A GENERAL LIFE HISTORY EXPLOITED POPULATION SIMULATOR WITH PANDALID SHRIMP AS AN EXAMPLE[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A general life history population simulator, GXPOPS, with provisions to exploit any age sector of the population is presented. In addition to the usual fish life history pattern, the model allows simulation of random mating, sex-differential maturation, and stepwise growth found in many crustacean and some fish populations. GXPOPS provides for monthly calculations and all rates may be as general as month specific. The generality of the model is illustrated with an examination of closed season management strategies for a pandalid shrimp population.

The advent of the digital computer has allowed simulation modeling to become the current vogue within nearly all fields of science; fisheries is no exception. The computer has freed mathematically inclined scientists from being able to examine only equilibrium or cursory transitional states and from the need for expressing relations in neat closed analytical forms. Numerical integration schemes and the speed of computation have made possible the examination of large systems of differential equations with feedback mechanisms, both from deterministic and stochastic standpoints. Even the simplest self-regenerating population model of Beverton and Holt (1957), which may be regarded as a simulation model in that it has a feedback mechanism, is largely intractable for looking at transitional states and parameter variability without the aid of a computer.

Paulik (1969) gives a good review of simulation modeling in fisheries. He divided the modeling of fishery systems in an admittedly arbitrary way into two categories, management models and scientific models, depending on the manner in which a model is utilized. Management models are employed for decision making in evaluating or planning strategies for management purposes, while scientific models are constructed to help elicit certain basic knowledge of a biological system. The actual implementation of models in the two categories, however, should be similar in utilizing the model for planning, alternative evaluation, organization, and identifying sensitive areas of the system.

There are at least two fishery simulation models currently in existence which were designed to be generally applicable to most exploited populations. The most comprehensive is GAMES (Gales, 1972). This simulator has seven interacting sectors from the fish stock to the marketing of the final fish product, is modular in structure, and uses the most updated means of input/output. Unfortunately, GAMES is still in a state of development. The other simulator, POPSIM, was written by Walters (1969). POPSIM's major feature is an optimization routine for planning harvesting strategies for a number of harvesting periods. Both of these simulation models are easily adapted to the life history characteristics of fish populations which have been traditionally studied in fisheries science. However, the FORTRAN IV computer simulation model, GXPOPS, was written to allow additionally for the life history pattern of many crustaceans and some fishes that require actual copulation in reproduction and a sex-differentiated maturation schedule.

MODEL STRUCTURE

A flow-chart of GXPOPS indicating the optional life history sectors is presented in Figure 1. Each sector is described by the equations below. The basic time period for calculations in GXPOPS is monthly with all processes summed or averaged annually. There are three output options: 1) annual summaries only, 2) monthly and annual summaries by age class, and 3) monthly listings by age class as well as monthly and annual summaries.
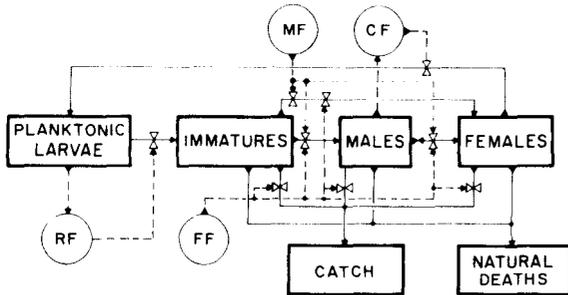

FIGURE 1.—Simplified flow chart of the computer program, GXPOPS. Boxes represent state variable compartments, solid lines represent material flows, dashed lines represent information flows, and circles represent regulatory functions; CF = copulation function, FF = fishing mortality function, MF = sex specific maturation function, and RF = recruitment function.

Mortality

Mortality may be age-specific on a monthly basis and is assumed to be representable by an exponential decline such that

$$N_{i, j + 1} = N_{ij}e^{-Z_{ij}} \qquad (1)$$

with

$$Z_{ij} = M_{ij} + A_{ij}F_{ij} \qquad (2)$$

where N_{ij} is the number of animals belonging to the ith year class at the beginning of month j, M_{ij} is the instantaneous coefficient of natural mortality, A_{ij} is an availability multiplier, F_{ij} is the potential instantaneous coefficient of fishing mortality of a fully available

year class, $i = 1. . . n$, and $j = 1. . . 12$. With natural and fishing mortality so general one can evaluate the effects of seasonal mortality patterns such as mass winter mortalities, closed seasons, etc. The coefficient A allows patterns of selectivity or seasonal availability, etc. to be incorporated. The average number alive of year class i during month j is given by

$$\overline{N}_{ij} = N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}. \qquad (3)$$

Growth

The growth in weight of the animals is represented by one of two options, the von Bertalanffy growth equation or a linear segmental growth curve as in POPSIM (Walters, 1969). The von Bertalanffy formulation is

$$w_{ij} = W_{\infty} [1 - e^{-K(12i + j - 13 - t_0)}]^3 \qquad (4)$$

where w_{ij} is the average weight of an individual in year class i at the beginning of the month j, and W_{∞}, K and t_0 are parameters of the von Bertalanffy growth equation. The segmental growth option is formulated as

$$w_{ij} = a + b \triangle t \qquad (5)$$

where $a = w_{i, j - 1}$, $b = (w_{ij} - w_{i, j-1})$ and $\triangle t = 1$. Using the segmental option, any shape growth curve may be approximated, including the stepwise growth pattern of crustaceans and many temperate fishes and mollusks.

Yield

Yield is computed monthly both in numbers and weight for each year class under either the von Bertalanffy or linear segmental growth option.

$$Y_{N_{ij}} = A_{ij}F_{ij}\overline{N}_{ij} \qquad (6)$$

where $Y_{N_{ij}}$ is the yield in numbers. Under the von Bertalanffy growth option, the yield in weight, $Y_{w_{ij}}$, is computed as

$$Y_{w_{ij}} = A_{ij}F_{ij}N_{ij}W_\infty \sum_{u=0}^{3} \frac{\Omega_u e^{-uK(12i + j - 13 - t_0)}}{Z_{ij} + uK}$$

$$x \, [1 - e^{-(Z_{ij} + uK)}] \qquad (7)$$

where $\Omega_u = 1, -3, 3, -1$, respectively. With the linear segmental growth option

$$Y_{w_{ij}} = Y_{N_{ij}} \{ w_{ij} + (w_{ij} + 1 - w_{ij})$$

$$[1/Z_{ij} - 1/(e^{Z_{ij}} - 1)] \} \qquad (8)$$

Equations (7) and (8) are modified for monthly calculations from Beverton and Holt's (1957) equations 4.4 and 9.5 respectively.

Maturation

A maturity schedule of the sexes is necessary to compute several relationships associated with the reproductive sextor of GXPOPS. This is accomplished in the simulator with two vectors of age-specific values, one denoting the average fraction of mature males in each year class during the breeding season, ϕ_{mi}, and the other denoting the female fractions, ϕ_{fi}. The mean number of mature males, $\overline{N}_{m_j}$, and mean number of mature females, $\overline{N}_{f_j}$, during month j of the spawning season are

$$\overline{N}_{m_j} = \sum_{i=1}^{n} \phi_{mi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij} \qquad (9)$$

and

$$\overline{N}_{f_j} = \sum_{i=1}^{n} \phi_{fi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij} \qquad (10)$$

with

$$s_j = \overline{N}_{m_j}/\overline{N}_{f_j}, \qquad (11)$$

where s_j is the mean monthly sex ratio. The mean sex ratio for the breeding season is given by

$$\bar{s} = [\sum_{j=t_s}^{t'_s} s_j]/(t'_s - t_s + 1) \qquad (12)$$

where t_s and t'_s are respectively the months that breeding begins and ends.

The maturation fractions, ϕ, are assumed to be constants in the present version of GXPOPS. It is possible that the ϕ may be density-dependent in certain populations. One can investigate the effect of differences in ϕ at equilibrium with the current version of GXPOPS, but it would be a simple matter to reprogram GXPOPS to examine the consequences of any functional hypotheses.

Reproduction

The major components of the reproduction sector of GXPOPS are copulation, egg-carrying (ovigerous period), and hatching. For the common spawing characteristics of freely casting both spermatozoa and eggs, the copulation and ovigerous period sector may be bypassed.

The traditional concept of fertilization success in fisheries population dynamics, excluding the salmonids, is described by Beverton and Holt (1957, p. 61) as:

> . . . if there is free liberation of gametes, with spermatozoa greatly in excess of eggs, and especially if the percentage of successful fertilisations is fairly high, then the number of fertilised eggs would tend to be a constant fraction of the numbers laid. In addition, a large spawning population would tend to distribute eggs over a rather wider area than a small one, so that the number of gametes per unit volume, which in such a situation determines the rate of fertilisation, would not be expected to change much.

Copulation is one mode of ensuring the fertilization of eggs in sexual reproduction. The success of fertilization, therefore, depends on the copulation rate which is at least some function of the sex ratio and density of the mature population. Beverton and Holt recognized this may be the case for a lobster population, in which copulation occurs.

Copulation is a part of reproduction in most commercially exploited crustaceans, and some fishes. With the exception of salmonid studies, where a form of pseudocopulation occurs, population dynamics studies of commercial fisheries have ignored the effects of exploitation on the rate of copulation. Conway (1969) presents the most extensive quantitative treatment of reproduction in insects, whose copulation parallels

that of many crustaceans. He recognizes three types of mathematical models for representing reproduction: 1) derivations from the Lotka-Volterra equations, 2) empirical models (essentially multiple regressions from data sets with a number of variables), and 3) structural models of the causal mechanisms likely to be involved.

Derivations from the Lotka-Volterra equations assume that if mating is random, then the rate of change of copulated females is proportional to the expected rate of contact per female times the number of uncopulated females. The rate of contact per female is assumed to be proportional to the number of males, giving

$$dN_f^*/dt = k_c N_m(N_f - N_f^*) \qquad (13)$$

where * denotes copulated females and k_c is the coefficient of copulation. The copulation coefficient may be thought of as consisting of two multipliers — the instantaneous coefficient of males contacting females at random and the fraction of these encounters that result in copulation. Equation 13 has the solution

$$N_f^* = N_f(1 - e^{-k_c N_m}) \qquad (14a)$$

or

$$p = (1 - e^{-k_c N_m}) \qquad (14b)$$

where p is the fraction of mature females that, at the end of the breeding season (scaled to be of one unit length for convenience), have been copulated. Equation (14b) may also be derived probabilistically by assuming the number of copulations is Poisson distributed such that k_c is the mean rate of contact resulting in copulation per male, then

$$P_r \, [x \text{ copulations}] = e^{-k_c N_m} \frac{(k_c N_m)^x}{x!}$$

with equation (14b), therefore, expressing the probability that at least one copulation per female has occurred in one unit of time (Klomp, Montfort, and Tammes, 1964 [cited in Conway, 1969]). This assumes that the population is not aggregated but is randomly distributed over the breeding grounds regardless of the size of the population. Philip (1957) has also derived

equation (14b) under slightly different circumstances. Writing equation (14a) in terms of the sex ratio (males: females), s, and total mature population, N_a, we have

$$N_f^* = (\frac{1}{1+s}) N_a \, [1 - e^{-k_c (\frac{s}{1+s}) N_a}]. \qquad (15)$$

Therefore, as the total mature population decreases, or as the sex ratio increases, the number of females being copulated with decrease under this model for reasonable values of s in the virgin state.

With the aid of equation (15) one can easily follow the reasoning of Beverton's and Holt's conclusions for large, long-lived fish populations with essentially a constant sex ratio. The maximum sustainable average yield (MSAY) in these populations is likely to occur at relatively low rates of fishing, hence there would be only a small reduction in population size from the virgin state. If k_c were high, then the reduction in N_f^* would be negligible. On the other hand, if the population is short-lived, the MSAY is likely to occur at a relatively lower population level. If fishing also increases the sex ratio, the deleterious effects on the size of N_f^* are compounded.

Equation (13) may be extended to become more realistic for a multiage population under exploitation. Often the mortality during breeding is neglected; however, exploitation may increase the mortality significantly and the breeding season may be protracted. Therefore, with the additional assumption that males make no distinction between year classes of females, for any year class i during month j

$$dN_{fi}^*/dt = k_c N_m(t) \, [N_{fi}(t) - N_{fi}^*(t)] - Z_i N_{fi}^* \qquad (16)$$

where

$$N_m(t) = \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij} t} \qquad (17)$$

and

$$N_{fi}(t) = \sum_{i=1}^{n} \phi_{fi} N_{ij} e^{-Z_{ij} t} \qquad (18)$$

Rewriting equation (16) in terms of the ratio of

copulated females to total mature females, $p(t)$, giving

$$dp(t)/dt = k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij}t} [1 - p(t)], \quad (19)$$

the solution obtained is

$$p_j = [1 - e^{-k_c} \sum_{i=1}^{n} \phi_{mi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}] \quad (20)$$

with $t = (0, 1)$ months and $p_0 = 0$. Equation (20) may be further simplified by substitution from equation (9) to give

$$p_j = [1 - e^{-k_c \overline{N}_{mj}}]. \quad (21)$$

Therefore, the fraction of the females in any year class that are copulated is the same for all year classes *provided that k_c is not age specific*. Given the fraction copulated in the previous month, p_{j-1} [where $p_{t_s - 1} = 0$], the fraction copulated at the end of the month j is

$$p_j = [1 - (1 - p_{j-1}) e^{-k_c \overline{N}_{mj}}]. \quad (22)$$

The total number of females in the population bearing fertile eggs at the end of the breeding season is then

$$N^*_{ft'_s} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it'_s}, \quad (23)$$

further assuming that one copulation results in fertilization.

Recounting the assumptions implicit in the simple model, equation (23), they are:

1. The instantaneous copulation rate per female is linear and proportional to the number of males.
2. The copulation coefficient is independent of the age of the males and females.
3. The copulation coefficient is independent of population size.
4. A single copulation results in fertilization.
5. Multiple copulations, if they occur, do not alter the fraction of each egg clutch that is fertilized from the first copulation.

In developing a reproduction model for insects, Conway (1969) criticized the first assumption as being unrealistic. Empirical evidence and biological induction suggest that the copulation rate should be concave downwards, rising to a maximum at some intermediate density and declining at very high densities owing to interference. Conway (1969) dismissed the second type of models (empirical) as lacking generality for a critical examination of reproduction, and developed three structural models based on nearest neighbor distances. Given the population size, density, and sex ratio, four parameters are contained in his models as compared with only one for the simple model. Conway fits each of his models to data obtained from the literature on insects. The fits he obtained are hardly remarkable considering that four parameters were estimated, and a number given, for only eight points. However, the fits are an indication of the flexibility and possible validity of Conway's structural concepts—especially since an irregularity in the data with biological significance was predicted with the fitted model. The decline in copulation rate in the data, however, occurs at very high population densities. The major use of GXPOPS will likely be for examining the dynamics of populations under exploitation, hence at less than virgin population densities. Also, since the two data sets given by Conway are adequately described by a straight line for the observations at population densities before the decline in copulation rate occurred, and lacking other empirical evidence to the contrary, equation (22) was adopted as the copulation model in GXPOPS.

Many exploited animals carry their fertilized eggs so that the number of eggs reaching the hatching period is intimately tied to the survival of the females during the ovigerous period. If it is assumed that all female mortality results in the loss of the eggs as well, then the number of copulated females reaching the hatching period is given by

$$N^*_{ft'_h} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it'_h} \quad (24)$$

where t_h is the time at hatching. Instantaneous

hatching is assumed, so t_h represents the mean hatching time.

Individual fecundity (eggs per female) is usually correlated with the size of the individual. Many plots of fecundity on length appear to be concave upward, which indicates that fecundity is closely proportional to the weight of the individual. In order to be more useful generally, however, fecundity in GXPOPS is represented by a vector of mean viable eggs per female at hatching by age class, λ_i, such that the total number of larvae hatched, L_h, is given by

$$L_h = P_{t'_s} \sum_{i=1}^{n} \lambda_i \phi f_i N_{it_h}. \qquad (25)$$

Recruitment

Any equilibrium point achieved with the population model as now formulated is likely to be unstable, such that with a sustained increase or decrease in mortality the population will decrease to extinction or increase to infinite size. Most successful natural populations are believed to achieve equilibrium through any of a number of homeostatic mechanisms associated with density-dependent reproduction or mortality. One such mechanism already mentioned is a decrease in copulation rate at high densities. Others include a lack or destruction of oviposition sites at high densities as in insects or salmonid fishes, an overutilization or competition for a fixed food supply, cannibalism, predator-prey interactions, etc. The usual mode of population regulation assumed in fisheries studies is through density-dependent early stage (or larval) mortality. Treatises on this subject can be found in Ricker (1954, 1958) and Beverton and Holt (1957).

Two models have been widely used in fishery population dynamics; GXPOPS allows the selection of one or the other. The first model, owing to Beverton and Holt (1957), states that the simplest assumption one can make is that the larval mortality coefficient can be expressed as a simple linear function of larval population size

$$dL_t/dt = -(\mu_1 + \mu_2 L_t) L_t \qquad (26)$$

where μ_1 and μ_2 are the density-independent and density-dependent larval mortality coefficients. Equation (26) integrates to

$$L_j = [\mu_2/\mu_1 (e^{\mu_1} - 1) + e^{\mu_1} /L_{j-1}]^{-1} \quad (27)$$

for the survival of larvae from month $j - 1$ to j. Collecting the constants we have

$$L_j = 1/(\alpha_1 + \alpha_2/L_{j-1}),$$

or

$$L_{h+t_r} = 1/(\alpha_1 \sum_{r=0}^{t_r-1} \alpha_2^r + \alpha_2^{t_r}/L_h) \quad (28)$$

for t_r months of larval existence. Equation (28) is a concave downward function that increases monotonically with L_j for a constant period of larval existence and it approaches an asymptote of $\sum_{r=0}^{t_r-1} \alpha_2^r/\alpha_1$ at an increasing rate as α_2 increases.

The second model, owing to Ricker (1954, 1958), simply assumes that the density-dependent coefficient, μ_2, may operate only until some critical size is reached and that the time to attain this critical size may be proportional to the size of the larval population at hatching, L_h, which gives

$$dL_t/dt = -(\mu_1 + \mu_2 L_h)L_t$$

or on integrating

$$L_{h+t_r} = L_h e^{-(\mu_1 t_r + \mu_2 L_h)} \qquad (29)$$

for t_r months of larval existence. Equation (29) is also concave downwards, but monotonically increases to a maximum at $L_h = 1/\mu_2$, and then monotonically decreases approaching zero as L_h becomes infinite.

Both equations (28) and (29) allow a population to achieve stability over a range of sustained mortality rates. Equation (29), additionally, will produce oscillations in the population (Beverton and Holt, 1957), the criteria for which are given by Paulik and Greenough (1966).

Constant recruitment of size $1/\alpha_1$ may be simulated with GXPOPS by selecting equation (28) and setting $\alpha_2 = 0$.

Timing in the Simulator

Reference in this study is made to a year divided into 12 mo because the reproductive cycles of many exploited fish populations are annual. It is just as easy to consider the "year" as a reproductive cycle (16 days, 3 yr, etc.) divided into 12 time periods of equal length.

The conventional notation, for numbering timestream entities, is for the initial or first instance to be denoted as 0. The computer, however, begins with 1 in executing "DO" loops, etc., therefore, the ordinal numbering system is used in GXPOPS. The first month and year are denoted as 1, as are the initial numbers and yields of the first month and year, and the young of the year. The simulator takes the hatching time, t_h, as time 1 (i.e., $L_h = L_1$) and the year is carried on a biological fiscal basis. For example, if hatching occurs on April 1, recruitment to the main population on July 1 of the first year of life, and breeding begins October 1 and ends December 1; then

$$t_h = 1, t_r = 3, t_s = 7, \text{ and } t_s' = 8,$$

respectively. If recruitment does not occur until July 1 of the third year of life, then $t_r = 27$.

EXAMPLE: A PANDALID SHRIMP POPULATION

GXPOPS was designed to be useful for examining the responses of many life history patterns to exploitation. The impetus, however, was to examine the response to exploitation of a pandalid shrimp life history (Fox, 1972). Pandalid shrimps are protandric hermaphrodites—i.e., individuals mature as males but later transform to function as females (Berkeley, 1930), fertilization is accomplished through copulation, the females carry fertilized eggs 3-9 mo until hatching, and they exhibit pronounced

stepwise growth. While the extensive simulation studies investigating the effects and management implications of all sectors of the pandalid shrimp model will be published subsequently, one particular study of the effect of season length on the simulated fishery is useful for illustrating the utility of GXPOPS.

Table 1 contains the parameters of the simulated pandalid shrimp population which 1) consists of six year classes, 2) is fully recruited to the fishable population during the third year of life (at 2 yr old), 3) breeds over 2 mo, 4) carries its eggs 5½ mo until hatching, 5) recruits to the main population during the fourth month of life (3 mo after hatching), 6) matures as males during the third year of life (at 2 yr old), and 7) transforms into females during the fourth year of life (at 3 yr old). The stepwise growth in weight is given in Figure 2.

Exploiting the simulated pandalid shrimp produced the relationship between equilibrium yield and fishing effort (= instantaneous fishing mortality coefficient since the catchability coefficient was assumed to be 1.0) given in Figure 3. An equilibrium yield was achieved with fishing effort up to 1.4, with the maximum equilibrium yield occurring at about 1.0. Fishing above a level of 1.4 did not result in equilibrium within 25 yr of simulated fishing, and continued fishing somewhere between 1.4 and 2.0 would eventually result in extinguishing the population. By not including the effect of random mating (copulation), i.e., $k_c = \infty$, the simulated population achieved equilibrium out to nearly $F = 1.8$ (Fox, 1972). This exhibits some need for considering the implications of copulation success in evaluating management alternatives.

The equilibrium yields given in Figure 3 are for an annual pandalid shrimp fishery. Several states, however, have closed seasons during that part of the year when females are carrying fertilized eggs — ovigerous period — (Dahlstrom, 1970). For the simulated pandalid shrimp population, the ovigerous period lasts 6 mo (months 7-12). It is of interest to compare the results of the closed ovigerous season strategy with other possible season lengths, all beginning subsequent to hatching and running continuously until reaching the closed season.

TABLE 1.—Parameters of the simulated pandalid shrimp population.

| Parameter	Symbol	Value
1. Number of year classes	n	6 ($i = 1$-6)
2. Instantaneous natural mortality coefficient	M_{ij}	0.06 (for all i and j)
3. Availability multipliers	A_{ij}	0.0 (for $i < 3$) 1.0 (for $i \geq 3$)
4. Month breeding begins	t_s	7
5. Month breeding ends	t_s'	8
6. Year of first maturity	t_m	3
7. Age (mo) at first recruitment	$t_r + 1$	4
8. Copulation coefficient	k_c	10^{-9}
9. Recruitment parameters of the Beverton and Holt model	α_1 α_2	3.2851×10^{-11} 1.01
10. Fecundity coefficients	λ_i	0.0 (for $i = 1$-3) 1314 (for $i = 4$) 1679 (for $i = 5$) 1997 (for $i = 6$)
11. Male maturity fractions	ϕ_{mi}	0.0 for $i = 1, 2$ and 4-6 1.0 for $i = 3$
12. Female maturity fractions	ϕ_{fi}	0.0 for $i = 1$-3 1.0 for $i = 4$-6
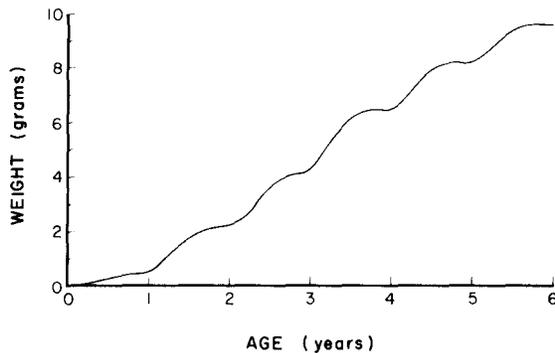
FIGURE 2.—Arbitrary growth curve exhibiting the stepwise growth pattern of pandalid shrimps.

The simulated pandalid shrimp population was fished for six different season lengths, from 12 to 2 mo after the hatching period (Table 2). The maximum equilibrium yield for each season length occurred with an *annual* fishing mortality coefficient, F, of 1.0. This means that the monthly fishing effort must increase proportionally to the inverse of the season length to obtain the maximum equilibrium yield (column 2, Table 2). Of those seasons simulated, the greatest equilibrium yield and

catch per unit effort were obtained with the 8-mo season (columns 3 and 4, Table 2). Compared with an annual fishery, however, the 8-mo season resulted in a 5% decrease in the average weight of a shrimp in the catch (column 5, Table 2). The 6-mo season (closure during the breeding, ovigerous, and hatching periods) was only slightly less than the 8-mo season in yield and catch per unit effort, but it was better than the annual fishery. However, there was an 11%
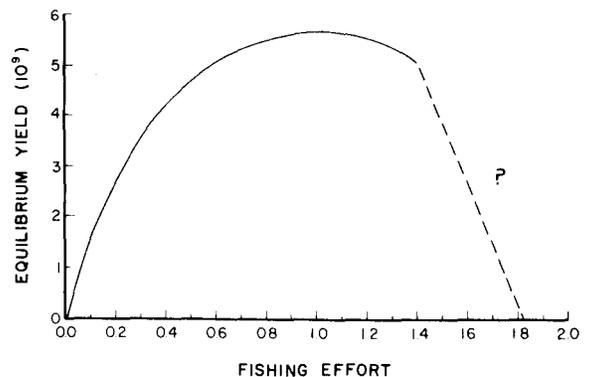

FIGURE 3.—Relationship between equilibrium yield and fishing effort for the simulated pandalid shrimp population. Dashed line represents nonequilibrium region.

TABLE 2.—Effect of season length, beginning subsequent to hatching, on maximum equilibrium yield and allied fishery parameters for the simulated pandalid shrimp population.

(1) Season length (months)	(2) Monthly fishing effort	(3) Season yield in weight	(4) Average monthly catch/effort	(5) Average individual weight	(6) Breeding success (percent)
12	1.0	5.60×10^9	0.467×10^9	3.7	85.5
10	1.2	5.68×10^9	0.474×10^9	3.6	82.0
8	1.5	5.70×10^9	0.475×10^9	3.5	76.1
6	2.0	5.67×10^9	0.472×10^9	3.3	71.3
4	3.0	5.63×10^9	0.469×10^9	3.1	71.3
2	6.0	5.57×10^9	0.464×10^9	2.9	71.3

decrease in average weight as compared to the annual fishery. The breeding success, defined as the fraction of available eggs which are fertilized, declined with the season length until a 6-mo season was reached.

An unknown factor not programmed into the simulation model, however, is the effect of trawling on the behavior of the shrimp during breeding or on the possibility of causing dislodgement of the egg clutches and a subsequent higher mortality rate. In view of these uncertainties, the adoption of a 6-mo season from hatching to the onset of breeding, as several states have, appears to be a biologically prudent approach for a natural population similar to the simulated population. The 6-mo season is only slightly lower in maximum equilibrium yield, catch per unit effort, and average size than the optimal 8-mo season, but is better than the annual fishery in the first two categories. The actual implementation of a 6-mo season on an annual fishery, however, would have to weigh socioeconomic factors because the maximum yield is obtained with twice the amount of fishing effort per month as compared with the annual season. If the fishery were only able, at the time of adopting the closed season, to exert a monthly effort of 1.0, the expected seasonal equilibrium yield is about 10-15% less than that for the annual fishery, but the expected equilibrium mean monthly catch per unit effort would increase 70-80%. The latter should provide a substantial increase in the economic standard of an average fisherman, provided that he has an alternative means of investment for the 6-mo closed season which would provide a sufficient return. The simulation model can be used also to evaluate the expected transitional states from an annual fishery to a seasonal closure fishery as well as the expected equilibrium results discussed here. A socioeconomically feasible strategy, then, may be determined given the current state of the fishery.

PROGRAM AVAILABILITY

A listing and card set-up documentation for program GXPOPS are available on request from the author.

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