COMPUTER SIMULATION MODELS FOR PREDICTING POPULATION TRENDS OF LARGEMOUTH BASS IN LARGE RESERVOIR

Donald J. Orth
Oklahoma Cooperative Fishery Research Unit*, Oklahoma State University, Stillwater, Oklahoma

Two computer simulation models of population dynamics of largemouth bass (*Micropterus salmoides*) are described. Model I is an age-structured, deterministic model with numbers as the only state vector. Constant age-specific fecundities and survival rates are required inputs. Model I simulates population trends based on an equilibrium population. Sensitivity analysis of this model indicates that density of bass is most sensitive to variations in survival from egg to age I. Multiple regression equations with water level during spawning and water level fluctuation since the end of the previous growing season as predictor variables resolved 88.2% of the observed variation in year-class strength and 86.7% of the observed variation in mortality from egg to age I of largemouth bass in Lake Carl Blackwell. Model II is similar to Model I except that the effect of reservoir water level and water level fluctuation on survival of the young-of-the-year is included. Predictions of number of age I recruits from Model II agree closely with population estimates for Lake Carl Blackwell.

INTRODUCTION

The largemouth bass, *Micropterus salmoides,* is one of the most important sport fishes in southern lakes and reservoirs. About 24% of the fishing trips on reservoirs in the southeastern states are specifically for centrarchid basses and another 18% for bass plus other species (1).

The management of largemouth bass in large reservoirs (larger than 200 hectares) is often difficult because reservoir size may prohibit the fishery manager from collecting enough data to allow rational decisions, and because unstable water levels may prevent the fish population of the reservoir system from attaining a stable (or steady) state. Thus, management of largemouth bass in large reservoirs must rely on few studies. What is needed is a reliable method for predicting the consequences of a proposed management action before its implementation.

One approach for development of reliable predictions is the use of models based on systems analysis, computer modeling, and simulation techniques. Mathematical models of fisheries have traditionally been used to assess fish stocks and to predict maximum sustainable yield (2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12). The basic weaknesses of these models are that they are deterministic and assume a steady-state fishery. These assumptions may not be unreasonable when one is dealing with a large marine fishery but are unreasonable when largemouth bass fisheries in large fluctuating reservoirs are being considered.

Watt (12) proposed a model which would include the influence of environmental factors on recruitment, growth, and natural mortality in an attempt to avoid the limitation of deterministic models. This model has been applied to a sport fishery for smallmouth bass in South Bay of Lake Huron (13); however, the analysis suffers from too few data.

This paper describes a computer simulation model that includes environmental factors and predicts year-class strength and population trends for largemouth bass populations. Ultimately, all of our existing knowledge of population dynamics of largemouth bass may be incorporated into such a model. The long-range objective of this research is to develop models of largemouth bass population dynamics that will provide biologists with useful management tools.

METHODS

Population dynamics of largemouth bass in reservoir environments are complex. Thus, these dynamics may best be studied

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in terms of Holling's (14, 15) experimental components approach, with emphasis on the processes of growth, mortality, reproduction, and year-class formation. Holling's approach involves determining which components of the reservoir ecosystem are limiting these processes, followed by definition of system variables and parameters and formulation of the mathematical model.

The objective of this study was to construct a model of the bass population in Lake Carl Blackwell, a 1400-hectare reservoir in north-central Oklahoma. This lake was chosen because several previous investigations have been made here on population dynamics of adult bass (16), growth, production and mortality of young-of-the-year bass (17), growth of bass in relation to water level (18), and the relationship between weather and other environmental factors and year-class strength (19, 20). The philosophy employed in this study was to begin with a simple model (Model I) which included only a few system variables and parameters, and to expand and modify this model so that it would include more of the relevant components. Data collected from Lake Carl Blackwell were analyzed by simple and multiple linear regression techniques (21) to arrive at the mathematical equations used in Model II.

Year-class strength of bass in Lake Carl Blackwell was estimated for 1965 through 1975, using ecological density on 13 August (20), and an additional estimate was made by the author in 1976, using the same sampling techniques (application of rotenone to coves). I estimated survival from egg to age I for 7 consecutive years, from estimates of the egg potential and number of age I recruits the following spring. Estimates of age-specific fecundities were based on the mean lengths presented in Zweiacker et al. (18) and a length-fecundity regression of log-transformed data from Kelley (22) and Coomer (23). Egg potential was calculated by

$$\text{number of eggs} = \sum_{i=3}^{8} N_i m_i (0.5) \qquad \text{Eq. 1}$$

where N_i = number of fish of age i and m_i = number of eggs per female of age i, assuming a 1: 1 sex ratio and maturity at age III. Zweiacker et al. (18) noted that in Lake Carl Blackwell a few age II bass spawned but most did not spawn until age III. Population estimates from Zweiacker (16) and Shirley (17, and unpubl. data) were adjusted to 15 May (the approximate midpoint of the spawning period) by assuming a constant exponential mortality and using age-specific rates (17, 18). Zweiacker's estimates were stratified by single age groups using percentage age composition in his samples.

I adapted the mathematical models for computer simulation, using FORTRAN IV programming language after the forms of the equations were specified. The FORTRAN computer programs were written with flexible input requirements to allow for manipulation of the simulated fish population and to accommodate different parameter values. Programs were run on the IBM System 370/Model 158 digital computer at the Oklahoma State University Computer Center. Program listing and sample outputs are available from the author.

Sensitivity analysis was performed to determine how varying the input parameters affected population size (density) after a 20-year simulation. Net sensitivity of the population side to a 10% change in any given input parameter was computed according to the formula given by Francis (24):

$$S(x,\ y,\ \Delta x) = \frac{y(x+\Delta x) - y(x)}{y(x)} \qquad \text{Eq. 2}$$

where S (x, y, Δ x) is the net sensitivity of y to a change, Δ, in x. The relative sensitivity was then obtained by dividing net sensitivity by the largest net sensitivity value.

Both models were age-structured, based on age-specific fecundities and survival rates, and similar to the Leslie matrix algorithm (25). The notation is as follows: N_i (t) = number of individuals of age i at time t, m_i = fecundity per individual of age i, and S_i = probability that an individual of age i will survive to age i+1. Fecundity per individual, m_i, would equal fecundity per female multiplied by 0.5, assuming a 1:1 sex ratio. The basic time unit is a year which commences at the time eggs are laid (approximately 15 May for Lake Carl Blackwell). The number of eggs produced is calculated by

$$N_o(t) = \sum_i N_i(t) m_i \qquad \text{Eq. 3}$$

and a new age distribution is obtained by

$$N_i(t+1) = N_{i-1}(t)S_{i-1} \qquad \text{Eq. 4}$$

for all i = 1, 2, 3,..., k, where k = maximum age.

Reliable estimates of S_o, survival from egg to age I, are difficult to obtain for natural populations. For this reason, S_o is estimated by assuming an equilibrium population and using age-specific fecundity and survival data. Vaughan and Saila (26) derive this estimation procedure on the basis of the Leslie matrix algorithm:

$$S_o = \frac{1}{\sum_{i=1}^{k-1} [m_{i+1}(\prod_{j=1}^{i} S_j)]} \qquad \text{Eq. 5}$$

RESULTS AND DISCUSSION

Model I

I made a simulation run using average age-specific survival rates from Zweiacker et al. (18), average age-specific fecundities from Kelley (22) (Table 1), and an initial population of 1000 age I fish (Figure 1). The simulated population initially oscillated due to the time-lag for the fish to reach maturity, and finally stabilized at about simulation year 18.

Simulation of Model I with a stable age structure and parameter values in Table 1 resulted in a total population of 2396 after a 20-year simulation. The effect of varying the survival rate of age 0 fish is shown in Figure 2. Results of the sensitivity analysis (Table 2) indicated that density was most responsive to changes in survival rates of age 0, age I, and age II bass, in that order. Therefore, on the basis of this model, it is important that one have accurate estimates of survival rates of these age groups to simulate population trends. Horst (27) also found that population growth of the cunner (*Tautogolabrus adspersus*) was most sensitive to changes in survivorship of younger ages, from a sensitivity analysis of the Leslie matrix model.

TABLE 1. *Initial age structure, age-specific fecundity and survival rates used in nominal simulation of Model I.*

Age (i)	Numbers (N_i)	Fecundity (m_i)	Survival (S_i)
0	--	--	0.00015
1	787	0	0.676
2	528	0	0.616
3	322	9335	0.659
4	210	4350	0.560
5	116	5750	0.375
6	43	13610	0.197
7	8	13610	0.071
8	1	13610	0.000

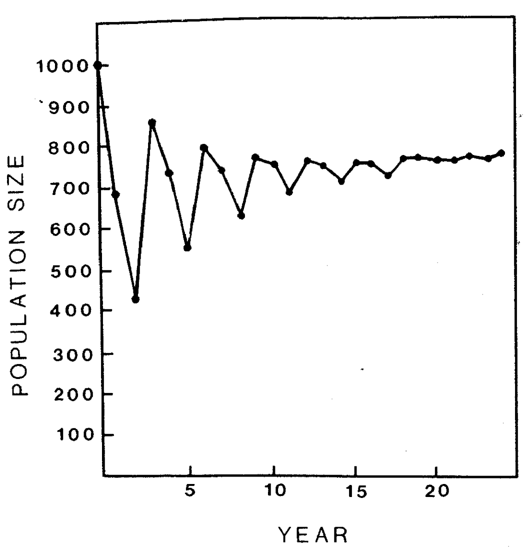

FIGURE 1. Model I simulation of population changes starting with 1000 age I fish.

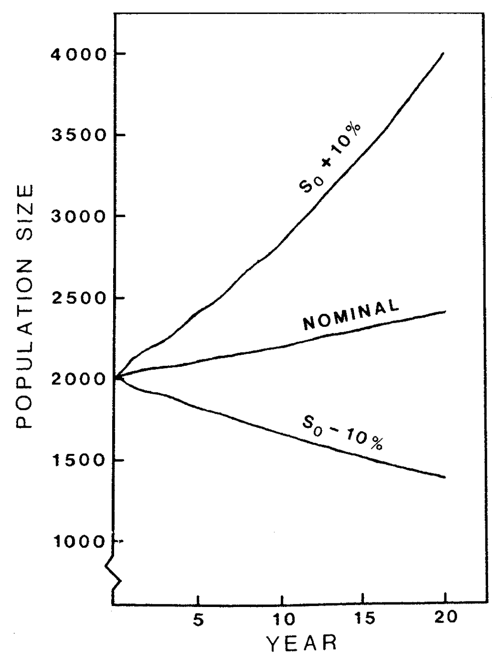

FIGURE 2. Model I simulation results with nominal and adjusted values for the survival rate of age 0 fish, S_o

In Model I, I assumed that the population operated in a deterministic fashion, with constant age-specific survival rates and fecundity. Consequently the simulated population trends beginning with 1000 age I fish (Figure 1) do not mimic the situation in new reservoirs, where in the first years of impoundment, large year-classes of bass are produced and the population exhibits a "boom and bust" phenomenon. Also, the effects of density and environmental factors were ignored in Model I. Since this omission was unrealistic, further development of this model should involve varying the age-specific survival rates or fecundity, or both, based on density or other environmental conditions. Also there is evidence for higher mortality of males than females among older bass (28, 29), which tends to shift the sex ratio away from unity. In many reservoirs this shift may be negligible but inclusion of an appropriate parameter would increase the flexibility of the model.

Model II

Sensitivity analysis of Model I showed that the population size was most sensitive to changes in survival from egg to age I. This conclusion is also supported by field studies in which the major factors influencing this mortality were environmental factors such as wave action, wind, and temperature (19, 30, 31, 32). In many reservoirs large year-classes of largemouth bass are produced in years of stable or rising water levels during spawning (33, 34, 35, 36), probably because the flooding of shoreline areas increases cover for nest sites and for shelter from predation, and releases nutrients into the littoral zone. Also, the increased depth of water over the nests decreases the effects of wind, wave action, and fluctuations in temperature.

The relation between environmental factors and year-class strength of largemouth bass in Lake Carl Blackwell was studied by Summerfelt and Shirley (20), who correlated year-class strength with a series of biotic and abiotic environmental factors. They showed that year-class strength was positively correlated with water level, change in water level, and turbidity; negatively correlated with hardness, alkalinity, and pH; and uncorrelated with wind, air and water temperature, and size of the spawning population. They concluded that the fluctuations in year-class size were due primarily to the water level and its effect on food and cover for young-of-the-year bass. Other significant correlations were attributed to the effects of changing water levels on the physical and chemical composition of the water.

Model II represents an attempt to include the effects of environmental factors on reproduction and year-class formation within the framework of Model I. Year-class strength of largemouth bass varied considerably in Lake Carl Blackwell, as indicated by ecological densities on 13 August (Figure 3). Regression analysis was performed to determine which of the variables in Table 3 would be useful in predicting year-class strength. The correlation coefficient between water level fluctuation and year-class strength (Figure 4) of 0.8779 was highly significant (P = 0.0002), and water

TABLE 2. *Total population sizes (N) and resulting sensitivities obtained after a 20-year simulation of Model I with adjusted input parameters.*

	+10%			−10%		
Parameter	*N*	Net sensitivity	Relative sensitivity	*N*	Net sensitivity	Relative sensitivity
S_0	3990	+0.6653	1.000	1374	−0.4265	1.000
S_1	3928	+0.6394	0.961	1388	−0.4207	0.986
S_2	3935	+0.6423	0.965	1390	−0.4199	0.984
S_3	2981	+0.2442	0.367	1891	−0.2108	0.494
S_4	2735	+0.1415	0.213	2079	−0.1323	0.310
S_5	2568	+0.0718	0.108	2232	−0.0684	0.160
S_6	2421	+0.0104	0.016	2366	−0.0125	0.029
S_7	2397	+0.0004	0.001	2396	0.0	0.0
m_3	3221	+0.3443	0.518	1762	−0.2646	0.620
m_4	2624	+0.0952	0.143	2184	−0.0885	0.207
m_5	2556	+0.0668	0.100	2236	−0.0668	0.156
m_6	2539	+0.0597	0.090	2256	−0.0584	0.137
m_7	2424	+0.0117	0.018	2369	−0.0113	0.026
m_8	2397	+0.0004	0.001	2396	0.0	0.0

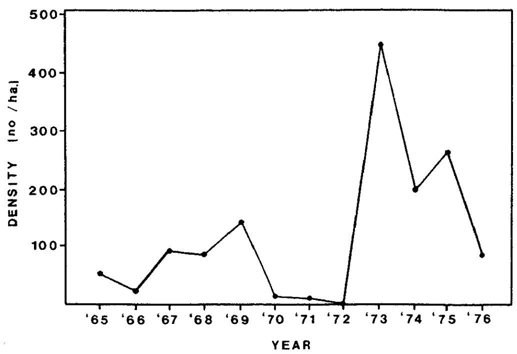

FIGURE 3. Estimated ecological density of young-of-the-year largemouth bass on 13 August in Lake Carl Blackwell, Oklahoma (1965-1976)

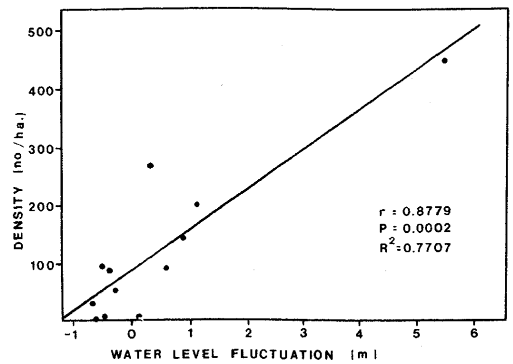

FIGURE 4. Relationship between year-class strength as indexed by ecological density of young-of-the-year largemouth bass on 13 August and water level fluctuation.

level fluctuation accounted for 77.07% (R^2 = 0.7707) of the observed variation in density. The residuals were greatest for 1970, 1971, 1972, when water level was extremely low, and 1975, when water level was at or near spillway level all year. These data indicate the importance of water level itself, in addition to water level fluctuation, in determining the strength of year-classes.

The correlation between water level during the spawning season and year-class strength (Figure 5) was not significant (r = 0.5337; P = 0.0739). However, analysis without the 1973 data yielded a highly significant correlation coefficient (r = 0.7828; P = 0.0044). Even though the water level during the 1973 spawning season was more than 2m below spillway level, it was nevertheless rising, and this condition resulted in very successful largemouth bass reproduction and survival and growth of young-of-the-year. Thus, there is apparently an important interaction between water level during spawning and water level fluctuation with respect to year-class formation.

Results of the multiple regression in which these two variables are used as predictor variables are summarized in Table 4. The equation for predicting density of young-of-the-year bass on 13 August (Y) is

$$Y = -7601.3833 + 62.5356(X_1) + 26.9689(X_2) \quad \text{Eq. 6}$$

where X_1 = water level fluctuation from 1 October of the previous fall to 15 May (m), and X_2) = mean water level during May, M.S.L.). This relationship is

TABLE 3. *Estimated ecological density of young-of-the-year largemouth bass, water level during spawning, and water level fluctuation in Lake Carl Blackwell, Oklahoma (1965-1976).*

Year class	Estimated density[a] (no./ha)	Water level during spawning[b] (m, M.S.L.)	Water level fluctuation[c] (m)
1965	54.6	285.62	−0.286
1966	24.8	284.66	−0.674
1967	95.2	283.77	−0.518
1968	87.8	284.39	0.600
1969	141.9	284.84	0.869
1970	7.4	284.81	0.104
1971	5.5	283.41	−0.472
1972	0.13	282.57	−0.613
1973	447.4	285.53	5.432
1974	200.5	287.81	1.122
1975	266.4	287.92	0.277
1976	88.9	286.99	−0.390
Mean:	118.4	285.19	0.4587
Standard deviation:	132.0	1.68	1.5526

[a]Adjusted to 13 August (1965-1975 data from Summerfelt and Shirley (20).
[b]Mean water level during May.
[c]Fluctuation in water level from 1 October of previous growing season to 15 May.

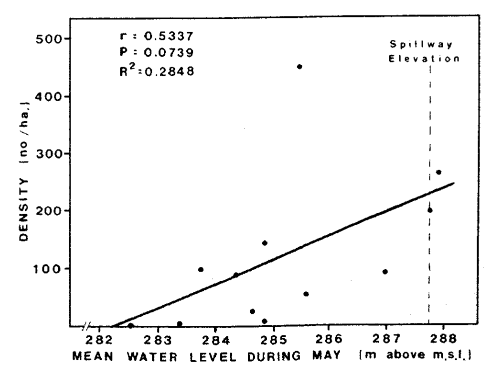

FIGURE 5. Relationship between year-class strength as indexed by ecological density of young-of-the-year largemouth bass on 13 August and water level during May

TABLE 4. *Analysis of variance table for multiple regression analysis of dependent variable — young-of-the-year density — and independent variables — water level fluctuation (X_1) and mean water level during May (X_2).*

Source	d.f.	S.S.	M.S.	F	P
Corrected total	11	191669.1068			
Regression	2	169042.7681	84521.3841	33.6198	0.0002
R ($b_1 \mid b_o$)	1	147714.9289	147714.9289	58.7560	0.0001
R ($b_2 \mid b_o$, b_1)	1	21327.8392	21327.8392	8.4835	0.0172
Residual	9	22626.3387	2514.0376		

highly significant because the calculated F = 33.6198 for regression has an associated probability of a greater F-value of 0.0002. Furthermore, these two variables account for 88.20% (R^2 = 0.8820) of the observed variation in density. This R^2 value is substantially higher than that observed for the regression with either water level fluctuation alone (R^2 = 0.7707), or water level during May alone (R^2 = 0.2848). Also, the addition of the second variable, water level during spawning, to the model was significant as evidenced by the sequential F-test (F = 8.4835; 1, 9; P = 0.0172). Water level fluctuation is more than twice as important as water level during May in predicting density of young of the year bass; the ratio of standardized regression coefficients was 2.317 (0.7959/0.3435).

For inclusion of this relationship in the population dynamics model, it was necessary to relate survival from egg to age I to these two variables. I therefore used estimates of age-specific fecundities for Lake Carl Blackwell (Table 5) and estimates of number of fish per age group in the spring, and total egg potential of the stock to calculate annual instantaneous mortality rates (Z_o) from egg stage to age I (Table 6). Annual instantaneous mortality rate (Z) is related to survival rate (S) by

TABLE 5. *Mean total length and estimated age-specific fecundity of largemouth bass in Lake Carl Blackwell.*

Age	Mean total length (mm)	Number of eggs per female
III	369	18487
IV	425	28917
V	462	37665
VI	485	43929
VII	504	49613
VIII	531	58527

$$S = e^{-Z} \quad \text{Eq. 7}$$

where e = the base of natural logarithm[5] (7).

Results of the multiple regression analysis in which water level fluctuation from 1 October of the previous fall to 15 May (m) (X_1) and mean water level during May (m, M.S.L.) (X_2) are used to predict

TABLE 6. *Estimated number of fish per age group in the spring, egg potential, and annual instantaneous mortality rate (Z_a) from egg to age I for largemouth bass from Lake Carl Blackwell, Oklahoma.*

Age	Number of fish per age group 1968[a]	1969[a]	1970[b]	1971[b]	1972[c]	1973[c]	1974[c]	1975[c]
I	1151	357	178[c]	360[c]	322	32[d]	78741[d]	12640[e]
II	305	766	241	120[c]	207	217	22[e]	--
III	192	138	472	148	74	127	134	14
IV	175	269	91	311	62	49	84	88
V	206	142	151	51	53	34	27	47
VI	78	70	53	57	27	20	13	10
VII	24	15	14	10	11	5	4	3
VIII	--	--	1	1	--	1	--	--
Egg Potential:	10493072	9748767	10063037	8354395	3444482	3115281	3346385	2580950
Z_o:	10.28849	10.91087	10.40079	10.16375	11.58655	3.67791	5.57877	

[a]Zweiacker (16, p. 54)
[b]From Spring 1969 estimates
[c]From Shirley's (unpubl. data) estimate of 6 October 1972
[d]Shirley (17, p. 32 & 39)
[e]From Summerfelt and Shirley (30, p. 34) estimate of 14 October 1974

the annual instantaneous mortality rate Z_o) from egg to age I are significant (Table 7). The equation for predicting Z_o is

$$Z_o = 230.8063 - 0.9689(X_1) - 0.7757(X_2) \quad \textbf{Eq. 8}$$

This regression equation is significant F = 13.1073; 2, 4; P = 0.0193) and accounts for 86.76% (R^2 = 0.8676) of the observed variation in Z_o. The observed and predicted values coincided well (Figure 6).

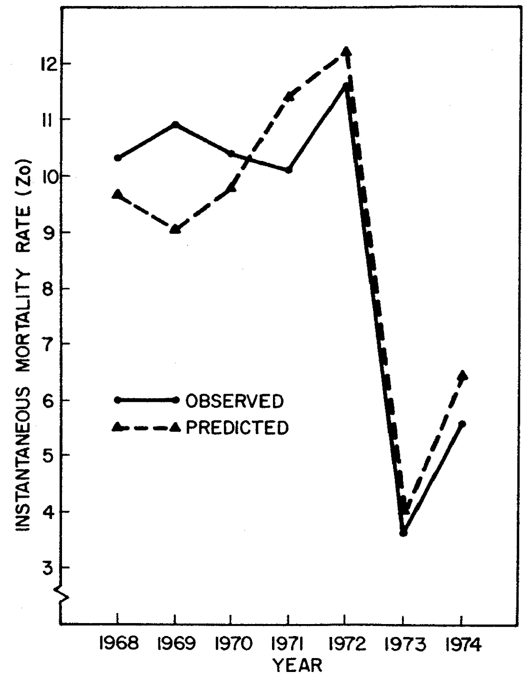

FIGURE 6. Observed and predicted annual instantaneous mortality rates (Z_0) from egg to age I for largemouth bass in Lake Carl Blackwell (1968-1974)

Model II is essentially the same as Model I, except that Model II includes the equation to predict the survival from egg to age I, parameters to account for the percentages for each age group that are mature and female (incorporated into equation 3), and the use of fecundity per female rather than fecundity per individual.

Simulation of the Lake Carl Blackell population was made using initial age structure for spring 1968 (Table 6), age-specific survival rates (Table 1) from Zweiacker et al. (18), age-specific fecundity from Table 5, and water level data for Lake Carl Blackwell from 1968 to 1977 (Table 3). Inasmuch as confidence limits on some of the input data vary widely, discrepancies between simulated and observed number of age I recruits could be attributed to either errors in the population estimates or errors in the model.

Comparison of the simulated predictions of year-class strength, as indicated by the number of age I recruits, with the observed number of age I recruits (Figure 7) show that precision of the estimates is high; however, the model cannot be soundly validated with data that were used for its derivation.

Model II should prove to be of value in largemouth bass fishery management by enabling fishery biologists to quickly and easily predict year-class strength for any given year, and hence the future population size and structure. With this information at hand, fishery managers can make better decisions on stocking recommendations and creel limits.

It is unlikely, though, that the parameters derived in this study for the relationship between year-class strength and water level fluctuation and water level during the spawning season will be the same for all reservoirs. Therefore research must be done on other reservoirs to evaluate the generality of this relationship and to determine the appropriate parameter values for individual reservoirs.

TABLE 7. *Analysis of variance table for multiple regression analysis of dependent variable — annual instantaneous mortality rate (Z_0) from egg to age I — and independent variables — water level fluctuation (X_1) and mean water level during May (X_2).*

Source	d.f.	S.S.	M.S.	F	P
Corrected total	6	55.3258			
Regression	2	48.0014	24.0007	13.1073	0.0193
R ($b_1 \mid b_0$)	1	40.0728	40.0728	21.8846	0.0095
R ($b_2 \mid b_0$, b_1)	1	7.9286	7.9286	4.3300	0.1059
Residual	4	7.3244	1.8311		

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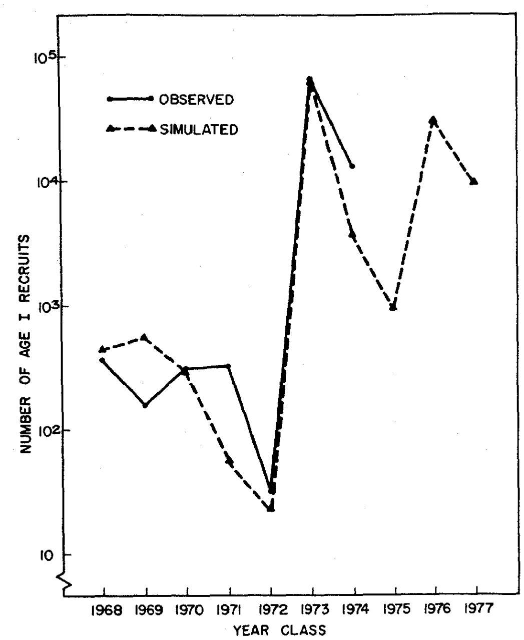

FIGURE 7. Observed estimates and Model II simulation of number of age I recruits in year-classes 1968 through 1977 in Lake Carl Blackwell

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