K) with an expanding variance of length at age shows that apparently most if not all, classes of recruitment patterns (i.e. normal, beta, trigonometric and retracted, protracted, continuum) result in similar length frequency distributions. This suggests that using modal analysis on even marginally fast growing stocks when the recruitment may be protracted leads to erroneous conclusions about

7

the population and its estimated rate parameters. This condition is exacerbated for analysis with short lived-fast growing (i.e. high M-high K ≡ HMHK) stocks. Only in the very long lived, slow growing (i.e. low M-low K ≡ LMLK) stocks were any "real" age related modes discernable, but those were strictly for the youngest age groups. In cases where "fast" growing animals were involved (i.e. K is 50% greater than for red abalone base parameters), as many as 10 annual age classes could be nested in no more than two discernable modes (c.f. Figure 3b).

YPR values became time constant (at $n \times m-1$ time steps) for quasi-continuous populations with time constant recruitments. Global maxima existed for the LMLK life history, and medium M-high K (i.e ≡ MMHK) stock cases. Maxima became more pronounced, but so did the YPR declines with a significant declines in YPR at high fishing mortality rates. The HMHK YPR maximizes close to the origin (Figure 4c).

For continuously recruiting populations averaged over a fixed time increment, there is a significant transition of the age of maximum biomass to the younger ages with increased fishing mortality. For an LMLK stock, the rate of transition with only moderate fishing mortality rates is comparatively much greater than for stocks with higher M & K values. For those higher M & K stocks, the age of maximum biomass remains relatively constant; however, the total percentage of biomass remaining declines markedly at that age.

LMLK relative reproduction is plotted against deterministic lengths for various levels of exploitation by nonlinear coupling of the functions describing recruitment, growth and survivorship along with age(size) specific information on maturation, fecundity and sex ratio (Figure 5). Seasonal variation in the inputs caused the annual maxima to shift seasonally (Figure 5b). Unexploited stocks appeared to receive the bulk of their reproductive potential from the older size strata. The stock's quantity of reproductive contribution declines markedly and shifts its major contribution towards the younger groups with only minor increases in the fishing mortality rates. For LMLK, moderate levels of fishing mortality (i.e. $F \leq 0.2$) reduced the stock's reproductive potential by more than 50 percent, and caused the strata of equilibrium maximum contribution to be shifted sharply to younger groups (Figure 5).

The transition of average length observed in the catch bears strong correlation to the recruitment pattern under a constant effort strategy (Table 3). The observed pattern is periodic; but annually stationary if the sampling is weighted intra-annually in proportion to the true effective fishing effort and population abundance. If sampling is proportional within months but not between months, then the annual stationary value will be biased, the degree to which is determined by the specific recruitment pattern (Table 4). In this study, pulsed retracted recruitments

8

had the largest coefficients of variation (CV) for all factor combinations of growth and catch aggregation. Continuous uniform recruitments produce time-constant average lengths. However, both unimodal (normal) and bimodal recruitments showed annual cycles of average lengths, the number of cycles being equal to the number of recruit modes. With beta recruitments, the progression of average lengths showed marked skewness which was inversely proportional to the type of recruitment pattern. The degree to which average length varied seasonally was also driven by the life history parameterization; for oscillations in average length increased with increased values of M and K.

Length cohort analysis (Jones 1981) was conducted on LMLK simulated length frequency distributions with an $F/\Delta t$ fishing mortality rate at an annual fishing mortality rate of 0.1 (Table 5). The bias in the total mortality estimation for various combinations of growth variance and catch aggregation ranged from 19.20 to 109.7 percent. The bias decreased with increasing aggregation for the deterministic and low stochastic growth functions. For increasing aggregation levels, bias increased or was approximately steady for increases from the 8 to the 16 power curves. The CV of Z decreased with increasing aggregation for deterministic growth; however, increases in the CV were proportional to the increased variation about the growth function. Estimates of total time to transit a given length increment were generally biased and estimates of Δt became grossly overestimated with increasing variance about the growth curve. This resulted in a upwardly biased allocation of individuals in given length classes. Estimated time in intervals were consistently positively biased and increased with increasing variance, but in most cases estimated values were within 10-15% of the actual. Because convergence was poor for LMLK at all levels of recruitment, growth and aggregation at low input Z; a similar analysis was conducted at an annual F of 0.4 (Table 5b). In general, these estimates were markedly improved, but still were significantly biased.

Discussion

The analyst's decision making power will be greatly enhanced with availability of models which emerge as syntheses of knowledge of a range of actual cases. COREX was effective depicting fishery resource dynamics. The general focus of this study was to deal with resource attributes by examining base parameter ranges in the continuous model, and then expand the interpretation by extrapolation to other stock-type variants of the base life history.

When tested against COREX simulated data most traditional fishery assessment techniques were biased, i.e.: (i) modal analysis was of dubious validity; (ii) length cohort analysis was consistently positively biased and was most affected by the shape of the annual recruitment, the technique was also biased by growth

9

variability and catch aggregation; (iii) yield-per-recruit may be useful for generalizations, but the eumetric fishing concept is weak for density-dependent or hermaphroditic populations; (iv) policy derived from logistic assessment models should be conservative in transitional dynamics as seasonal recruitments influenced the observed catch-per-unit-effort and catch average length statistics.

Precise interpretation of catch length frequency distributions depends strongly upon the manner in which the data are collected and assimilated. Simulation with COREX has shown that when abalone catch distributions exhibiting stochastic growth are aggregated, the majority of the older age groups become occluded due to significant overlap of age strata. The situation is exacerbated for stocks with two or more annual recruitment modes. Thus, under certain conditions statistical fitting of dynamic population trends may cause mis-estimation of key management variables including total mortality and its correlates, sustainable yield and optimum fishing effort. For stocks with substantial seasonal variation in recruitment, an abundance of small samples taken at multiple intervals of the recruitment domain and pooled, would be superior to a single large sample taken at an arbitrarily fixed point in time.

Both age- and length-based cohort analysis are based on the assumption that information about numbers caught provides useful information about the total stock. The rapidity of convergence is a function of total mortality from the youngest to the oldest ages. It is not a function of the number of time-steps involved. The length cohort analysis technique: (i) makes no allowance for fish of different ages to be of the same length, (ii) assumes that the CV of length for a given time interval is less than the CV of age for a given length interval. These facts contribute to bias in Z estimation. Because LMLK have a relatively low Zs tolerance, depending upon the specific size of first capture regulations, significant numbers of individuals may contribute to catch at all levels of age. This would also inflate the cumulative mortality estimates in the older age groups. On the other hand, abalone with increased M and K were much more reliably estimated than red abalone due primarily to higher Z rates. Z estimation bias seemed to peak at intermediate levels of stochastic growth. The general failure of cohort analysis to provide any meaningful results in a situation where all the inputs were completely specified to the routine, suggests a lack of robustness and concern for its use without some modification of the existing theory. Much of the bias generated by Jones' analysis may be reduced by using larger length intervals so that cumulative fishing mortality within intervals is larger and the approximate conditions of Pope's (1972) approximation are met. A more appropriate extension of the methodology might be to use the catch equation (Murphy 1965) and directly substitute the representation of time in terms of length analogous to the Δt equation of Jones (1981) and then solve the

system numerically.

We have shown that LMLK with protracted normal recruitments have biomass on length structures exhibiting series of local maxima and a global maximum. Translated as age-independent relative to the stock's nonlinear reproductive potential two facts become apparent: (1) the continuous function has time-bound peaks, and (2) the global maximum occurs at the older ages(sizes) for a 1:1 sex ratio. For distorted (i.e. unbalanced) sex ratios the peak will move towards the younger ages. Therefore, if seasonal or temporal shifts in the stock's reproductive activity occurs, some cohorts may produce sub-optimal reproductive output in a given season. This will not be the result of poor spawn quality, but rather because the cohort's may miss their "reproductive window" (Bakun et al 1979; Pauly & Navaluna 1983). Fishing also promotes shifts in biomass maxima to the younger age groups, the rate of transition is exacerbated for slow growing stocks. When continuous recruitment following some distribution is coupled with high stock growth rates and low survivorship to age probabilities, then biomass peaks passing certain ages (sizes) at critical periods may implicate increased recruitment instability. In addition, population density-dependence or competitive cohort influence could also adversely impact age-specific reproductive values. Thus, certain stock genera may oscillate more within years. This class of effects may have important and resounding stock implications: For example, consider the bioenergetics of two fish, both past minimum reproductive age and of identical length but with four years difference in age. These two LMLK individuals may, with probability, have the same body weight but they undoubtedly have different potentials to produce viable gametes. Several authors have shown that the quality of ova produced by given age strata of fishes can vary, and Hunter (1985) has indicated that the quality of ova produced per age strata in serially spawning fish can also vary within a year. In our example, the older individuals would possess a gonad which is four years more reproductively advanced (i.e. more extensive trabecular development), and this fact would seem to imply a higher expectation of fecundity relative to the younger individual, sans the effect of reproductive senility and necrosis (Giorgi & DeMartini 1977).

Although the birth functions presented here are only a few of the myriad of possible models of seasonally protracted recruitments the conclusions for stationary populations may have more general interpretations. Seasonal variation of parameters is not likely to be of importance to population behavior from a long term point of view, other than determining those factors which may force the seasonal oscillations and if those oscillations have domains of attraction. If growth, survivorship or any other factors are seasonally variable, or density-dependent (i.e. from competition or predation), then the resultant estimates may be directionally biased. We have shown that LMLK stocks are very sensitive to exploitation and will respond with significant reductions in stock

11

biomass and reproductive potential at even relatively low fishing mortality rates. "Optimal" stock reproductive properties are probably achieved at low fishing mortality rates. This suggests that optimal long-term benefits from stocks with LMLK characteristics are enhanced by a low fishing mortality. Finally, the consequences of interactions for management may depend on a number of factors such as the time relations between the fishing season and the growth and recruitment seasons and the interaction magnitude between biophysical forces (Rothschild 1986). Catches unevenly distributed throughout the year can lead to significantly large relative errors in stock sizes estimated from VPA. In most cases, analytical formulations are not robust to dynamical phenomena. Thus, decision makers can benefit from using a risk analysis based approach versus the very simple expectation of fixed-point equilibrium outcomes.

The power of the COREX model for use in fishery management assessments resides principally in its ability to produce high dimensional intricate population structured effects and policy scenarios for highly dynamic stocks. By identifying areas of special stock sensitivity to exploitation, strategies which minimize the chance of biological failure (i.e. spawning stock potential falling below given levels) and maximize the net economic rent from the resource may be determined. This feature allows fishery managers to establish effective optimum policy benefit strategies.

Glossary of Key Parameters

$N(\gamma,j,t)$ $\equiv$ total number of fish in cohort γ aged j at the beginning of period t.

$F(j,t)$ $\equiv$ instantaneous rate of fishing mortality of a fully available cohort.

$A(j,t)$ $\equiv$ size- or age-specific availability factor for the jth cohort in period t. If partial selection is required then the availability multiplier is $A(j,t)SL(j)f(j,t)$, where $f(j,t)$ is the level of effective fishing effort on cohort j in period t.

$SL(j,t)$ $\equiv$ selectivity or catchability coefficient for the jth cohort in period t.

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

$W(\gamma,j,t)$ $\equiv$ ensemble average weight of an individual in cohort γ aged j at the beginning of interval t.

t_m $\equiv$ minimum age of sexual maturity.

t_λ $\equiv$ oldest age observed in the stock.

$\sigma(j,t)$ $\equiv$ standard error of length for fish aged j at some time t.

AGE $\equiv$ the continuous age of a fish at time t.

α_2 $\equiv$ α-coefficient of the length standard error power curve model.

β_2 $\equiv$ β-coefficient of the length standard error power curve model.

$R(\tau-j)$ $\equiv$ Recruitment at $\tau-j$ periods ago.

$S(j)$ $\equiv$ Survivorship to at least an age j.

$p(L|j)$ $\equiv$ probability of a fish being length L at a given age j.

$Y_w(t)$ $\equiv$ yield in weight in period t.

$Y_n(t)$ $\equiv$ yield in number in period t.

$\varsigma(j,t)$ $\equiv$ average measure of production of viable ova of a female fish aged j at time t.

α_3 $\equiv$ α-coefficient of the fecundity power curve model.

β_3 $\equiv$ β-coefficient of the fecundity power curve model.

$R(t+\tau)$ $\equiv$ Recruitment of recruits produced at the instantaneous slice of time $(t-\tau)$, where τ is defined as the time lag between spawning and subsequent recruitment.

α_4 $\equiv$ age of recruitment to the reproductive portion of the stock for fish following the equations specified.

β_4 $\equiv$ average measure of egg production for fish aged j during the period t.

$\theta(j,t)$ $\equiv$ proportion of females in the jth age group during period t.

$\omega(j,t)$ $\equiv$ proportion of female in the jth 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.

$\Psi(t)$ $\equiv$ potential of the spawning stock to produce recruits in some period t.

$f[\Psi(t)]$ $\equiv$ some function of the parent stock, most often represented by the spawning biomass (Doubleday 1975; Deriso 1980; Shepherd 1982).

υ $\equiv$ normally distributed random variable with a mean of 0.0 and a variance of σ^2.

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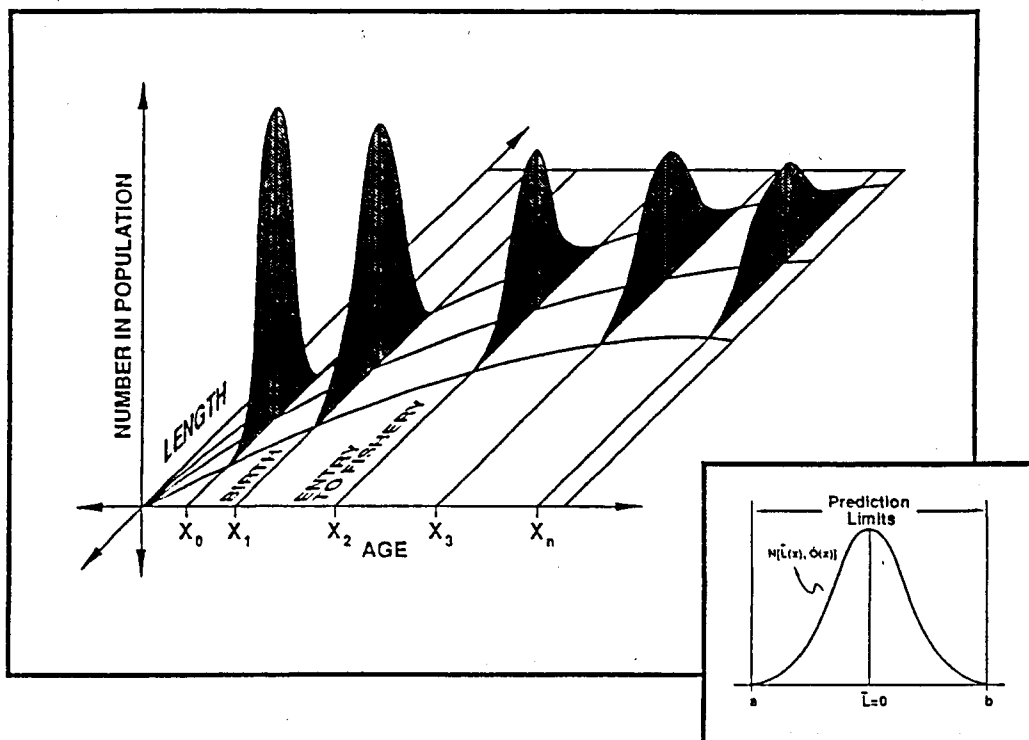
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List of Figures

(A)

(B)

(A)

(B)

(C)

Figure 2:

(A)

(B)

Figure 3:

A

13
8
5
2
0

AGE
OF FIRST
CAPTURE

0.5

1.0

FISH MORTALITY

Low M
Low K

B

10
6
4
2

AGE
OF FIRST
CAPTURE

Mid M
High K

0   1.0   2.0
FISH MORTALITY

C

6
5
4
3
2
1
0

AGE
OF FIRST
CAPTURE

High M
High K

0   1.0   2.0
FISH MORTALITY

Figure 4:

22

(A)

(B)

Figure 5:

Table 1a: Life history parameters developed for model stock dynamics (A) grouper, (B) scombrid, (C) engraulid.

1A Grouper

Description	Parameter	Value
Oldest annual age in the Catch	t_λ	13.0 years 22.0 years
Recruitment to Exploited Phase	t_ρ	13.0 months
Minimum age of Reproductive Maturity	t_m	49.0 months 28%-III,51%-IV
Size/age of First Capture	t_ρ'	13.0 months
Ultimate Length Ultimate Weight Time at which weight/ length of fish equals zero Growth coefficient	L_∞ W_∞ t_o K	1290.0(1122.6) mm 25.032719(16.30) kg -1.127(4.0514E-3) years 0.122(0.18343) year^{-1}
Natural Mortality	M	0.2 year^{-1}
Fishing Mortality	F	Variable
α-coefficient from fecundity on weight relation β-coefficient from fecundity on weight relation	α β	10899.5251 2.58077181
A-coefficient from weight on length relation B-coefficient from weight on length relation	a b	1.2E-08(3.971E-8) 2.996(2.8238)
α-coefficient from $\bar{L}$ stnd error on age relationship β-coefficient from $\bar{L}$ stnd error on age relationship	α_{sI} β_{sI}	0.10398 0.75865
$L_c = 304.90623$ $L_\lambda = 1059.81036$		

1B Scombrid

Description	Parameter	Value
Oldest annual age in the Catch	t_λ	10.0 years
Recruitment to Exploited Phase	t_ρ	11.0 months
Minimum age of reproductive maturity	t_m	13.0 months
Size/age of first capture	t_ρ'	11.0 months
Ultimate length Ultimate weight Time at which weight/ length of fish equals zero Growth coefficient	L_∞ W_∞ t_0 K	1690.0 mm 99.1272728 0.83333333 years $0.60(0.42)$ year^{-1}
Natural mortality	M	0.80 year^{-1}
Fishing mortality	F	Variable
α-coefficient from fecundity on weight relation β-coefficient from fecundity on weight relation	α β	13226.0815 1.44288696
A-coefficient from weight on length relation B-coefficient from weight on length relation	a b	3.894E-08 3.020
α-coefficient from $\bar{L}$ stnd error on age relationship β-coefficient from $\bar{L}$ stnd error on age relationship	α_{sI} β_{sI}	0.10398 0.75865
$L_c = 82.42223078$ $L_\lambda = 1683.09336$		

1C Engraulid

Description	Parameter	Value
Oldest annual age in the Catch	t_λ	7.0 years
Recruitment to Exploited Phase	t_ρ	7.0 months
Minimum age of reproductive maturity	t_m	6.0 months
Size/age of first capture	t_ρ'	7.0 months
Ultimate length Ultimate weight Time at which weight/ length of fish equals zero Growth coefficient	L_∞ W_∞ t_o K	159.1 mm 4.6826E-2 kg -2.08 years 0.32 year^{-1}
Natural mortality	M	0.80 year^{-1}
Fishing mortality	F	Variable
α-coefficient from fecundity on weight relation β-coefficient from fecundity on weight relation	α β	111.75 1.47632
A-coefficient from weight on length relation B-coefficient from weight on length relation	a b	1.21E-5 2.9733
α-coefficient from $\bar{L}$ stnd error on age relationship β-coefficient from $\bar{L}$ stnd error on age relationship	α_{si} β_{si}	0.026947 0.7.593E-1
L_c = 91.2522463 L_λ = 150.394692		

26

Table 2A: Classes of dimensioned factors and ranges used in the fishery model efficacy examination.

Main Factor	Nested Factor	Numerical Designation
	Discrete	11
	Continuous	12
Recruitment	Protracted I (Normal)	13
	Protracted II (Beta Skewed Left)	14
	Protracted III (Beta Skewed Right)	15
	Protracted IV (Bimodal)	16
	Deterministic	21
Growth	Probabilistic I $[1 \times \sigma (j)]$	22
	Probabilistic II $[8 \times \sigma (j)]$	23
	Probabilistic III $[16 \times \sigma (j)]$	24
	1.0 mm	31
Catch Aggregation	2.5 mm	32
	5.0 mm	33

Table 2B: Factorial design for the simulation experiment to systematically examine the influence of the main dimensional factors of recruitment, growth, and catch data length increment aggregation. The factorial analysis was conducted on every combination for each of two generic life history groups: (1) groupers, and (2) scombrids.

Factorial Permutations & Combinations			
σ_0	1.) 11,21,31 2.) 11,21,32 3.) 11,21,33	25.) 13,21,31 26.) 13,21,32 27.) 13,21,33	49.) 15,21,31 50.) 15,21,32 51.) 15,21,33
σ_1	4.) 11,22,31 5.) 11,22,32 6.) 11,22,33	28.) 13,22,31 29.) 13,22,32 30.) 13,22,33	52.) 15,22,31 53.) 15,22,32 54.) 15,22,33
σ_2	7.) 11,23,31 8.) 11,23,32 9.) 11,23,33	31.) 13,23,31 32.) 13,23,32 33.) 13,23,33	55.) 15,23,31 56.) 15,23,32 57.) 15,23,33
σ_3	10.) 11,24,31 11.) 11,24,32 12.) 11,24,33	34.) 13,24,31 35.) 13,24,32 36.) 13,24,33	58.) 15,24,31 59.) 15,24,32 60.) 15,24,33
σ_0	13.) 12,21,31 14.) 12,21,32 15.) 12,21,33	37.) 14,21,31 38.) 14,21,32 39.) 14,21,33	61.) 16,21,31 62.) 16,21,32 63.) 16,21,33
σ_1	16.) 12,22,31 17.) 12,22,32 18.) 12,22,33	40.) 14,22,31 41.) 14,22,32 42.) 14,22,33	64.) 16,22,31 65.) 16,22,32 66.) 16,22,33
σ_2	19.) 12,23,31 20.) 12,23,31 21.) 12,23,33	43.) 14,23,31 44.) 14,23,32 45.) 14,23,33	67.) 16,23,31 68.) 16,23,32 69.) 16,23,33
σ_3	22.) 12,24,31 23.) 12,24,32 24.) 12,24,33	46.) 14,24,31 47.) 14,24,32 48.) 14,24,33	70.) 16,24,31 71.) 16,24,32 72.) 16,24,33

Table 3: Effects of intra-annually periodic recruitment on the observed average lengths from the simulated catch over a one year cycle for annually stationary, deterministic populations for two stock genera under six recruitment hypothesis delineated in Table 2B. C.V = coefficient of variation.

(A) LMLK (Stationary average length in the catch = 574.5925903).

Time-Step	Recruitment Types					
	11	12	13	14	15	16
1	536.1960	574.5926	586.9229	584.5286	565.1949	579.7186
2	543.8209	"	591.6614	570.5530	572.4560	576.5786
3	551.3687	"	591.8207	562.1321	579.3581	572.1748
4	558.8399	"	586.5562	558.6614	585.4366	569.6138
5	566.2357	"	577.5657	559.0503	589.9351	571.2499
6	573.5566	"	568.0766	562.2532	591.8564	578.5203
7	580.8037	"	561.1080	567.3681	590.1684	579.7186
8	587.9774	"	558.4203	573.6552	584.2076	576.5786
9	595.0784	"	560.2958	580.5421	574.1873	572.1748
10	602.1077	"	565.6959	587.6398	561.6787	569.6138
11	609.0658	"	572.7674	594.7390	550.3112	571.2499
12	615.9536	574.5926	580.0223	601.7716	557.7933	578.5203
Weighted avg.	574.5926	574.5926	574.5926	574.5926	574.5926	574.5926
Arithmet.avg.	574.7504	"	575.0761	575.2412	575.2153	574.6427
C.V (%)	4.5326	0.0	2.1564	2.5225	2.4224	0.6939

29

(B) MMHK (Stationary average length in the catch = 637.160767).

Recruitment Types

Time-Step	11	12	13	14	15	16
1	432.4848	637.9161	728.6788	668.4839	606.8442	668.2767
2	482.6075	"	749.7890	589.4332	649.6105	646.4812
3	530.5176	"	736.6697	555.6447	688.8627	621.4312
4	576.7239	"	689.8386	549.9246	721.3037	610.0477
5	621.0891	"	631.1790	562.1509	741.1935	621.9846
6	663.6860	"	583.3896	586.3124	741.3644	664.5179
7	704.5856	"	557.3621	618.3630	716.8347	668.2767
8	743.8553	"	554.8454	655.1700	669.6260	646.4811
9	781.5599	"	573.3675	694.1475	610.2159	621.4312
10	817.7619	"	607.6261	733.2924	553.4821	610.0476
11	852.5215	"	649.3032	771.3772	515.2013	621.9846
12	885.8958	637.9161	690.7698	807.9844	561.9677	664.5179
Weighted Average	637.9161	637.9161	637.9161	637.9161	637.9161	637.9161
Arithmetic Average	674.4416	"	646.0682	649.3750	648.0422	638.7899
C.V. (%)	22.0253	0.0	11.1243	13.4816	12.0202	3.6564

Table 4: Annual average lengths in the catch and the associated
coefficients of variation for elements of the factorial
design for the simulation experiment to systematically
examine the influence of the main dimensional factors of
recruitment, growth, and catch data length increment
aggregation on the behavior of the length frequency and
average length statistics for: (A) LMLKs, and (B) MMHKs.

(A) LMLK (Stationary average length in the catch = 574.59259).

Average Length (Coefficient of Variation %)		
1.) 568.57(4.67)	25.) 566.88(2.25)	49.) 567.05(2.63)
2.) 567.74(4.82)	26.) 566.83(2.23)	50.) 567.00(2.61)
3.) 568.64(4.61)	27.) 567.01(2.29)	51.) 567.17(2.64)
4.) 569.11(4.60)	28.) 567.43(2.20)	52.) 567.60(2.57)
5.) 569.16(4.71)	29.) 567.45(2.23)	53.) 567.62(2.61)
6.) 569.07(4.54)	30.) 567.44(2.20)	54.) 567.60(2.56)
7.) 569.44(4.64)	31.) 567.75(2.20)	55.) 567.92(2.58)
8.) 569.46(4.63)	32.) 567.77(2.20)	56.) 567.93(2.57)
9.) 569.31(4.66)	33.) 567.61(2.22)	57.) 567.78(2.60)
10.) 569.46(4.65)	34.) 567.76(2.21)	58.) 567.93(2.58)
11.) 569.41(4.64)	35.) 567.71(2.20)	59.) 567.05(2.64)
12.) 569.34(4.70)	36.) 567.63(2.24)	60.) 566.96(2.69)
13.) 566.38(0.0)	37.) 567.02(2.53)	61.) 566.43(0.69)
14.) 566.34(0.0)	38.) 566.97(2.51)	62.) 566.39(0.74)
15.) 566.50(0.0)	39.) 567.15(2.56)	63.) 566.54(0.60)
16.) 566.95(0.0)	40.) 567.57(2.47)	64.) 567.00(0.69)
17.) 566.96(0.0)	41.) 567.59(2.51)	65.) 567.01(0.73)
18.) 566.96(0.0)	42.) 567.58(2.47)	66.) 567.00(0.63)
19.) 567.26(0.0)	43.) 567.89(2.48)	67.) 567.17(0.72)
20.) 567.28(0.0)	44.) 567.90(2.47)	68.) 567.33(0.71)
21.) 567.12(0.0)	45.) 567.75(2.50)	69.) 567.17(0.72)
22.) 567.27(0.0)	46.) 567.90(2.48)	70.) 567.32(0.71)
23.) 567.23(0.0)	47.) 567.85(2.47)	71.) 567.28(0.71)
24.) 567.13(0.0)	48.) 567.77(2.52)	72.) 567.18(0.71)

(B) MMHK (Stationary average length in the catch = 637.91608)

Average Length (Coefficient of Variation%)		
1.) 568.57(24.00)	25.) 601.64(12.43)	49.) 605.07(15.07)
2.) 631.38(24.63)	26.) 601.65(12.43)	50.) 605.09(15.09)
3.) 632.71(24.54)	27.) 603.10(12.31)	51.) 606.51(14.93)
4.) 631.47(24.58)	28.) 601.81(12.45)	52.) 605.25(15.09)
5.) 631.47(24.59)	29.) 601.57(12.44)	53.) 605.01(15.09)
6.) 632.55(24.52)	30.) 602.99(12.33)	54.) 606.41(14.94)
7.) 633.51(24.09)	31.) 605.33(12.25)	55.) 608.62(14.77)
8.) 633.60(24.05)	32.) 605.47(12.22)	56.) 608.74(14.73)
9.) 633.93(23.98)	33.) 605.88(12.18)	57.) 609.15(14.68)
10.) 633.53(24.14)	34.) 612.45(11.84)	58.) 615.41(14.11)
11.) 633.54(24.10)	35.) 612.54(11.83)	59.) 615.50(14.10)
12.) 633.96(24.19)	36.) 613.03(11.82)	60.) 615.99(14.08)
13.) 593.16(00.00)	37.) 603.70(13.43)	61.) 594.09(04.15)
14.) 593.13(00.00)	38.) 603.71(13.43)	62.) 594.11(04.23)
15.) 594.64(00.00)	39.) 605.14(13.29)	63.) 595.55(04.04)
16.) 593.31(00.00)	40.) 603.96(13.44)	64.) 594.23(04.13)
17.) 593.07(00.00)	41.) 603.63(13.44)	65.) 594.01(04.20)
18.) 594.52(00.00)	42.) 605.04(13.22)	66.) 595.41(03.99)
19.) 595.99(00.00)	43.) 607.34(13.24)	67.) 597.85(03.94)
20.) 597.14(00.00)	44.) 607.47(13.21)	68.) 597.96(03.94)
21.) 597.57(00.00)	45.) 607.88(13.16)	69.) 598.41(03.90)
22.) 604.44(00.00)	46.) 614.34(12.81)	70.) 605.17(03.60)
23.) 604.53(00.00)	47.) 614.43(12.80)	71.) 605.26(03.60)
24.) 604.53(00.00)	48.) 614.92(12.79)	72.) 605.92(03.63)

Table 5: Estimates of the total instantaneous mortality rate ([annual Z]/Δt) and the associated bias generated using Jones(1981) length cohort analysis technique for the various stationary combinations specified in Table 2B for LMLKs and MMHKs each with an annual F = 0.1 expressed as a continuous stationary distribution of Δt = 30 days. The values of M and F relate to MΔt and FΔt, where Δt is the time interval used - normally a year, but arbitrary in a stationary population. (C.V. = coefficient of variation, n = number of length intervals, $\sum$ Δt = total time in months embedded in length frequency estimation). Z^* and $\sum \Delta t^*$ are inputs.

(A) LMLK (Z^* = .025, $\sum \Delta t^*$ = 148).

Combination	Mean Z	Bias (%)	C.V.	n	$\sum$ Δt
13	.03436	37.44	.3471	76	142
14	.03329	33.16	.3268	31	147
15	.0395	23.80	.2039	19	143
16	.04576	83.04	1.256	78	158
17	.03313	32.52	.3193	31	147
18	.03095	23.80	.1996	19	143
19	.04310	72.40	.5967	89	219
20	.05242	109.7	.5898	31	151
21	.03850	54.00	.4225	22	229
22	.02980	19.20	.1712	102	473
23	.03333	33.32	.2078	40	288
24	.03016	20.64	.1695	25	317

(B) MMHK (Z^* = .075, $\sum \Delta^*$ = 109)

Combination	Mean Z	Bias (%)	C.V.	n	$\sum$ Δt
13	----	----	----	----	----
14	.07620	1.60	.0978	65	92
15	.07915	5.53	.0667	41	106
16	.08345	11.27	.2752	165	----
17	.08230	9.73	.1327	66	129
18	.09008	20.11	.1175	40	81
19	----	----	----	----	----
20	.08294	10.59	.1047	66	143
21	.08463	12.84	.0952	41	130
22	----	----	----	----	----
23	.08245	9.93	.0732	66	138
24	.08485	13.13	.0813	41	129

(C) LMLK (Z^* = .05, $\sum \Delta^*$ = 148).

Combination	Mean Z	Bias (%)	C.V.	n	$\sum$ Δt
14	.05297	5.94	.2785	31	149
15	.05116	2.32	.1641	19	145
17	.05272	5.44	.2721	31	149
20	.08341	66.82	.5026	31	153
23	.05303	6.06	.1771	40	291

Table 6: Percent bias in estimation of total instantaneous mortality as determined by Ehrhardt & Ault's (in press) equation from average lengths in the simulated catch over a one year cycle for annually stationary deterministic populations with six different recruitment hypotheses as delineated in Table 2B for (a) LMLKs and (b) MMHKs.

(A) LMLK

Recruitment Types

Time-Step	11	12	13	14	15	16
1	28.22	0.24	-8.21	-6.70	6.16	-3.61
2	22.03	"	-11.15	2.40	1.19	-1.56
3	16.20	"	-11.25	8.32	-3.37	1.38
4	10.68	"	-7.98	10.81	-7.27	3.11
5	5.44	"	-2.20	10.53	-10.08	2.00
6	0.45	"	4.17	8.23	-11.27	-2.83
7	-4.31	"	9.05	4.65	-10.23	-3.61
8	-8.87	"	10.98	0.38	-6.49	-1.56
9	-13.24	"	9.63	-4.14	0.03	1.38
10	-17.44	"	5.81	-8.66	8.64	3.11
11	-21.48	"	0.98	-13.03	17.00	2.00
12	-25.38	0.24	-3.81	-17.24	11.44	-2.83
Weighted Avg.	0.24	0.24	0.24	0.24	0.24	0.24
Arithmetic Avg.	-1.67	"	-0.67	-0.67	-0.65	-0.27

(B) MMHK

Recruitment Types

Time-Step	11	12	13	14	15	16
1	86.73	-0.10	-21.49	-7.99	8.82	-7.94
2	57.65	"	-25.70	14.27	-3.21	-2.39
3	35.73	"	-23.11	25.95	-12.84	4.51
4	18.48	"	-13.06	28.09	-19.96	7.85
5	4.61	"	1.75	23.58	-24.02	4.35
6	-6.80	"	16.25	15.28	-24.05	-7.01
7	-16.38	"	25.32	5.40	-19.02	-7.94
8	-24.54	"	26.25	-4.65	-8.27	-2.39
9	-31.61	"	19.63	-14.05	7.80	4.51
10	-37.80	"	8.58	-22.43	26.75	7.85
11	-43.30	"	-3.13	-29.76	42.23	4.35
12	-48.23	-0.10	-13.28	-36.18	23.64	-7.1
Weighted Avg.	-0.10	-0.10	-0.10	-0.10	-0.10	-0.10
Arithmetic Avg.	-9.44	"	-2.28	-3.15	-2.80	-0.33