A Computer Simulation Model of a Multispecies Centrarchid Population Complex

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Abstract—The development and structure of STOCKS, a computer simulation model of a multispecies centrarchid population complex, is discussed. STOCKS emphasizes dynamic interrelationships among three game fishes: bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and black crappie (*Pomoxis nigromaculatus*). Required input data for each species are: (1) an initial population estimate; (2) estimated high, medium, and low annual recruitment with a standard deviation for each; (3) annual natural mortality rate; and (4) annual fishing mortality rate. Simulator output is: (1) a population estimate for each species each year; (2) catch of each species for each year; and (3) mean catch of each species for all years. Analysis of a large number of computer runs under various input conditions is discussed. STOCKS is not offered as the solution to the multispecies management problem, but rather as an approach to better understanding the dynamics of centrarchid population complexes.

Effectively managing multispecies fish population complexes is a perpetual enigma in fisheries management. Successfully managing a single species is difficult at best, but managing a complex with two, three, or more competing populations is a formidable, if not impossible, task (Lackey 1974). To enhance understanding of fisheries and thereby increase management capabilities, mathematical models have been formulated which attempt to describe how populations function. Some of these models have become classical tools in fisheries management. Unfortunately, none of the models is particularly applicable in multispecies situations which are characteristic of nearly all freshwater and marine fisheries. The classical models best apply to single species fisheries as found in a few marine commercial situations. For example, the Ricker (1954) stock recruitment model applies to a population where fish spawn once and die, as with the Pacific salmon.

The two best known single stock models are the dynamic pool model (Beverton and Holt 1957) and the logistic model (Schaefer 1954). The dynamic pool model describes a fish population in terms of the vital parameters of recruitment, growth, and mortality.

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Implementing this model requires a large amount of data and can generally be successful only after substantial information has been collected on a fish population. The logistic model, also called the surplus-yield model, combines the effects of recruitment, growth, and natural mortality into a single-valued function of population biomass. The logistic model, usually employed when information on a fish population is relatively scanty, requires only catch and effort data for a series of years.

Both the dynamic pool and the logistic models have been applied, with some success, in the management of marine commercial fisheries. The dynamic pool model has been used in the North Sea plaice fishery and provides an adequate description of the fishery (Gulland 1972). The logistic model has been useful in managing the Eastern Tropical Pacific yellowfin tuna fishery (Schaefer 1957, Gulland 1972). Neither, however, has been applied with much success in freshwater sport fisheries. Watt (1959) did an extensive study of the smallmouth bass population of South Bay, Lake Huron. He applied four different population models to the fishery, including the logistic and dynamic pool models, and found that all models were deficient in one or more respects. He attributed the weaknesses of the models to lack of adequate input data. He had "relatively small amounts of information collected over *only* a ten year period" (emphasis added). In comparison to data available on most freshwater sport fisheries, Watt had an abundance of information. Watt's conclusion illustrates one of the main problems with classical population models: to be accurate predictive tools they simply require more data than are available from most sport fisheries.

An additional problem with all commonly used fisheries models is the deterministic description of stochastic population phenomena. Models that incorporate stochastic processes may provide better descriptions of population dynamics. An example of deterministic versus stochastic processes should illustrate why the latter is to be preferred for sport fisheries. A deterministic model predicts that for a given value of the independent variable, X, we can expect the dependent variable to have a corresponding value, Y. A stochastic model predicts that for a given value of X we can expect any one of a number of Y_i

values, with a probability of P_i attached to the occurrence of each Y_i (Watt 1959). The stochastic approach is appropriate where a steady state situation cannot be safely assumed, which is the case in most fisheries.

There are many computer-implemented stochastic fisheries models described in the literature. Royce et al. (1963) developed a simulation model to investigate economic and biological consequences of various strategies for restricting entry of gear into the salmon net fisheries. Larkin and McDonald (1968) used a computer simulation model to synthesize the main features of the population biology of sockeye salmon of the Skeena River. Paulik and Greenough (1966) used computer simulation for management analysis of a salmon resource system. Southward (1966) developed a large-scale simulation model to study three management strategies for limiting halibut catch in the northeastern Pacific. Mathews (1967) developed a simulation model to determine potential economic benefits to the canning industry of varying degrees of forecast reliability of the size of sockeye salmon runs to Bristol Bay, Alaska. Pella (1968) employed Monte Carlo simulation techniques to study the effectiveness of mark-recapture experiments for estimating population parameters of tuna. Riffenburgh (1969) developed a stochastic model of inter-population dynamics based on energy flow through an ecological system composed of the Pacific sardine, the northern anchovy, and their competitors, predators, and prey. These models and others are discussed in more detail by Paulik (1969).

Large-scale models of marine commercial fisheries are not easily applicable to a freshwater sport fishery. Walters (1969) developed a general computer simulation model which may have application in sport fisheries, but the basic model structure is deterministic. Also, his model is designed to describe a single species population and, therefore, its predictive value in most freshwater fisheries is limited.

The purpose of this paper is to describe a stochastic population dynamics model which was designed to be generally applicable to multispecies freshwater sport fisheries. The model, STOCKS, is not offered as the panacea for multispecies management, but rather as a methodological approach to the problem.

The Conceptual Model

STOCKS is based on a three-species freshwater centrarchid population complex. Much of the basis for the model was derived from 10 years of creel census data from Lake Brittle, Virginia. Each species is considered to be a single stock (a manageable unit in itself). The three stocks used in the model are black crappie (CR), largemouth bass (LMB), and bluegill (BG) (Fig. 1). Total size of the combined three stocks (N) is represented by the outer line. Crappie, bass, and bluegill were selected for modeling because of the readily available data on the population dynamics of these species. However, any three game fishes that meet the requirements of the model could have been used. The model in Fig. 1 is an extension of the unit stock model of Ricker (1958). Recruitment (R) acts to increase the total number of recruited fish in the fishery. Total annual natural mortality rate (D) and

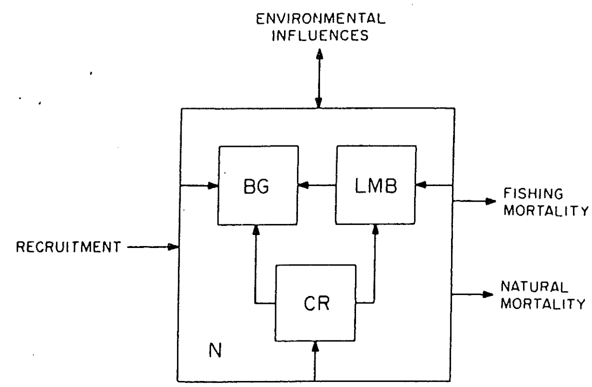

FIG. 1—Conceptual model of a three-species fishery which is the basis for STOCKS.

fishing exploitation rate (E) act to decrease N. Environmental effects (V) either increase or decrease N, depending on whether the effects are favorable or unfavorable.

Since the model includes three stocks, there must be a mechanism to account for interspecific competition and predation. Interspecific competition and predation in STOCKS is based on spawning sequence and is predicated on the theory that density-dependent factors control animal populations (Nicholson 1933, 1954). Thompson (1941) describes a situation where a large year-class of crappie dominated the abundance of all fishes in a lake for the duration of the age class. Swingle (1950) has described how bass and bluegill interact to control each other. Bass and bluegill, although not strong competitors, may each curtail the population of the other (Bennett 1971). An assumption in STOCKS is that the population which first produces a strong year-class will have a competitive advantage over other species. Crappie spawn first (by water temperature), largemouth bass second, and bluegill last (Calhoun 1966). There is some overlap (i.e., crappie are still spawning when largemouth bass begin spawning) but spawning times are distinct enough to be considered discrete. If crappie exhibit high spawning success, they will exert a controlling effect over the spawning success of largemouth bass and bluegill. In turn, the spawning success of largemouth bass affects the spawning success of bluegill. The spawning success of bluegill does not directly affect spawning of either crappie or largemouth bass, but does have an indirect effect in that it contributes to N, which affects future spawning success of all three stocks.

Growth in biomass per individual is not considered explicitly in STOCKS, only increase in numbers. For a simulator with general application it is more practical to deal with numbers of fish rather than individual growth rates. Average sizes for each species vary substantially from fishery to fishery and only a few realistic situations could be easily incorporated into a simulator. Rather, the user should consider the model to be operating under the average conditions of a particular fishery and assume that the results reflect these conditions. For example, the catch of bluegill predicted by STOCKS for a given year should be considered as comprising average size bluegills found in that body of water in an average year. If stunting occurs, STOCKS provides a statement to this effect in the output. In practice, stunting (extreme overpopulation as shown by STOCKS) is rare, and generally happens only when the initial population estimates are very high.

The Computer Simulator

Program Structure

STOCKS is coded in FORTRAN IV on an IBM System 370. A fully documented program listing and user guide is available from the authors. The simulator comprises a main program and five subroutines. The main program serves to read in data, call various subroutines, and write out results. The program iterates on a daily basis for a simulation of 10 years.

The first subroutine, RC, generates recruitment for each stock. Recruitments are generated from the following functions:

$R_{cr} = f(N)$,
$R_{lmb} = f(N, R_{cr})$, and
$R_{bg} = f(N, R_{cr}, R_{lmb})$.

This subroutine incorporates a process generator which generates values for recruitment from a normal distribution. The process generator provides stochastic rather than deterministic recruitment values. There are three possible recruitment distributions for each stock: high, medium, and low. The user (manager) must provide high, medium, and low recruitment values. Interaction between stocks in the main program determines from which distribution the recruitment will be generated for each year. The RC subroutine is provided with the mean and standard deviation of the appropriate distribution, and from this it generates recruitment within three standard deviations of the mean. For example, suppose it is determined that the current year will produce a high recruitment of crappie. The mean for the high recruitment value and corresponding standard deviation that were read in as input data are sent to the RC subroutine. Suppose these values are 30,000 and 5,000 respectively. The RC subroutine will generate a recruitment from a normal distribution with mean 30,000 and standard deviation 5,000, within the limits of three standard deviations. A value for recruitment will be generated from the interval 15,000 to 45,000, and 68% of the time the value will be within one standard deviation of the mean (25,000–35,000).

The F subroutine estimates the number of fish in each stock that die due to fishing on a given day, using instantaneous rates. The total number of fish of each stock alive on a given day is then multiplied by the daily fishing mortality rate to obtain the number of fish in each stock that died due to fishing on that day. These values are returned to the main program where they are subtracted from the current population size.

The M subroutine estimates the number of fish in each stock that die due to natural mortality on a given day by converting annual rates to daily rates. The number of fish in each stock alive on a given day is multiplied by the daily rate and the results are subtracted from the current values of each stock.

RANDU, the fourth subroutine, is the random number generator. It generates a uniformly distributed random number on the interval (0.0, 1.0). RANDU is used in the RC subroutine to provide random numbers required by the normal process generator. RANDU is also used in the main program as one determinant of the level of recruitment.

TPLOT is the final subroutine and it plots catch of each stock over 10 years (three separate graphs). The plot routine is optional and must be requested.

Input Data Required

The type of input data selected was in part determined by what could be realistically expected from a reasonably well-studied fishery. Detailed instructions describing input data requirements are given in the program listing available from the authors.

The user is required to enter a 5-digit, odd, random number. This number sets the random number generator which then generates all the random numbers called for in the program. More sophisticated means could be used to seed RANDU (e.g., calling the number from the computer system clock), but giving the user control over the initial random number has a distinct advantage. When the user wishes to experiment with the simulator, he can make various runs by adjusting different system parameters, while holding the random number constant. The whole series of random numbers generated in the simulator will remain the same and changes in output can be attributed to the specific variables that were manipulated.

An initial population estimate of each stock present at the end of the last angling season must be provided because simulation begins by adding recruitment for the first year to the initial population estimate.

The user must also provide high, medium, and low estimates of the mean annual recruitment for each stock, with a standard deviation for each. A simple way of determining the approximate standard devia-

TABLE 1
Results of testing STOCKS with selected initial random numbers (table values are estimated 10-year average catch of each stock)

Stock	Random Number					
	12693	15973	45239	78965	53261	*99999
Bluegill	7,423	8,182	7,729	6,622	7,259	6,161
Largemouth Bass	176	150	188	121	205	94
Crappie	11,046	10,425	10,958	12,101	9,699	11,814

TABLE 2
Results of testing STOCKS with high, medium, and low initial population estimates

Stock	Initial Population Estimate	10-Year Average Catch
Bluegill	10,000	15,230
	50,000	17,224
	80,000	16,981
Bass	100	204
	750	275
	2,000	251
Crappie	5,000	11,314
	40,000	11,161
	70,000	12,524

tion is to estimate the range of the distribution in which 95% of the possible values is included. This range is approximately four standard deviations and one-fourth of this range equals one standard deviation. For example, suppose mean annual high recruitment of bluegill in a particular fishery is estimated to be 50,000 fish. The extremes are grossly estimated to be 30,000 and 70,000. Thus, the range is 40,000 with an approximate standard deviation of 10,000. The user enters 50,000 for the mean high recruitment and 10,000 for the high recruitment standard deviation. The same procedure is followed for the high, medium, and low recruitment values for all three stocks.

The proportion of each stock that will be removed each year due to natural mortality must also be estimated. If it is estimated that 40% of the crappie stock will die due to natural mortality each year, then .40 is entered on the data card. The estimates of annual fishing mortality, E, for each stock are determined in the same manner. If E for bluegill is 25% then .25 is entered on the data card.

Analysis of Simulator Runs

Numerous simulation runs were made with STOCKS during its development and after its completion. The simulator was tested at the extremes, such as using zero population estimates, and at extraordinarily high population estimates. It was also tested with various combinations of recruitment and mortality estimates. Simulation runs were also extended to 100 years to determine performance over an extended time frame. STOCKS performed acceptably; i.e., it delivered output values that appeared realistic as compared to Lake Brittle data. STOCKS was also tested for sensitivity to variations in input parameters.

Sensitivity Analysis

Six different initial random numbers were tested while holding other system components constant. The model was relatively insensitive to different random numbers as ascertained by comparisons of the 10-year average catch of each stock (Table 1). The variation in catch due to the random number is roughly similar to actual catches from Lake Brittle.

Three initial population estimates were tested to determine how their magnitude affected average catches (Table 2). Initial population estimates had little effect on the overall average catch. This is a highly desirable property because it affords the user a large margin for error in making initial population estimates.

The level of the recruitment estimates has a more profound effect on average catch than does the random number or the initial population estimate. Recruitment estimates and average catch appear to vary in direct proportion; that is, a 10% decrease in recruitment decreases average catch approximately 10%, while a 10% increase in the recruitment increases average catch approximately 10%. Standard deviations must be adjusted in proportion to the adjustment in the recruitment estimate if the proportional relationship is to hold for all cases. Based on these results, the user should attempt to provide the best possible estimate of recruitment.

The model was tested for reaction to simulated changes in fishing mortality by varying fishing mortality of one stock from a very low to a very high value while holding the parameters of the other two stocks constant. Bluegill exploitation was varied from .10 to .70 while holding largemouth bass exploitation at .25 and crappie exploitation at .10 (Table 3). Largemouth bass exploitation was varied from .10 to .75 while holding bluegill exploitation at .30 and crappie exploitation at .10 (Table 4). Crappie exploitation was varied from .10 to .70 while holding bluegill exploitation at .30 and largemouth bass exploitation at .25 (Table 5). In every case catch increased until E = .50 and then declined. This response is not unexpected because one of the assumptions of the model is the parabolic relationship of yield on fishing effort as exemplified in the logistic model (Royce 1972). If some other assumptions were warranted, STOCKS could be modified to reflect another relationship. The model was tested to determine the effect of simulated fishing of all three stocks at E = .50. The result was a higher yield of each stock

TABLE 3
Results (expressed as catch) of testing STOCKS by varying bluegill exploitation rate from .10 to .70 (other parameters constant with E = .25 for largemouth bass and E = .10 for crappie). Each column represents a 10-year simulation at a particular E level

Stock	Exploitation Rate for Bluegill						
	.10	.20	.30	.40	.50	.60	.70
Bluegill	7,423	13,495	17,224	19,933	24,180	18,438	19,534
Largemouth Bass	242	245	275	291	286	459	459
Crappie	11,046	11,161	11,161	11,493	12,616	11,099	11,099

TABLE 4

Results (expressed as catch) of testing STOCKS by varying largemouth bass exploitation rate from .10 to .75 (other parameters constant with E = .30 for bluegill and E = .10 for crappie). Each column represents a 10-year simulation at a particular E level

Stock	Exploitation Rate for Largemouth Bass						
	.10	.25	.30	.40	.50	.60	.75
Bluegill	17,224	17,224	17,224	17,224	17,224	26,228	26,228
Largemouth Bass	145	275	305	353	390	108	116
Crappie	11,161	11,161	11,161	11,161	11,161	10,514	10,514

as compared to any other combination of exploitation rates tested.

Natural mortality was not tested for two reasons. First, it operates in the same mode as fishing mortality in the simulator and will cause similar trends in catches. Secondly, in most management situations, natural mortality is only slightly under the control of the fisheries manager. Therefore, to vary it in simulation would not be very realistic. The best estimate of natural mortality for each stock should be obtained and then held constant; E, which is under control of the manager, can be varied.

Validation

One approach to validation is to assume that a model is valid if, despite its inexactness in representing the system, it can give a reliable prediction of the system's performance (Taha 1971). In freshwater sport fisheries it is probably currently impossible to validate a model according to this definition because adequate data are lacking. Data that are available are generally used in developing the model and thus cannot be used to validate it. In the case of STOCKS, the model was based on 10 years of creel census data from Lake Brittle and thus cannot be validated by using the same Lake Brittle data.

Although the model cannot be validated, its performance in relation to the Lake Brittle system can be examined (Figs. 2, 3, and 4). Closer correlation between the real and model catches could be obtained by varying the combinations of input parameters, but such an effort would not validate the model.

Discussion

The key results from the analysis of many runs of STOCKS are: (1) the proportional relationship of recruitment and catch in the model; (2) the effect of varying exploitation of one stock on the catch of the other stocks; (3) an indication of the expolitation level which produces the maximum sustainable yield; and (4) the graphical analysis showing that STOCKS may possibly mimic a multispecies population complex.

The average catch of a stock was found to be about proportional to the recruitment values specified for that stock as input data. This relationship may prove useful for discovering what the average recruitment levels really are since it is difficult to get accurate population estimates, much less good estimates of recruitment in most fisheries. Perhaps through use of the proportional recruitment relationship we can address the problem in a different manner. For example, the manager designs a strategy to obtain good estimates of natural and fishing mortality for each stock. He then uses these estimates in the simulator along with his best intuitive estimates for recruitment and initial population levels. He runs the simulation to estimate average catches for each stock and then compares these to average catches on the fishery. If the simulated catches are low compared to actual catches, he would increase input recruitment values and rerun the simulator. He would continue iterating until the simulated catch approximated the real catch level. He should finally arrive at a reasonable approximation to the recruitment values. Once he has recruitment values, he can then begin to experiment with the simulator by varying exploitation.

The response of STOCKS to varying exploitation rate for one stock while holding the others constant appears to verify interaction effects. When a stock was increasingly exploited, the average catch of that stock increased until the level of overexploitation was reached, and then the catch took a drastic decline (Tables 3, 4, and 5). Concurrently, the catches of the other two stocks were not significantly affected until the stock which was being increasingly exploited reached an overexploitation level. Catches from one of the two other stocks would increase sharply and act to exert control over the third stock. This can be seen by following the exploitation sequences through the tables.

TABLE 5

Results (expressed as catch) of testing STOCKS by varying crappie exploitation rate from .10 to .70 (other parameters constant with E = .30 for bluegill and E = .25 for largemouth bass). Each column represents a 10-year simulation at a particular E level

Stock	Exploitation Rate for Crappie						
	.10	.20	.30	.40	.50	.60	.70
Bluegill	17,224	18,722	19,356	18,466	19,979	18,671	18,671
Largemouth Bass	275	302	327	285	279	674	674
Crappie	11,161	21,645	26,658	32,699	36,457	16,052	17,301

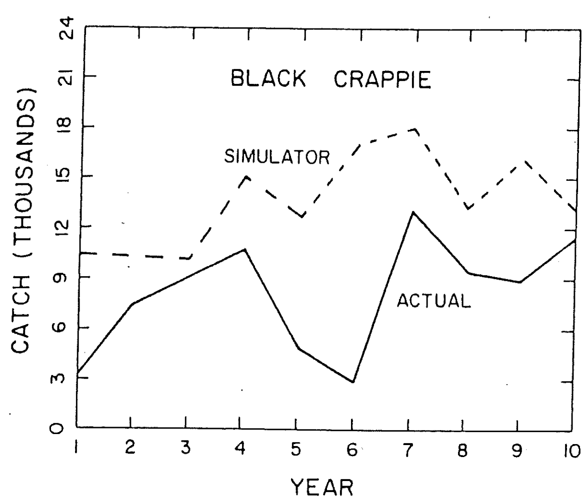

FIG. 2—Plot of STOCKS-generated crappie catches vs. Lake Brittle crappie catches.

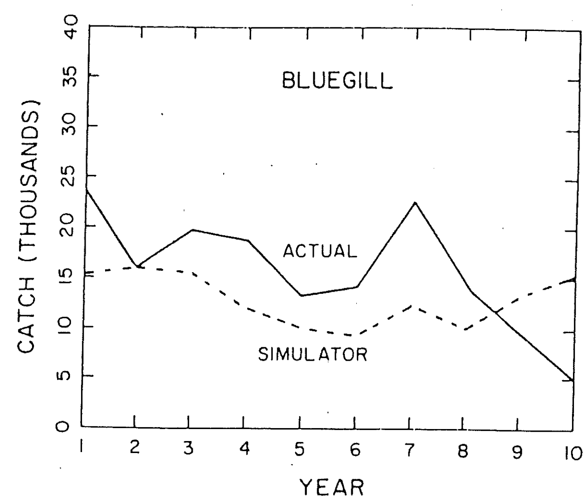

FIG. 4—Plot of STOCKS-generated bluegill catches vs. Lake Brittle bluegill catches.

A key question in fisheries management is how to optimize output (however it is to be defined) from each stock at the level of maximum sustainable yield. If we assume that all fish in the creel are approximately equally desirable, then all stocks should be exploited at E = .50. But, in reality, would this strategy work? Perhaps if all three stocks were fished at this level, predation on and/or competition with bluegill, for example, would be reduced to a low level. In this situation the bluegill stock may increase tremendously, causing stunting and thereby decreasing yield in the long run. Perhaps a better strategy would be to fish one of the highly reproductive stocks for maximum sustainable yield and fish the other stocks at some lower level. Or, perhaps none of the stocks should be fished at maximum sustainable yield but at some intermediate level which would result in the highest total yield. STOCKS indicates that the intuitive answer may apply in this case.

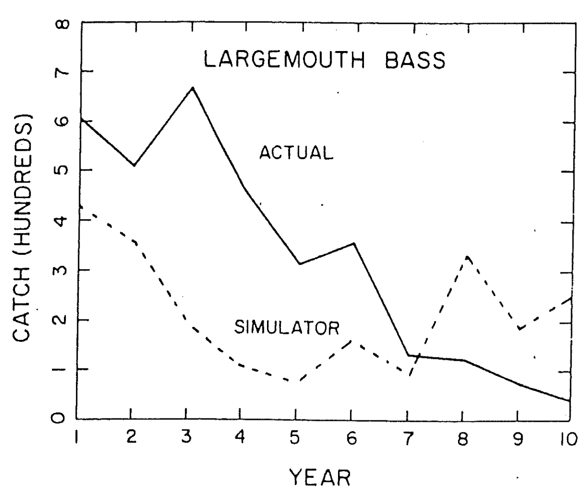

FIG. 3—Plot of STOCKS-generated largemouth bass catches vs. Lake Brittle largemouth bass catches.

Simulations were based on the aforementioned strategies and showed that fishing all three stocks simultaneously at the maximum sustainable yield provides the maximum yield of each over the long run. This is not surprising, considering the reproductive potentials of the species and the fact that most of the catch is represented by one year-class. Larkin (1963), using the Lotka-Volterra equations (Lotka 1932, Volterra 1931) to explore competitive interactions between two species, also found that the yield of either species is greater in any set of conditions when its competitor is also harvested.

Validation of a computer simulation model is important in any discipline. Any model can be made to deliver the desired results by appropriate manipulations of its parameters. Although we can show graphically that a model may mimic the real system, the key question is not merely whether the output from the model looks good but whether it meets the management objectives of allowing a choice among various relevant decisions or identifying weaknesses in existing knowledge.

Currently STOCKS can only be used to simulate three relatively discrete stocks. This of course limits the complexity of the fishery to which STOCKS would be applicable. If the fishery is so complex that there are perhaps two discrete stocks of largemouth bass, for example, the simulator must be modified. The simulator can, however, be used for a one- or two-stock system by simply entering zero values for the input parameters of the other stock or stocks. The other significant limitation is the restriction of the simulator to a discrete spawning sequence, or a sequence that overlaps to such a minor degree that it can be considered discrete. Modifications to account for this should not be difficult if the overlap is reasonably well understood.

STOCKS is not presented as the solution to the multispecies management problem, but rather as a foundation on which to build. It demonstrates one approach to the multispecies problem, a problem that cannot easily be solved (if it can be solved at all) with a system of deterministic equations. STOCKS currently simulates a small sport fishery population complex, but this application can be expanded and refined as better data on population dynamics are collected. STOCKS provides a way to put new data to immediate use and in the process should help to guide efforts to collect further appropriate data.

STOCKS and similar simulators provide a heuristic device by which the fisheries manager may gain insight into the workings of a fishery. By manipulating input parameters he can observe how populations may respond and perhaps test a "best" simulator strategy in the real world and evaluate if populations respond as the simulator predicted. The heuristic value to the fisheries manager is limited only by his imagination.

Finally, STOCKS may be used in training students to be fisheries managers. STOCKS can easily be developed into a teaching game such as TROUT (Titlow and Lackey 1973) or DAM (Titlow and Lackey 1974). Thus, the problem of multispecies management can be brought into the classroom where future managers may get some idea of the complexities involved in managing fisheries resources.

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