DEVELOPMENT OF A COMPUTER SIMULATION MODEL OF LARGEMOUTH BASS POPULATION DYNAMICS

By

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DEVELOPMENT OF A COMPUTER SIMULATION MODEL OF

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PREFACE

Many aspects of the population dynamics of largemouth bass have been investigated in Lake Carl Blackwell by the Oklahoma Cooperative Fishery Research Unit. The objective of this study was to incorporate these research findings into a computer simulation model of population dynamics. Funds were provided by Federal Aid to Fish and Wildlife Restoration, Oklahoma D-J Project F-36-R, Job 3.

I would like to thank my Graduate Committee--Dr. Michael D. Clady, Dr. O. Eugene Maughan, Dr. Ronald W. McNew, and Dr. Robert J. Mulholland--for their assistance and their critical reviews of the manuscript. I would also like to thank Dr. Robert C. Summerfelt for the encouragement and guidance he offered me during the initial phases of this study. The work of all Unit personnel during the many years of studies on Lake Carl Blackwell is appreciated; without it this research would never have been accomplished.

To my wife, Martha, I extend my gratitude for her patience and understanding during the many nights I spent either preoccupied with my computerized bass population, or electrofishing until 2 a.m. And finally, I am grateful to my parents, William John and Marie Joanne Orth, for their moral and financial support.

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CHAPTER I

INTRODUCTION

The largemouth bass, *Micropterus salmoides* (Lacépède), is one of the most important sport fishes of warmwater lakes and reservoirs. Many anglers fish exclusively for largemouth bass, others fish for it only incidently, but most consider this species an outstanding sport fish. Horvath (1974) reported that about 24 percent of the fishing trips on reservoirs in the southeastern states are specifically for bass and another 18 percent for bass plus other species (Jenkins 1975). The largemouth bass is also an economically important species because these anglers spend a considerable amount of money on boats, motors, gasoline, bait, tackle, and licenses; therefore, waters which support healthy populations of largemouth bass become valuable natural resources.

Careful management of natural resources is necessary to ensure proper protection and preservation while allowing some type of utilization by society. In the case of largemouth bass, we would like to regulate the fisherman's harvest to ensure that the resource is not depleted. To do this we must understand how regulations and environmental factors influence population processes and ultimately yield. We must also understand the ecological role (or niche) of the largemouth bass in the fish community. In multispecies fisheries largemouth bass serve a dual function. They regulate the size of sunfish populations, thereby allowing these fish to grow to a larger size, and they convert the biomass of many non-game fish (e.g., shad, Dorosoma spp.) to a more usable and aesthetic form.

The management of largemouth bass fisheries in large reservoirs (greater than 200 hectares) is often difficult because reservoir size may prohibit the fishery manager from collecting enough data to propose rational management strategies. Also, most of these reservoirs have unstable water levels which prevent the reservoir system fish population from attaining a stable (or steady) state. Management of largemouth bass fisheries in large reservoirs must thus rely on very few experimental studies on the response of the fish populations to the implementation of various management strategies. What is needed is a reliable method for predicting the consequences of a proposed management decision prior to implementation.

One approach that has been utilized in the management of other sport and commercial fisheries is the use of systems analysis, computer modeling and simulation techniques to develop a model to aid in management. The objective of this study is to develop a computer simulation model which will predict year-class strength, production and yield for the largemouth bass population of Lake Carl Blackwell. The long-range objective of this type of research is to develop a largemouth bass management model that will provide biologists with a useful tool for optimizing the yield from the fishery.

CHAPTER II

LITERATURE REVIEW

Models in General

The term, model, can be defined generally as any physical or abstract representation of a real system. Models may be categorized as mental, verbal, graphical, physical, or mathematical. Each of us has a mental image of how a pair of guppies in an aquarium will increase in numbers, slowly at first and then more rapidly as more individuals become sexually mature, until the population finally stabilizes at a certain level. Our mental image, when put into words, becomes a verbal model which can be more vividly expressed by means of a graphical model (Figure 1). The aquarium which the guppies occupied was a physical representation of the real system (i.e., a tropical aquatic ecosystem) which the guppies normally inhabit. Physical models such as this one are useful in that many variables are controlled allowing us to study the effect of only a few. Mathematical models are the most rigorous type of models and permit us to say precisely how the components of our simplified system are related. The rate of change in the number of guppies in our aquarium at any instant is described by a mathematical model:

$$\frac{dN}{dt} = r\left[\frac{K - N}{K}\right]N \tag{2.1}$$

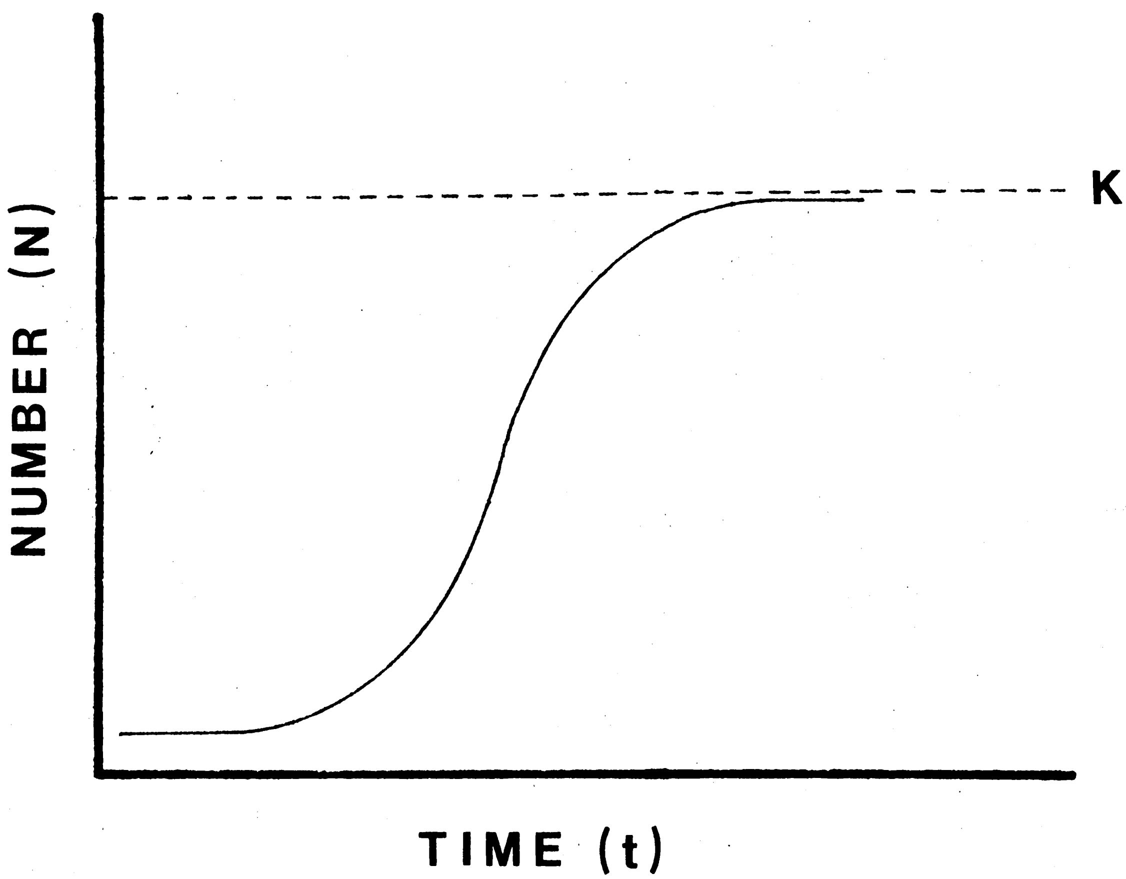

Figure 1. Graphical model of the increase in a population of guppies over time.

where N = number of guppies, K = number of guppies at the stabilization level (asymptote), r = intrinsic rate of population increase, and t = time. Integrating (2.1) we get an equation for the S-shaped logistic curve for population growth in Figure 1:

$$N(t) = \frac{K}{1 + N(0)e^{-rt}} \tag{2.2}$$

This is a simple mathematical model which relates only two components of the system, i.e., rate of population change and population density.

More complex mathematical models consist of (i) system (or state) variables, (ii) transfer functions, (iii) forcing functions, and (iv) parameters (Walters 1971). System variables are sets of numbers used to represent the state of the system at a given time. One or more system variables are used to characterize a particular component of the system. Transfer functions are equations which represent flows or interactions between components, forcing functions are equations which represent inputs to the system, and parameters are constants of the mathematical equations. Depending on the description of the parameters and the form of the transfer functions and forcing functions, a model may be deterministic or stochastic. The deterministic model tells us that for given values of the independent variables we should expect the dependent variables to have a single corresponding value. The possibility of chance variation is ignored. Stochastic models attempt to include the effects of random variability so that for any given values of the independent variables we might expect the dependent variable to have a series of values, each with an associated probability.

All of the models referred to hereinafter are similar in that they are mathematical, but they differ in the level of hierarchial organization of the system's components and the choice of system variables. The components and system variables used in the development of a particular model depend on the fishery under study, the amount and type of available data, and the questions the model is intended to answer.

Models may be evaluated in terms of their resolution, realism, precision, and generality (Holling 1966a). Resolution is a depth criterion related to the number of essential features in the real system that the model is intended to mimic. A model that includes only a few simple components is said to have low resolution and, conversely, if it includes many of the attributes of the system it is said to have high resolution. Realism refers to the degree to which the mathematical equations correspond to the biological processes which they describe. A model which predicts the growth rate of a fish simply on the basis of its age ignores the true components of the growth process, i.e., feeding energetics, and loses a degree of realism. The third criterion, precision, is concerned with the ability of the model to generate values for a component that compare with the values observed in the real system. Generality is a breadth criterion related to the ability of the model to work in a variety of real world systems. Holling (1966b) has shown that by dividing relevant components into basic (universal) and subsidiary (sporadic) components, generality becomes theoretically possible. Components shared by all examples are called basic in that they underlie all manifestations of the process. Those that are present in only some situations are called subsidiary.

Classical Models of Fisheries

Mathematical models of fishery systems have traditionally been used for fish stock assessment and prediction of maximum sustained yield. Baranov (1918) was the first to develop a theoretical model of an exploited fish population. The dynamics of this model were governed by recruitment, growth, natural mortality and fishing mortality. The total biomass of usable stock (P), i.e., fishes large enough to be harvested, was increased by the recruitment of new individuals to the usable stock and by growth of individuals and decreased by both natural and fishing mortality. A general model can be constructed expressing the relative rate of change in biomass of the usable stock in these terms:

$$\frac{dP}{Pdt} = R(P) + G(P) - M(P) - F(E) + e, \qquad (2.3)$$

where R, G, and M = rates of recruitment, growth, and natural mortality, respectively, and are functions of the biomass of usable stock (P) and its age composition (Beverton and Holt 1963). F = fishing mortality and is a function of fishing effort (E), and e is a variable rate of change in the biomass due to environmental factors. In the steady state, with population in equilibrium under average environmental condition, $\frac{dP}{dt} = 0$ and e = 0, so that

$$F(E) = R(P) + G(P) - M(P), \qquad (2.4)$$

and the equilibrium harvest, Y = F(E)P, will equal the additions due to recruitment and growth minus the loss due to natural mortality, i.e.,

$$Y = F(E)P = [R(P) + G(P) - M(P)]\ P. \qquad (2.5)$$

Ricker (1975) discussed various methods to compute equilibrium harvest and Paulik and Bayliff (1967) have developed a computer program for

Ricker's method.

The two general approaches most often used to predict the yield of exploited fish populations are (i) dynamic pool models and (ii) logistic models. Dynamic pool models are the most widely employed. In these models the elemental rates of recruitment, growth and natural mortality are estimated separately and combined into an appropriate form of the general model (2.5) assuming a steady state. These models, elaborated by Beverton and Holt (1957), are especially applicable to fisheries where one may regulate both fishing effort and minimum size of capture.

The other approach, which has been developed most completely by Schaefer (1954, 1957), was modified by Fox (1970) and Pella and Tomlinson (1969), and reviewed by Silliman (1971). It involves combining the rates of recruitment, growth and natural mortality into a single function of the biomass of usable stock (P). Models of this type, called logistic or surplus production models, are useful in that the only data needed are total catch, total effort and the instantaneous rate of fishing mortality. However, predictive reliability of this model is not very dependable due to the inherent assumptions (Watt 1956).

The basic weakness of these existing mathematical models is that they are deterministic and assume a steady-state fishery, i.e., one in which recruitment, growth and natural mortality are constant from year to year. This assumption may not be too unreasonable when dealing with a large marine fishery but in general, the smaller the fishery, the more chance there is that results predicted by a deterministic model will not match the actual results. To avoid this limitation

Watt (1956) proposed a model which would include the influence of environmental factors on recruitment, growth and natural mortality, and has applied this model to a sport fishery for smallmouth bass in South Bay of Lake Huron (Watt 1959). However, this type of model will work only where fishing intensities have covered a wide range of values, and a great amount and variety of population data are available.

Systems Analysis, Computer Modeling and Simulation Applied to Fisheries

The availability of electronic digital computers has enhanced the growth and development of new quantitative techniques, such as systems analysis, computer modeling and simulation. Considerable progress has also been made in the application of these techniques to ecology (Patten 1971, 1972, 1975a; Watt 1966, 1968) and fisheries science (Saila 1972).

Systems analysis involves determining which variables are most important in regulating the system, and incorporating these variables into a mathematical systems model. Computer implementation and the concurrent ease of bookkeeping and computation has allowed these models to become more complex and include more of the relevant variables than was previously possible.

Once the mathematical model has been formulated and programmed for the computer the behavior of the system can be simulated. Hence, computer simulation models have evolved. Simulation can also be used for determining parameter values by varying input values until simulated results agree with observed data. Sensitivity analysis involves simulation using variations in input variables and parameters to determine the magnitude of input effect on system behavior. Validation of the model involves testing to see if the model adequately predicts observed system behavior. Another technique of systems analysis involves optimization of an objective function by manipulation of control variables (Farrell et al. 1975). Saila and Hess (1975) have applied optimization techniques to fisheries management using maximum biomass yield as the objective function and rate of fishing as the control variable for the Beverton-Holt and Schaefer models.

Paulik (1969, 1972) has reviewed the literature on computer simulation models in fisheries research, management and teaching and has predicted that the resource management agency of the future will maintain a hierarchy of simulation models to serve as basic planning tools for studying system response to natural and artificial change. Lackey (1975) also foresees a much closer involvement between modelers and decision-makers in natural resource management. Simulation in fisheries is commonly used to evaluate costs and benefits of management strategies and to learn basic system properties, especially ecological properties.

Two main tactical approaches to development of simulation models in fisheries and ecological systems can be categorized as the "experimental components" (Holling 1963, 1966a, 1966b) and the "compartmental system" (Patten 1971) approaches. The experimental components approach emphasizes a detailed analysis of ecological processes by breaking them down into simple subprocesses or experimental components. This approach would seem well suited for a model of population dynamics in which the processes of growth, mortality, reproduction, predation, and competition would be analyzed as subprocesses. The compartmental system approach emphasizes the quantities of energy and materials in ecosystem compartments. Complex processes associated with populations making up the compartments are assumed to counter-balance one another resulting in simple behavior of the compartment as a whole. Models developed using the experimental components approach have tended to be realistic and precise and those using the compartmental system approach have tended to be general, but not realistic (Walters 1971).

Current Simulation Models in Use

Simulation models for many of the important commercial fisheries have been developed using a detailed analysis of the population processes. Most of these have been developed for a specific fishery (Francis 1974; Jensen 1975; Jones and Hall 1973; Larkin and Hourston 1964; Larkin and McDonald 1968; Paulik and Greenough 1966) but a few models are available that are generally applicable (Silliman 1966, 1969; Walters 1969).

The development of simulation models for inland recreational fisheries has encountered many difficulties. First, there is relatively little data available for these fisheries when compared to commercial marine fisheries and second, the dynamic pool and logistic models are inadequate in describing multispecies fisheries in which a steady state cannot be safely assumed. Some progress has been initiated toward simulating multispecies centrarchid fisheries (Zuboy and Lackey 1975) and put-and-take trout fisheries (Hammond and Lackey 1976), providing a foundation on which to build more complex models. Another promising approach has been to model fish biomass dynamics by analyzing the ecological processes involved (Hackney and Minns 1974;

Kitchell et al. 1974).

Recent authors (Dickie 1973; Lackey 1975; Patten 1969; Regier and Henderson 1973; Schaaf 1975) have emphasized the need for a more general modeling approach directed explicitly at the ecosystem level of organization. This approach stresses the importance of the interactive system aspect of fisheries and consequently efforts would be devoted to measurement of overall system properties and proposing generalizations which would enable us to simplify the systems that must be managed. These models usually analyze the flow of energy and/or biomass through several gross compartments of the fishery system (Riffenberg 1969; Patten 1969; Walters and Efford 1972).

Computer simulation models are also valuable tools in teaching natural resources management and evaluating management strategies since they allow the student and/or manager to make and test decisions on a simulated resource and analyze their consequences almost immediately (Clark and Lackey 1975; Li and Adams 1976; Titlow and Lackey 1973, 1974).

CHAPTER III

DESCRIPTION OF STUDY AREA

Lake Carl Blackwell (Figure 2) is a shallow, turbid reservoir located in north-central Oklahoma, about 12.8 kilometers west of Stillwater in Payne and Noble Counties. Dam construction on Stillwater Creek, a Works Progress Administration project, began in 1936 and was completed in 1938 with the primary purpose of providing erosion control although the lake has also been used for outdoor recreation, municipal water supply, and flood control. The reservoir and some of the surrounding land was leased to Oklahoma State University in 1948 and deeded to the University in 1954. From 1950 to 1974, it also served as the sole water supply for municipal Stillwater but with the completion of nearby Lake McMurtry, it now serves as an alternate water supply (Shirley 1975).

The original spillway elevation was 288.37 meters above mean sea level (M.S.L.) but in 1948 the spillway was reconstructed and lowered to an elevation of 287.78 meters above M.S.L. At this elevation the surface area is 1400 hectares, volume is 67.8 million cubic meters, mean depth is 4.8 meters, and the shoreline development index (S.D.I.) is 6.8. The reservoir is situated in a relatively small watershed (approximately 14 times the surface area of the lake) in a region characterized by cyclic rainfall, and thus has been subject to water level fluctuations since its impoundment (Figure 3). In October 1972 the reservoir

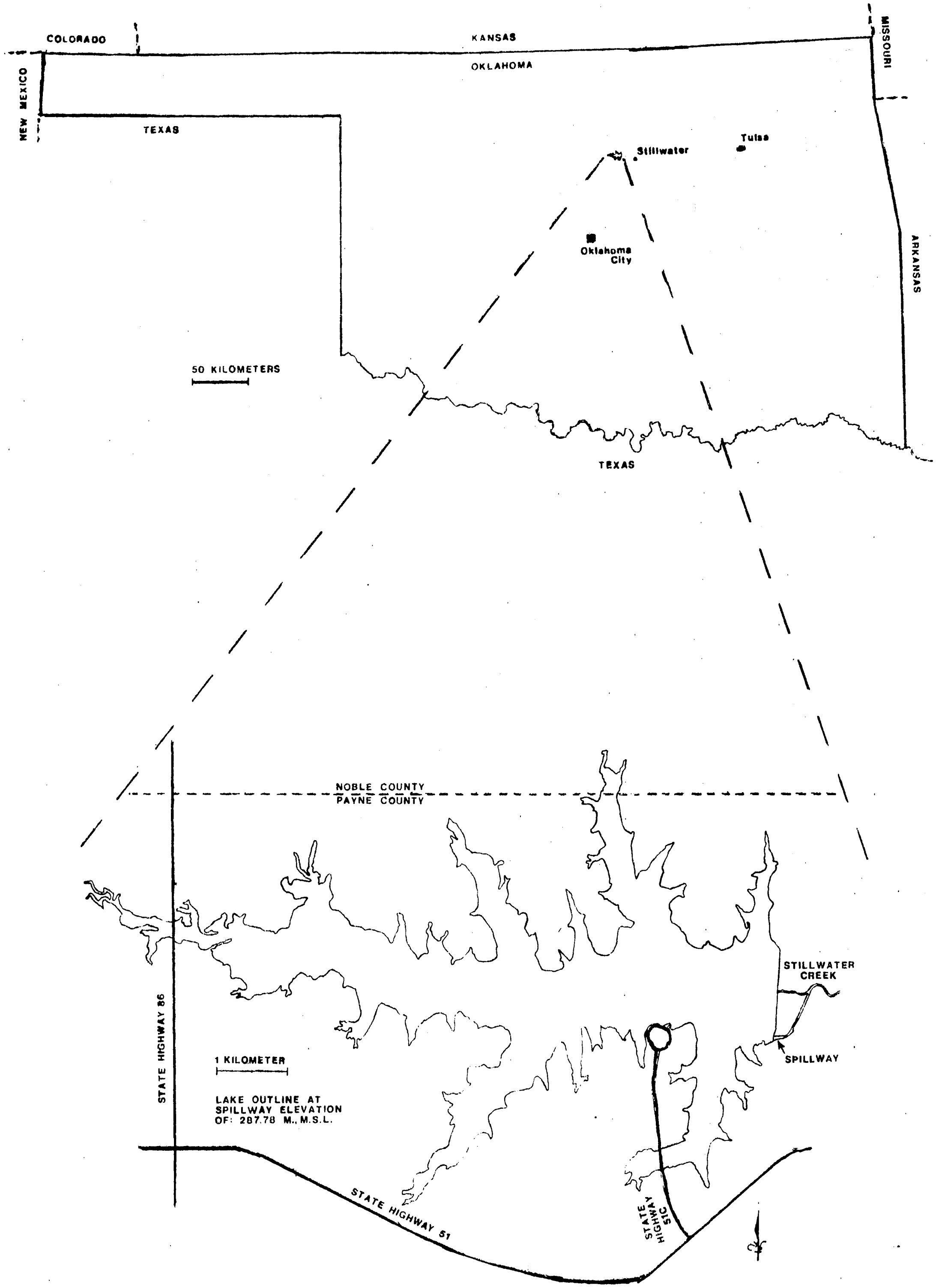

Figure 2. Lake Carl Blackwell and its location relative to Oklahoma and surrounding states.

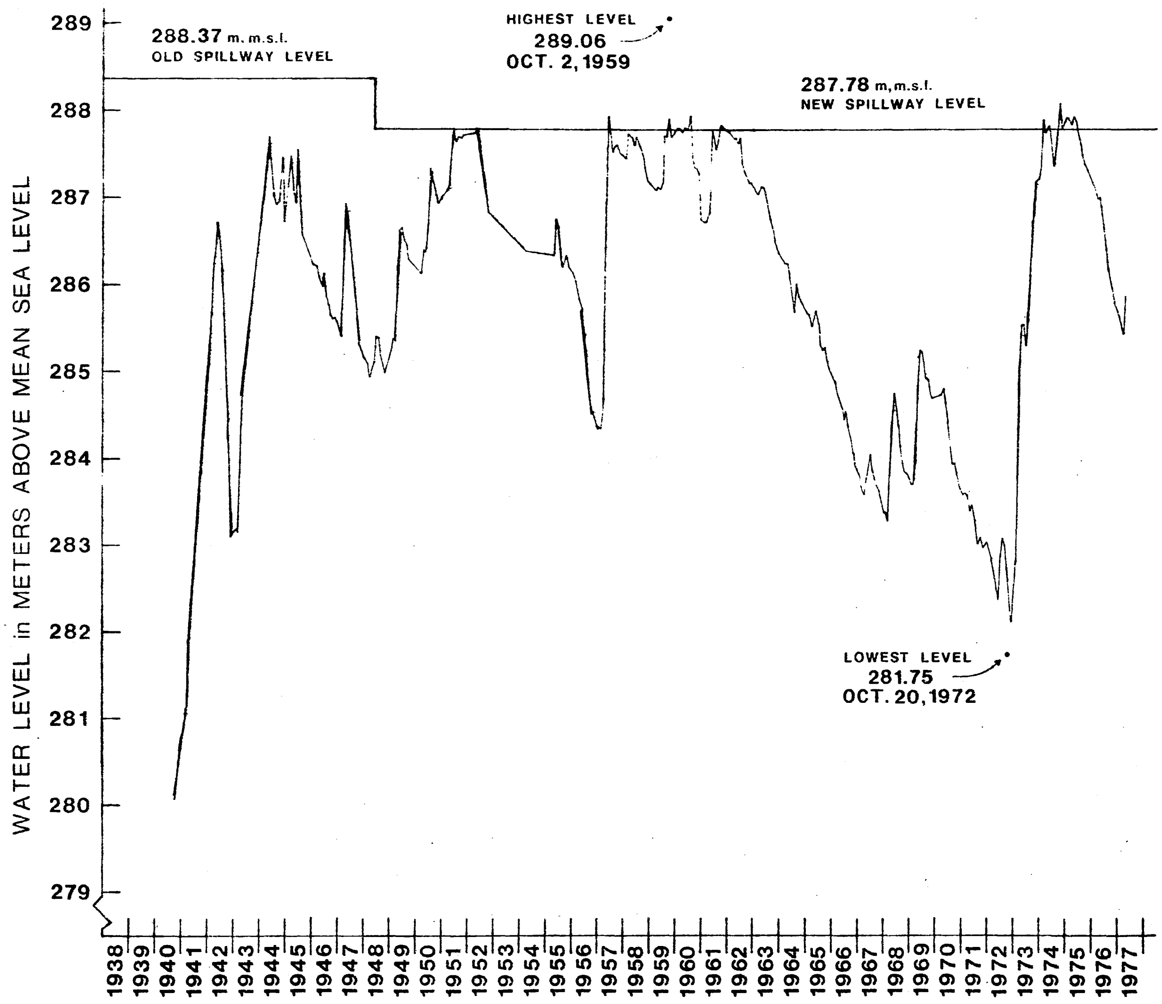

Figure 3. Water level in meters above mean sea level for Lake Carl Blackwell from impoundment to May 1977.

reached the lowest recorded elevation of 281.75 meters above M.S.L., over 6 meters below spillway elevation. At this level, the surface area was only 491.7 hectares, volume was 11.0 million cubic meters, mean depth was 2.2 meters, and the S.D.I. was 3.5. Maximum depth occurs in the old stream channel near the dam and the shallowest depths occur at the west end.

The reservoir is contained within the Redbeds Plains physiographic region, characterized by fine red soils derived from Permian clays and shales. The rolling hills surrounding Lake Carl Blackwell are partially wooded, but pastures of native grasses prevail. Wind-generated wave action resulting from the high average wind velocities of the prevailing southwest winds along with the relatively low, unprotected shoreline, shallow depth, and east-west orientation of the reservoir allow almost continuous vertical and horizontal water circulation. Consequently, temperature and dissolved oxygen curves are generally orthograde and the water remains turbid. Thermal stratification occurs occasionally during the summer months with coincidence of high ambient air temperatures and decreased wind velocities. The turbidity seems to be a result of resuspension of shallow sediment by wave action in the western end of the lake, and movement of sediment to the eastern end by wind-driven currents (Norton 1968; Hysmith 1975). In 1968 and 1969, Hysmith (1975) measured turbidities ranging from 17.0 to 109.7 ppm SiO_2 and averaging 42.5 ppm. He was, however, unable to show that primary productivity was limited by turbidity, although Leonard (1950) felt that turbidity rather than chemical conditions was the primary factor limiting primary productivity during the first 12 years of impoundment.

Almost the entire lake is devoid of submergent and emergent aquatic macrophytes, apparently due to turbid water conditions, unstable bottom sediments, and fluctuating water levels. Potamogeton nodosus, American pondweed; Scirpus spp., bulrushes; and Typha spp., cat-tails, do occur occasionally under stable water levels in coves protected from prevailing winds. A periodic sequence of natural drawdowns, plant succession, and flooding is a recurring phenomenon of the lake, as was noted during the first 12 years following impoundment (Loomis 1951; de Gruchy 1952). Cyperus spp., sedges; Amannia coccinea, scarlet amannia; and Polygonum spp., smartweeds, are the predominant terrestrial macrophytes that follow the receding water line (de Gruchy 1952).

The following fish species are known to occur in Lake Carl Blackwell, and are listed in order of decreasing relative abundance based on cove rotenone samples taken from 1966 to 1975.

	Scientific Name	Common Name
1)	Dorosoma cepedianum (LeSueur)	Gizzard shad
2)	Lepomis macrochirus Rafinesque	Bluegill
3)	Pomoxis annularis Rafinesque	White crappie
4)	Lepomis megalotis Cope	Longear sunfish
5)	Aplodinotus grunniens Rafinesque	Freshwater drum
6)	Lepomis humilis (Girard)	Orangespotted sunfish
7)	Lepomis cyanellus Rafinesque	Green sunfish
8)	Micropterus salmoides (Lacépède)	Largemouth bass
9)	Ictalurus punctatus (Rafinesque)	Channel catfish
10)	Cyprinus carpio Linnaeus	Carp
11)	Carpiodes carpio (Rafinesque)	River carpsucker
12)	Morone chrysops (Rafinesque)	White bass
13)	Pylodictis olivaris (Rafinesque)	Flathead catfish

14) *Pimephales* spp. Minnows

15) *Ictalurus melas* (Rafinesque) Black bullhead

16) *Notropis lutrensis* (Baird and Girard) Red shiner

17) *Notemigonus chrysoleucas* (Rafinesque) Golden shiner

18) *Gambusia affinis* (Baird and Girard) Mosquitofish

19) *Lepomis microlophus* (Günther) Redear sunfish

In addition to these species, a few black crappie, *Pomoxis nigromaculatus* (LeSueur), were collected in 1973 and 1974. Loomis (1951) reported black crappie to be the fourth most abundant fish species in the lake. Walleye fry, *Stizostedion vitreum vitreum* (Mitchill), were stocked in 1969, 1970, and 1971, and northern pike, *Esox lucius* Linnaeus, in 1968, but there was no evidence of natural reproduction (Johnson 1974). The fish population is unusual for an Oklahoma reservoir in that the gars (*Lepisosteus* spp.) and the buffalofishes (*Ictiobus* spp.) are absent.

The fishery of Lake Carl Blackwell is concentrated on channel catfish, largemouth bass, white crappie, and white bass. Based on a creel survey conducted in 1969, 61.8% of the anglers were fishing for channel catfish, and 13.8%, 11.1%, and 10.9% were fishing for largemouth bass, white crappie, and white bass, respectively (Zweiacker 1972).

Lake Carl Blackwell was chosen for the study area since several investigations have been made on aspects of the ecology of largemouth bass, including population dynamics of adults (Zweiacker 1972), growth, production, and mortality of young-of-the-year (Shirley 1975), growth in relation to water level (Zweiacker et al. 1973), and the relationships between weather and other environmental factors and year-class strength (Summerfelt 1975; Summerfelt and Shirley 1976).

CHAPTER IV

MODELING PROCEDURE

Population dynamics of largemouth bass in reservoir environments are very complex and may best be studied in terms of Holling's experimental components approach with emphasis on the processes of growth, mortality, reproduction and year-class formation. Each of these processes is influenced by the life history stage or age of the fish, many density dependent and density independent factors, and the season of the year. A population dynamics model must reflect these ecological processes if it is to be a realistic representation. Since the model will be intended for use in evaluating management strategies, considerable flexibility of input requirements is needed because the same amount and type of data will not be available for all reservoir bass fisheries.

The first step in developing a model of reservoir bass populations is to determine which components of the reservoir ecosystem are relevant to the analysis of these ecological processes. Initial analysis of each process involves construction of box-arrow diagrams to indicate paths of cause-and-effect relationships (Figures 4, 5, and 6). Development of these diagrams was the result of review of the literature on these topics. The purpose of these figures is to provide a reference point and a guide for modeling and to aid in conceptualization of the interrelationships.

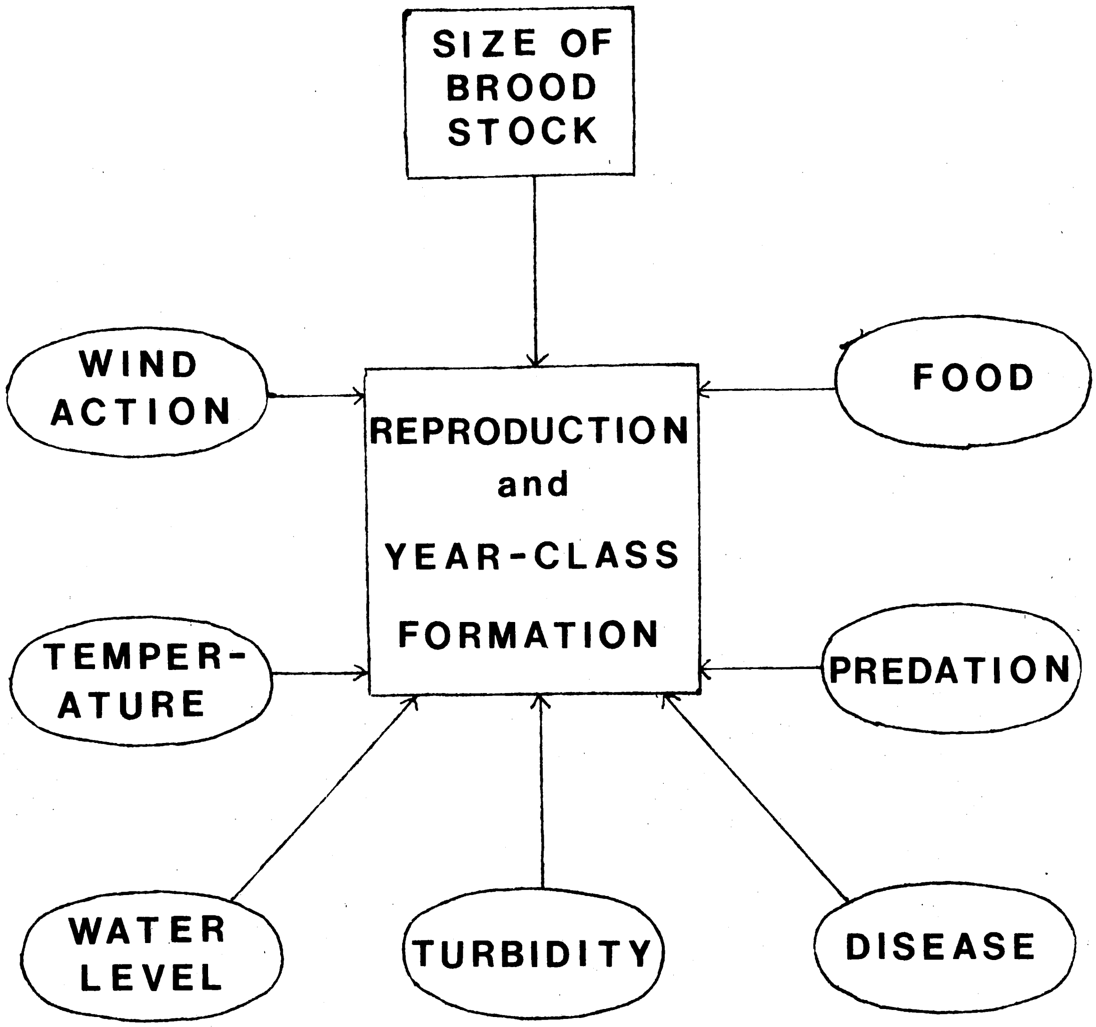

Figure 4. Factors influencing the reproductive process and year-class formation in largemouth bass.

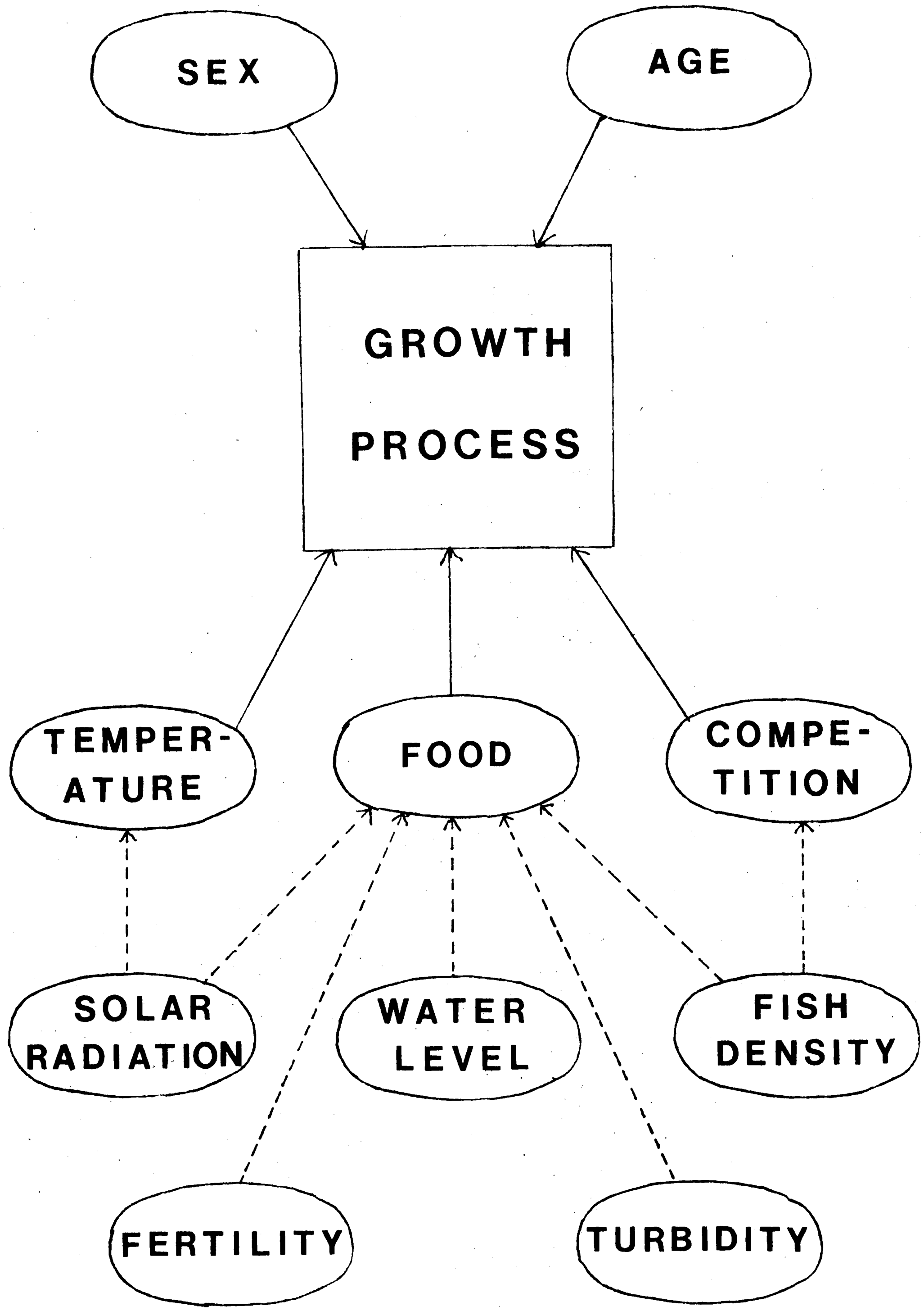

Figure 5. Factors influencing the growth process of largemouth bass. Solid lines and broken lines indicate direct and indirect influences, respectively.

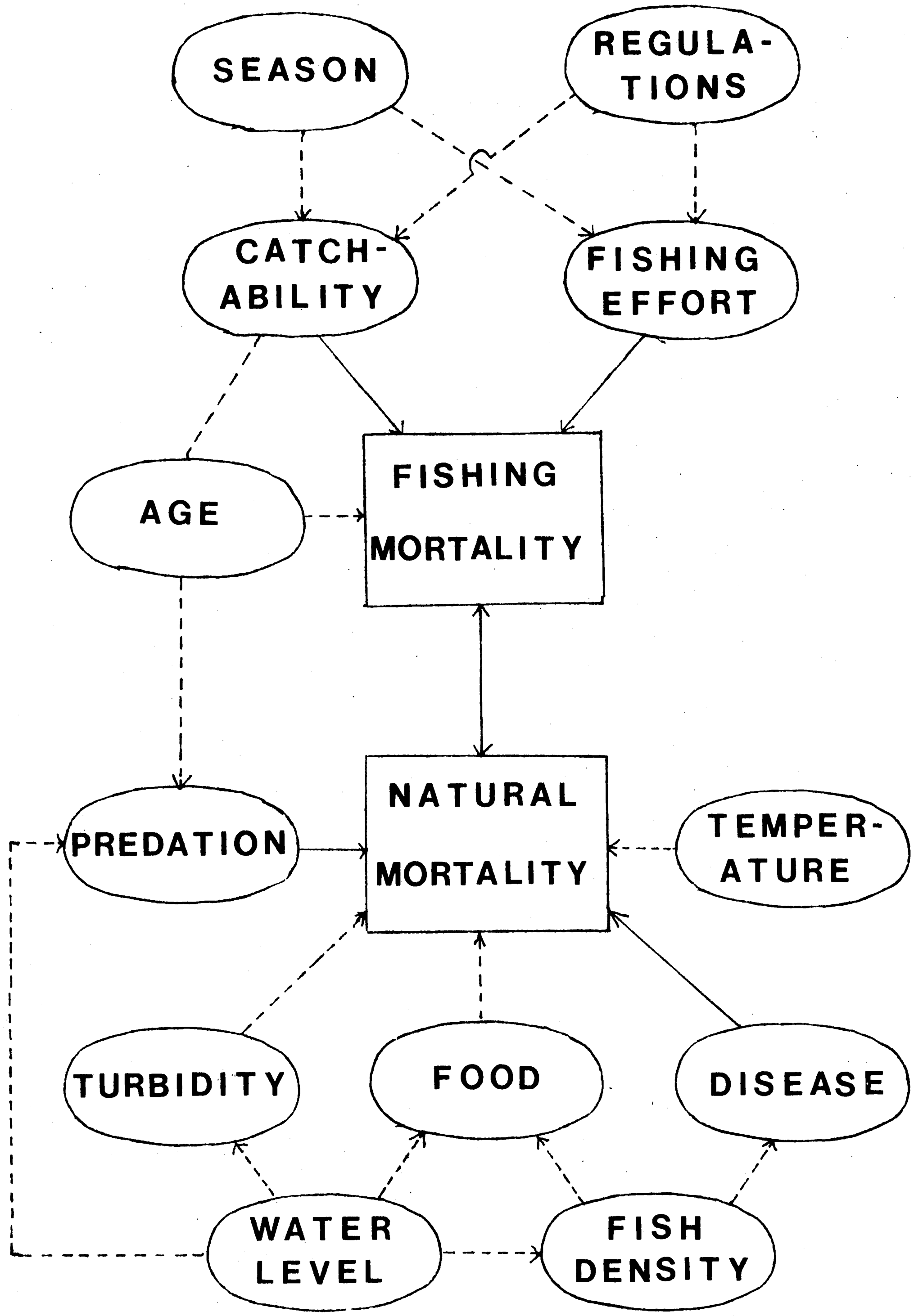

Figure 6. Factors influencing mortality of largemouth bass. Solid lines and broken lines indicate direct and indirect influences, respectively.

Selection and definition of system variables and parameters is the next step in the modeling procedure. 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 relevant components.

Construction of the mathematical model is the third and most rigorous task and involves specifying the form of the transfer functions, forcing functions and estimation of parameter values. The relationships between population size, growth, recruitment, and survival rates, and the relation of these factors with environmental factors must also be determined and quantified. Data collected from Lake Carl Blackwell were analyzed by simple linear and multiple linear regression techniques, described by Draper and Smith (1966), to arrive at the mathematical equations.

After the forms of the equations were specified, the mathematical model was adapted for computer simulation using FORTRAN IV programming language. For each model a computer program was written with considerable flexibility of input requirements to allow for manipulation of the simulated fish population by varying the input data. The FORTRAN language was chosen because it is generally available on most computer systems and most recently-trained fishery biologists have had some exposure to it. Programs were run on the IBM System 370/Model 158 digital computer at the Oklahoma State University Computer Center.

CHAPTER V

MODEL I

Model Description

Model I was age-structured, utilized age-specific fecundities and survival rates and was similar to the Leslie matrix algorithm (Leslie 1945) since fecundity, vulnerability to predators, and susceptability to angling change as a fish grows older, and since a new cohort is added to the population each year. The notation used is as follows: $N_i(t)$ = number of individuals of age i at time t, m_i = fecundity (number of eggs) per individual of age i, 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 times 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

$$N_o(t) = \sum_i N_i(t)m_i \quad (5.1)$$

and a new age distribution is obtained by

$$N_i(t+1) = N_{i-1}(t)S_{i-1} \quad (5.2)$$

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

Reliable estimates of S_o, survival from egg stage to age I, are difficult to obtain for natural populations. For this reason, S_o is estimated indirectly assuming an equilibrium population and using age-specific fecundity and survival data. Vaughan and Saila (1976) derive this estimation procedure based on the Leslie matrix algorithm.

$$S_o = \frac{1}{\sum_{i=1}^{k-1} [m_{i+1} (\prod_{j=1}^{i} S_j)]} \tag{5.3}$$

A program listing is given in Appendix A and a sample output is in Appendix B.

Results and Discussion

Simulation runs were made using the average age-specific survival rates from Zweiacker et al. (1973) and the average age-specific fecundities from Kelley (1962) which appear in Table 1. Figure 7 illustrates the results of a simulation run starting with 1000 age I fish. The simulated population initially oscillated due to the time-lag required for the fish to reach maturity and finally stabilized at about simulation year 18.

Sensitivity analysis was performed to determine how the population size after a 20-year simulation was affected by varying the input parameters. Net sensitivity of the population size to a 10% change in any given input parameter was computed according to the formula given by Francis (1974):

$$S(x, y, \Delta x) = \frac{y(x+\Delta x) - y(x)}{y(x)} \tag{5.4}$$

where $S(x, y, \Delta x)$ 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.

Initial age structure and values of population parameters (Table 1)

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

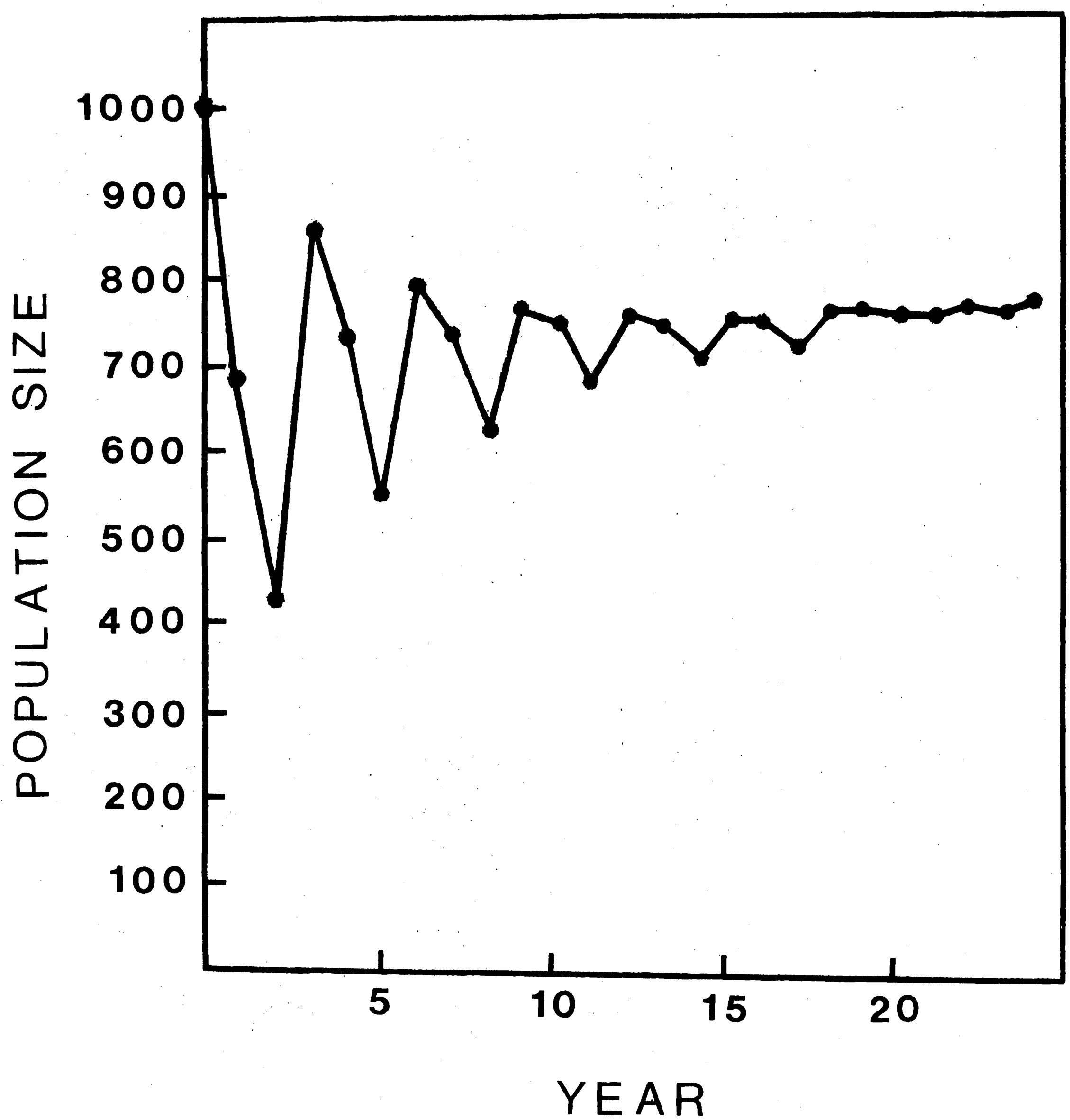

Figure 7. Model I simulation of population changes starting with 1000 age I fish.

used in simulation resulted in a total population size of 2396 after a 20-year simulation. The effect of varying the survival rate of age 0 fish is shown in Figure 8. Results of the sensitivity analysis (Table 2) indicate that the total population size is most responsive to changes in survival rates of age 0, age I, and age II fish, respectively. Therefore, based on this model, it is most important that we have accurate estimates of survival rates of these age groups in order to simulate population trends. Horst (1977) also found that population growth rate was most sensitive to changes in survivorship of younger ages from sensitivity analysis of the Leslie matrix model.

The next step in any modeling problem is to analyze the assumptions on which the initial model is based. In Model I, I assumed that the population operated in a deterministic fashion with constant age-specific survival rates and fecundities. Thus, simulated population trends beginning with 1000 age I fish (Figure 7) do not mimic the situation encountered 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 are ignored in Model I. Since this assumption is unrealistic, further developments of this model will involve varying the age-specific survival rates and/or fecundity based on density or environmental factors. Also there is evidence for differential mortality of older male bass (Bryant and Houser 1971; Hubert 1976) which tends to shift the sex ratio away from unity. In many reservoirs this shift may be negligible but inclusion of a parameter in the model to account for this variation would increase the model's flexibility.

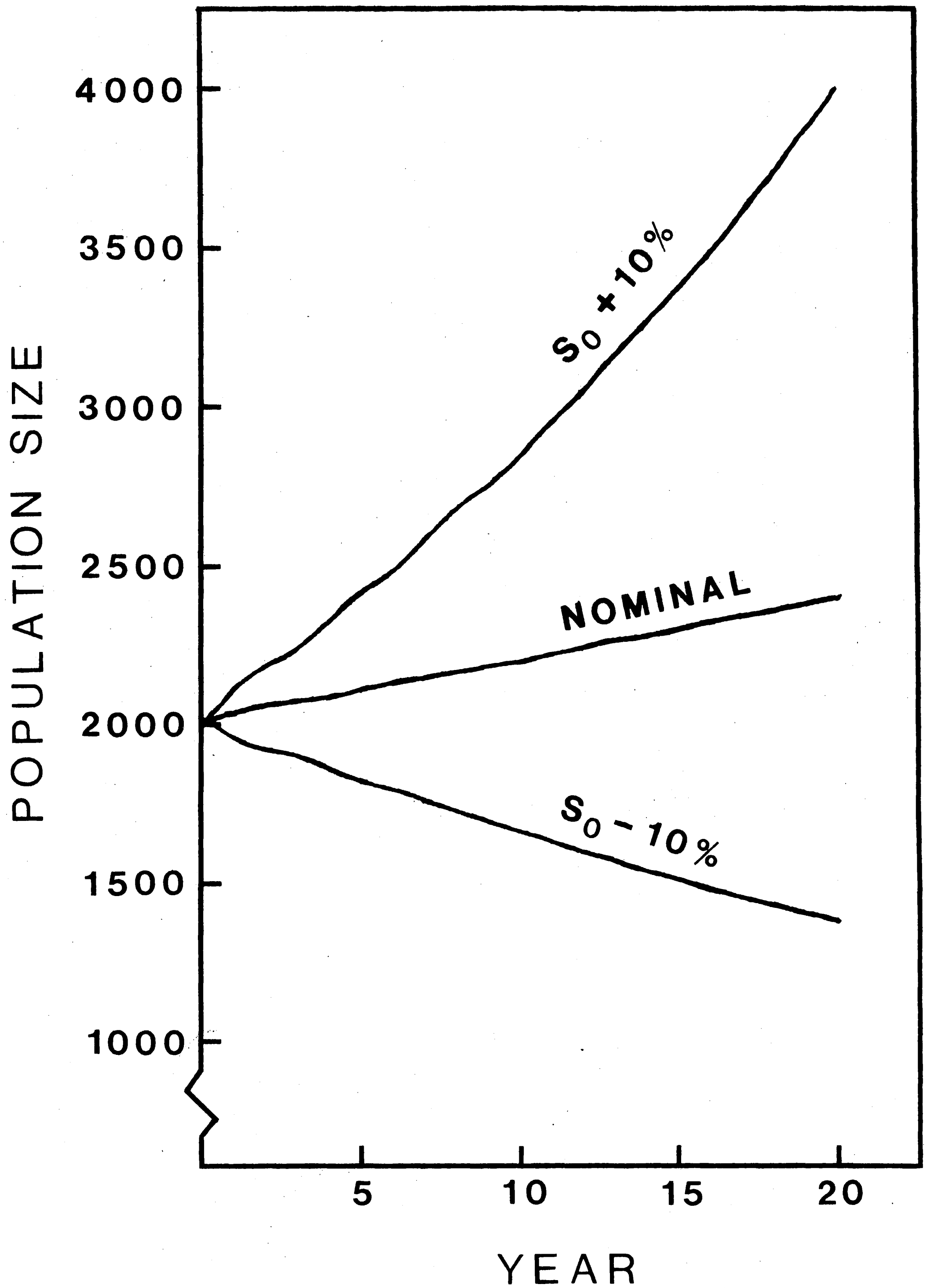

Figure 8. Model I simulation results with nominal and adjusted values for the survival rate of age 0 fish, S_0.

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

Parameter	+10%			-10%		
	N	Net sensitivity	Relative sensitivity	N	Net sensitivity	Relative sensitivity
S_o	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

CHAPTER VI

MODEL II

Introduction

Sensitivity analysis of Model I showed that the population size was most sensitive to changes in the survival rate from egg stage to age I. This stage is also the one at which natural mortality of largemouth bass is the greatest. Summerfelt and Shirley (1975) found that in Lake Carl Blackwell, the 1973 year-class, a large year-class, suffered 95% mortality from the time of hatching (5 May) until 1 October of their first growing season, and 66% of that mortality had occurred during the first 40 days after hatching. The authors inferred that wave action was the major limiting factor during this period. Kramer and Smith (1962) also considered wind the single most important factor in year-class formation in Lake George, Minnesota. Summerfelt (1975) has also found that in Lake Carl Blackwell year-class strength is determined by events occurring during the first few weeks of fish life; passage of frontal systems associated with strong winds and cooler temperatures apparently disrupt spawning and result in increased mortality of bass embryos and larvae. Conversely, spawning success was greatest during short intervals when weather was stable. Eipper (1975) has concluded that generally year-class strength fluctuation is the result of the very high mortality during the period between egg fertilization and the end of the first few weeks of life. He also concluded that strong winds and the various indirect influences of low temperature probably are most responsible for mortality during this period.

In many reservoirs large year-classes of largemouth bass are produced in years of stable or rising water levels during spawning (Aggus and Elliot 1975; Bross 1969; Keith 1975; von Geldern 1971). It is postulated that increasing water levels favor the survival of young-of-the-year largemouth bass by the flooding of shoreline areas containing terrestrial vegetation, which increases cover for nest sites and for shelter from predation and releases nutrients into the littoral zone thereby promoting production of food for the young bass (Shirley 1975). Also, the increased depth of water over the nests decreases the effects of wind, wave action and temperature fluctuation (Kramer and Smith 1962).

The relation between environmental factors and year-class strength of largemouth bass in Lake Carl Blackwell was studied by Summerfelt and Shirley (1976) by correlating these factors with the estimated ecological density of 11 consecutive year-classes (1965-1975). Cove poisonings with rotenone were used to make late summer estimates of numerical density of young-of-the-year (YOY) bass and these estimates were adjusted to a constant date (13 August) using an estimated daily instantaneous mortality rate of 0.0015. Year-class strength was estimated in this way for 1966, 1967, 1968, 1971, 1973, 1974, and 1975. The cove rotenone samples probably reflect the ecological density (number per unit of acceptable habitat) of Odum (1971:163-166) assuming that YOY bass are largely limited to the littoral zone. The 1965 and 1970 estimates were back-calculated from estimates of number of age I bass in the 1966 and 1971 cove poisoning collections using the daily instantaneous mortality rate of 0.0015. The 1972 year-class was estimated during the fall of 1972 by the mark-recapture technique developed by Lewis et al. (1963) in which bass were collected by shoreline electrofishing, marked and released for recapture in subsequent trips around the lake. This estimate was then divided by the area of water less than 2 meters deep to make it more comparable with the cove rotenone estimates. The 1969 year-class was estimated by comparing the electrofishing catch rate of that year-class with that of the 1968 year-class which had been estimated by cove poisoning. Catch rates were taken from Zweiacker (1972) and the density of the 1969 year-class was calculated by multiplying the ratio of the electrofishing catch rates. Summerfelt and Shirley (1976) discussed the comparability of the 1969 and 1972 year-class estimates with those estimated by cove poisoning.

Using their estimates of ecological density of YOY bass, Summerfelt and Shirley (1976) correlated these values with a series of biotic and abiotic environmental parameters including: water level, change in water level, pH, methyl orange alkalinity, hardness, turbidity, wind velocity, and number of spawners. Correlations were made using monthly maximum, minimum and mean and seasonal mean for each parameter except number of spawners and water levels. Correlations were also made between YOY bass density and the water level on the 1st and 15th of each month (January - August), monthly change in water level, change in water level since the end of the previous growing season (water level on the 1st and 15th of each month minus water level on 1 October the previous fall) and the estimated number of spawners in those years when reliable mark-recapture estimates of adult bass were made.

The results of their study 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 to the water level and its effect upon food and cover for YOY 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. An additional cove rotenone collection was made in August 1976 resulting in 12 consecutive estimates of ecological density of YOY bass in Lake Carl Blackwell (Figure 9).

Model Description

Mean water level[1] during May, water level fluctuation from 1 October of the previous fall to 15 May, and density of YOY bass (Table 3) were analyzed by regression (Draper and Smith 1966) to determine how useful these variables were in predicting year-class strength. These variables were chosen because they were most significantly correlated with year-class strength and thus probably the most meaningful.

The relationship between water level fluctuation and year-class strength and results of linear regression are illustrated in Figure 10. The correlation coefficient of 0.8779 was highly significant (P=0.0002)

[1]Water levels were obtained courtesy of the Hydraulics Research Laboratory, U.S. Department of Agriculture.

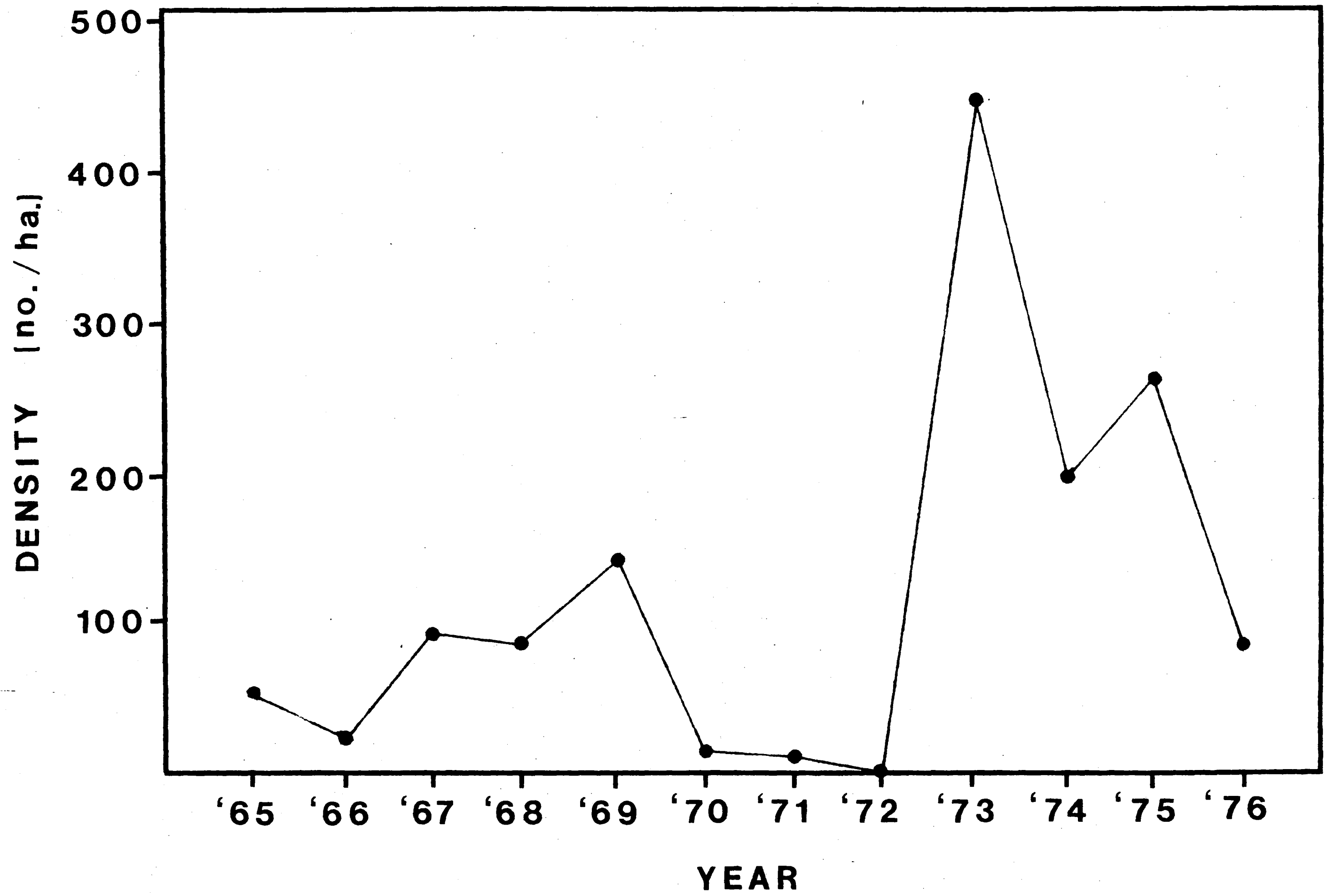

Figure 9. Estimated ecological density of young-of-the-year largemouth bass on 13 August in Lake Carl Blackwell, Oklahoma (1965-1976).

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 1976, unpubl. manuscript).

[b]Mean water level during May.

[c]Fluctuation in water level from 1 October of previous growing season to 15 May.

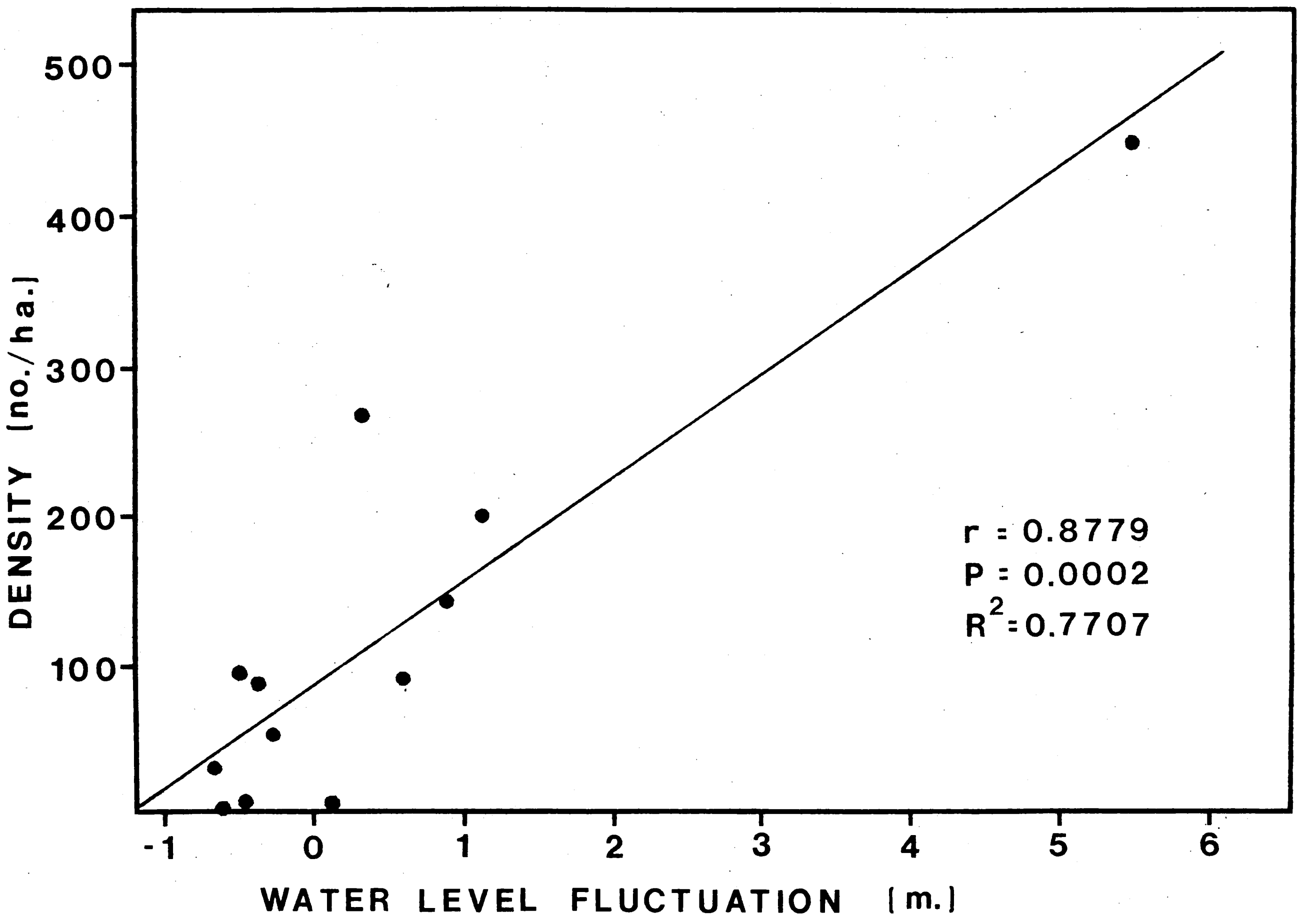

Figure 10. Relationship between year-class strength as indexed by ecological density of young-of-the-year largemouth bass on 13 August and water level fluctuation.

and water level fluctuation accounted for 77.07% (R^2=0.7707) of the observed variation in density. The residuals in this analysis were greatest for 1970, 1971, and 1972, when the water level was at an extreme low, and 1975, when water level was at or near spillway all year. These data indicate the importance of actual water level in addition to water level fluctuation in year-class formation.

The relationship between water level during spawning and year-class strength and results of linear regression are illustrated in Figure 11. Although this correlation (r=0.5337) was not significant (P=0.0739), analysis without the 1973 data yielded a highly significant (P=0.0044) correlation coefficient of 0.7828. Even though the water level during the 1973 spawning season was more than 2 meters below spillway, the water level was rising rapidly which resulted in very successful largemouth bass reproduction and YOY survival and growth. Thus, it appears that there is an important interaction between water level during spawning and water level fluctuation.

Results of the multiple regression using these two variables as predictor variables is summarized in Table 4. The equation for predicting YOY bass density on 13 August (Y) is

$$Y = -7601.3833 + 62.5356(X_1) + 26.9689(X_2) \qquad (6.1)$$

where X_1 = water level fluctuation from 1 October of previous fall to 15 May (meters), and X_2 = mean water level during May (meters, M.S.L.). This relationship is highly significant since 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 value is a

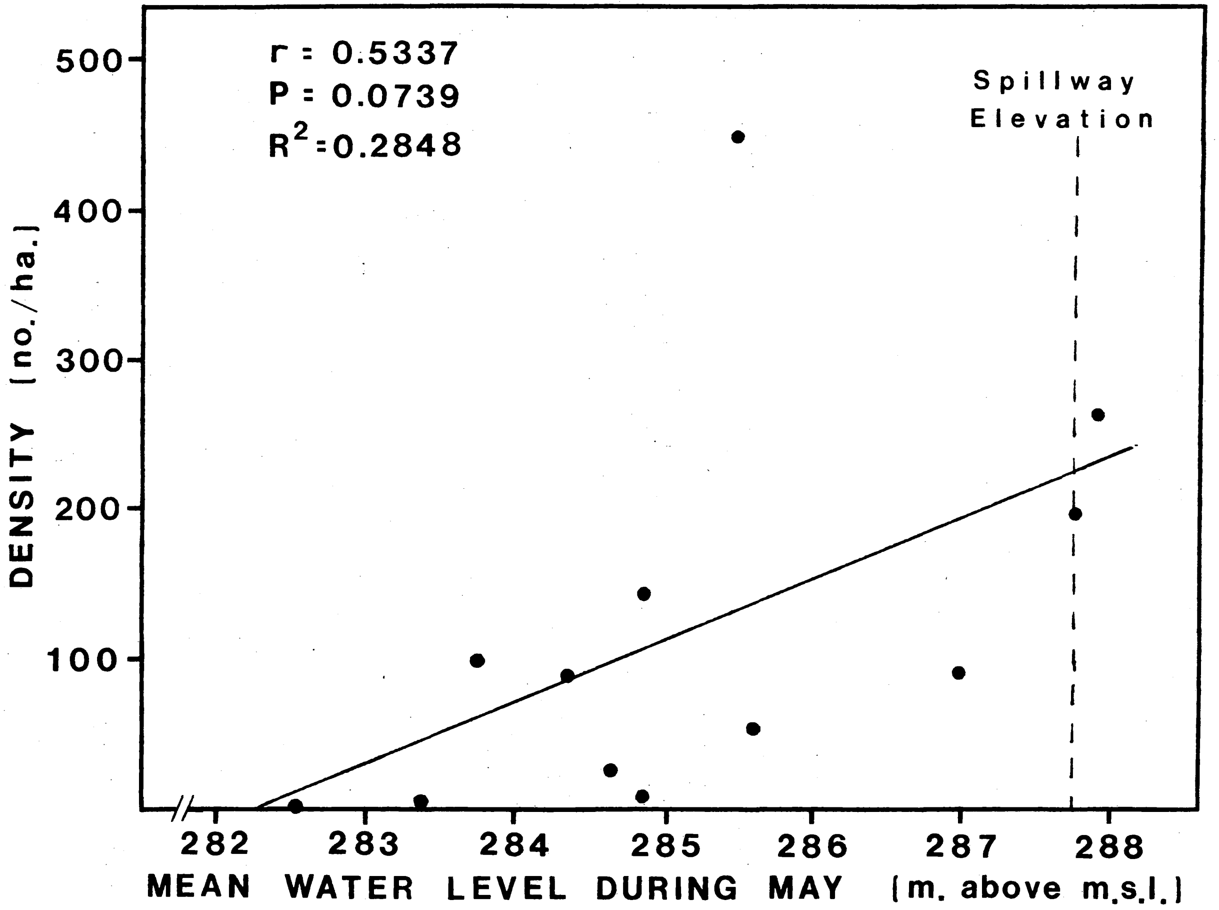

Figure 11. Relationship between year-class strength as indexed by ecological density of young-of-the-year largemouth bass on 13 August and water level during May.

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 $(b_1 \mid b_0)$	1	147714.9289	147714.9289	58.7560	0.0001
R $(b_2 \mid b_0, b_1)$	1	21327.8392	21327.8392	8.4835	0.0172
Residual	9	22626.3387	2514.0376		

substantial increase in the R^2 observed for the regressions with either water level fluctuation alone (R^2=0.7707) or water level during May alone (R^2=0.2848). Also, the addition to the model of the second variable, water level during spawning, was significant as evidenced by the sequential F-test (Draper and Smith 1966:71-72) (F=8.4835; 1, 9; P=0.0172). Water level fluctuation is over twice as important as water level during May in predicting YOY bass density because the ratio of standardized regression coefficients was 2.317 (0.7959/0.3435).

In order to include this relationship in the population dynamics model, it was necessary to relate survival from egg stage to age I to these two variables. Survival rates were estimated for years when reliable population estimates were available for the spawning population in the spring and the number of yearlings the following spring. Population estimates were adjusted to 15 May (the approximate midpoint of the spawning period) by assuming a constant exponential mortality and using the average age-specific survival rates from Zweiacker et al. (1973). Using a logarithmic transformation of fecundity and length data from Kelley (1962) and Coomer (1976) a linear regression equation was derived. Age-specific fecundities were then estimated based on the mean lengths presented in Zweiacker et al. (1973) for age groups of largemouth bass from Lake Carl Blackwell (Table 5). Egg potential was estimated by the equation

$$\sum_{i=3}^{8} N_i m_i (0.5) \qquad (6.2)$$

where N_i = number of fish per age i, and m_i = number of eggs per female of age i. This equation assumes a 1:1 sex ratio and that females mature at age III. Zweiacker et al. (1973) noted that in Lake Carl Blackwell,

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

a few age II bass spawned but most do not spawn until age III. The resulting estimates of number of fish per age group in the spring, egg potential, and annual instantaneous mortality rates (Z_o) from egg to age I are presented in Table 6. Annual instantaneous mortality rate (Z) is related to yearly survival rate (S) by

$$S = e^{-Z} \qquad (6.3)$$

where e = the base of the natural logarithm.

Results of the multiple regression analysis using water level fluctuation from 1 October of the previous fall to 15 May (meters) (X_1) and mean water level during May (meters, M.S.L.) (X_2) to predict the annual instantaneous mortality rate (Z_o) from egg to age I are summarized in Table 7. The equation for predicting Z_o is

$$Z_o = 230.8063 - 0.9689(X_1) - 0.7757(X_2). \qquad (6.4)$$

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. Figure 12 shows how well the observed and predicted values coincide. Regression coefficients were converted for use with water level data recorded in feet rather than meters since lake levels for Lake Carl Blackwell and most reservoirs are recorded in feet. This equation was then incorporated into the framework of Model I. If water level data are not available, the computer program will use the average survival rate of age group 0 as computed in Model I. A program listing of Model II is given in Appendix C and a sample output is in Appendix D. Model II is essentially the same as Model I except for the equation to predict mortality from egg to age I, parameters to account for the percentage of each age group that are mature and female, and use of

Table 6. Estimated number of fish per age group in the spring, egg potential, and annual instantaneous mortality rate (Z_o) from egg to age I for largemouth bass in 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]	306[c]	322	32[d]	78741[d]	12640[e]
II	305	766	241	120[c]	207	217	22[d]	-
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 (1972: 54)

[b] From Spring 1969 estimates

[c] From Shirley's (unpubl. data) estimate of 6 October 1972

[d] Shirley (1975: 32 & 39)

[e] From Summerfelt and Shirley (1975: 34) estimate of 14 October 1974

Table 7. Analysis of variance table for multiple regression analysis of dependent variable - annual instantaneous mortality rate (Z_o) 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 ($b_1 \| b_0$)	1	40.0728	40.0728	21.8846	0.0095
R ($b_2 \| b_0$, b_1)	1	7.9286	7.9286	4.3300	0.1059
Residual	4	7.3244	1.8311		

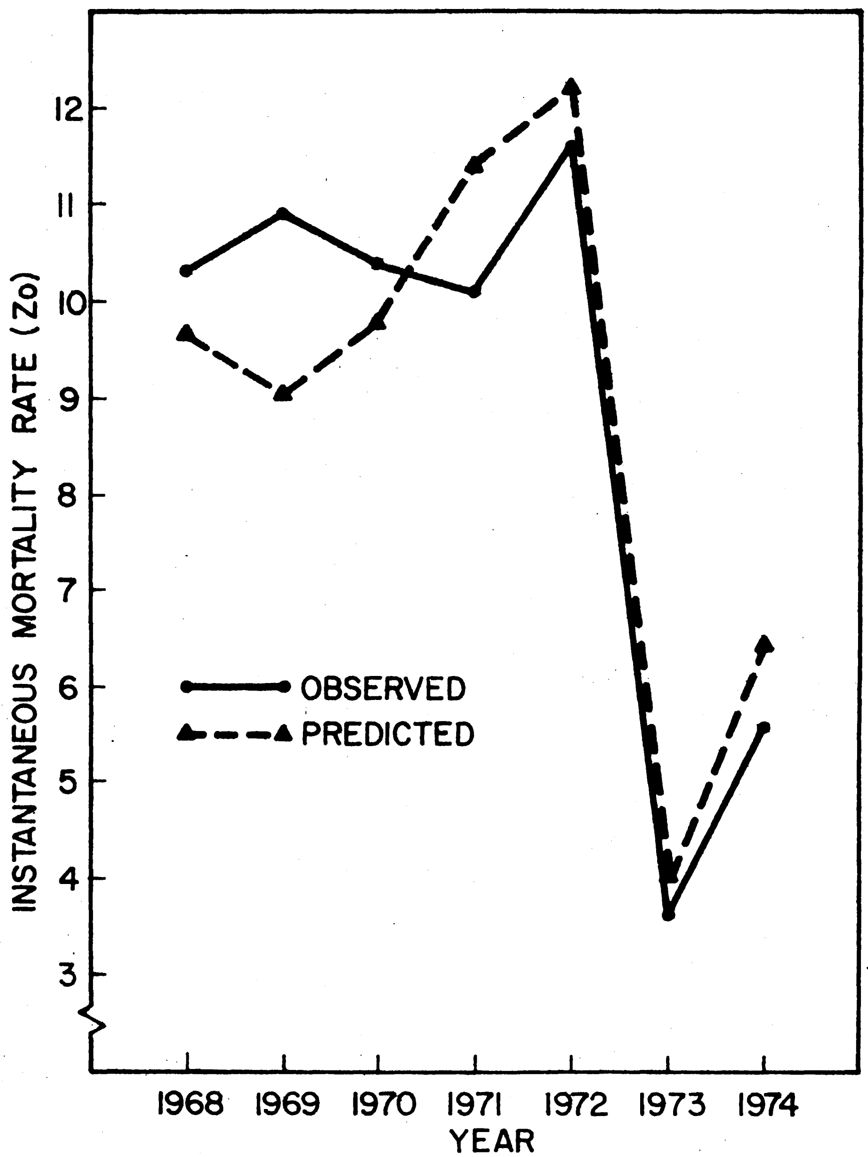

Figure 12. Observed and predicted annual instantaneous mortality rates (Z_o) from egg to age I for largemouth bass in Lake Carl Blackwell (1968-1974).

fecundity per female rather than fecundity per individual.

Results and Discussion

Simulation of Model II was made using initial age structure for spring 1968 (Table 6), age-specific survival rates from Zweiacker et al. (1973), age-specific fecundity from Table 5, and water level data for Lake Carl Blackwell from 1968 to 1977. The simulated predictions of year-class strength as indicated by the number of age I recruits is compared with the observed number of age I recruits in Figure 13. In terms of precision, Model II would rate very highly because of the close agreement between observed and simulated values. However, the model cannot be validated with data that was used for its derivation. An effort should be made in the future to collect data from the Lake Carl Blackwell bass population to validate the model, but this is beyond the scope of the present project.

Also we must take note of the confidence limits on the population estimates used before we condemn or praise the model. For example, Shirley's (1975) Schnabel estimate of the number of age I recruits in the 1973 year-class was 79,098 with 95% confidence limits of 51,718 and 135,825. Discrepancies between simulated and observed number of age I recruits could be attributed to errors in the population estimates or errors in the model.

Model II should prove to be of value in largemouth bass fishery management by enabling the 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 the fishery managers can make better decisions on stocking recommendations

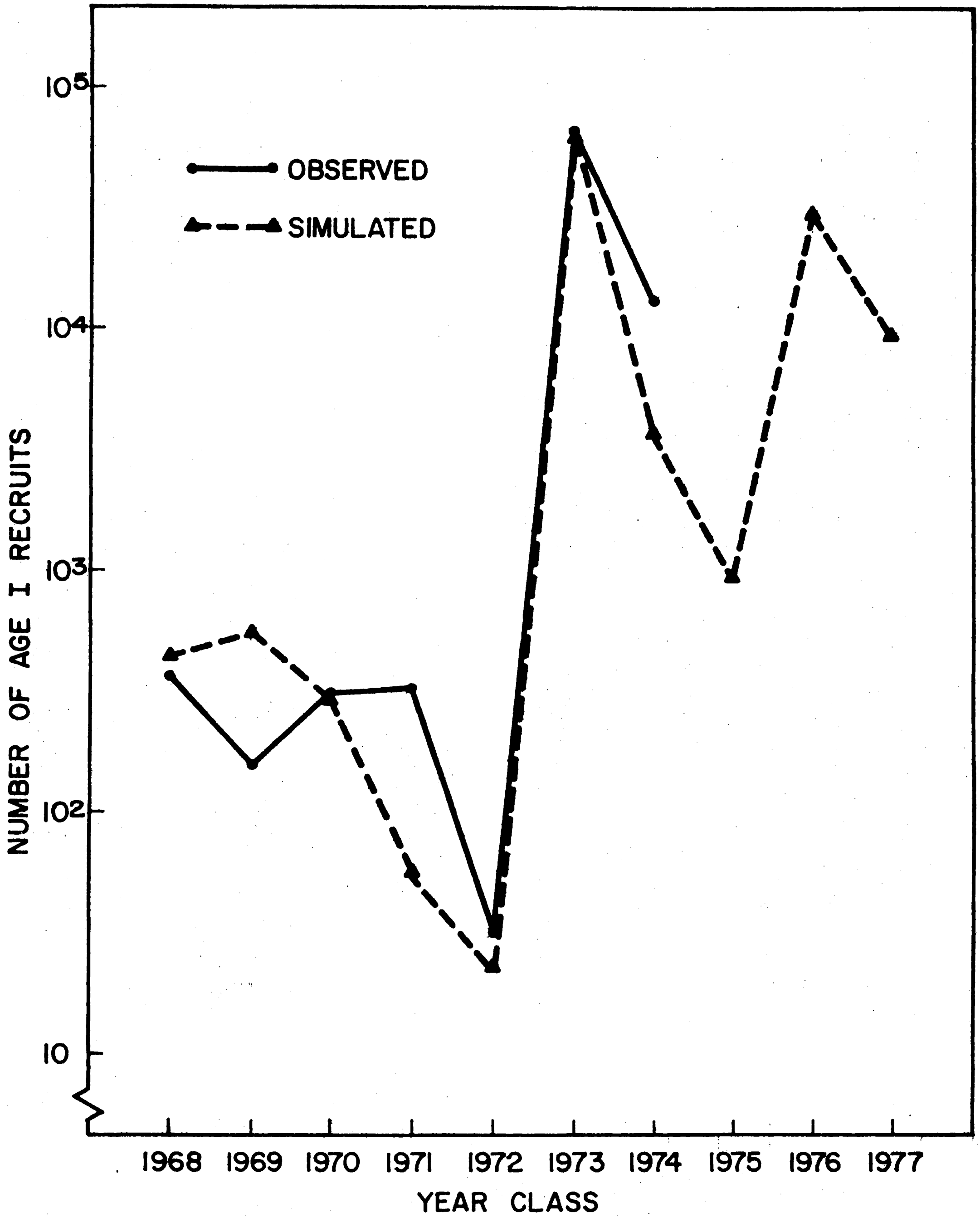

Figure 13. Observed estimates and Model II simulation of number of age I recruits in year-classes 1968 through 1977 in Lake Carl Blackwell.

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 spawning will be exactly the same for all reservoirs. Therefore, it is necessary that research be done on other reservoirs to evaluate the generality of this relationship and to determine the appropriate parameter values for these reservoirs. The program has been written so that different parameter values for this relationship can be used by changing only one program statement in SUBROUTINE YOYSRV. This subroutine could also be easily adapted to use other equations to predict survival from egg to age I.

CHAPTER VII

MODEL III

Introduction

Model III is an extension of the previous models to allow the prediction of production and yield. Production is the total elaboration of fish tissue during any time interval, and yield is that portion of production that is used by man. Estimates of production and yield of largemouth bass populations are extremely useful to fishery managers and ecologists since the largemouth bass is an important game fish and also one of the top carnivores of aquatic ecosystems.

Production and sustainable yield of a fish stock should, according to the logistic model (Schaefer and Beverton 1963), be at a maximum when biomass is at one-half of carrying capacity. Traditionally, maximum sustainable yield of fish stocks has been the objective of fisheries management but more recently the concept of optimum sustainable yield has become the accepted philosophy (Larkin 1977; Nielsen 1976; Roedel 1975). Roedel (1975) defined optimum sustainable yield as

> ... a deliberate melding of biological, economic, social and political values designed to produce the maximum benefit to society from stocks that are sought for human use, taking into account the effect of harvesting on dependent or associated species (p. 85).

Model Description

Model III is similar to the previous models in that it is age-structured and its basic time unit is a year. Survival from egg to age I is calculated as in Model II. Other state variables are computed as follows with FORTRAN variable names given in parentheses when different from those used here.

$N_{i+1}(t+1)$ = number of fish in age group i+1 (i = 0, 1, 2, ...k) at time t+1

$$= N_i(t)\ e^{-Z_i(t)} \quad (7.1)$$

where

k = maximum age (INPUT),

e = the base of the natural logarithm,

$Z_i(t)$ = instantaneous annual total mortality rate on age group i during time period t, t+1

$$= F_i(t) + M_i(t), \quad (7.2)$$

$F_i(t)$ = instantaneous annual fishing mortality rate on age group i during time period t, t+1 (INPUT)

$$= q_i(t)\ f(t), \quad (7.3)$$

$q_i(t)$ = catchability coefficient (vulnerability) of age group i during time period t, t+1,

$f(t)$ = fishing effort during time period t, t+1,

and $M_i(t)$ = instantaneous annual natural mortality rate on age group i during time period t, t+1 (INPUT).

$N_o(t)$ = number of eggs produced at time t

= (TOTEGG)

$$= \sum_{i=1}^{k} N_i(t)\ m_i(t)\ PF_i\ PM_i \quad (7.4)$$

where

$m_i(t)$ = number of eggs produced per female of age group i at time t

= (FECND)

$$= a\ \bar{l}_i(t)^b, \qquad (7.5)$$

$\bar{l}_i(t)$ = average total length (mm) of individuals of age group i at time t

= (AVGTL),

a = constant in fecundity estimation equation (INPUT)

= (AFEC),

b = exponent in fecundity estimation equation (INPUT)

= (BFEC),

PF_i = proportion of age group i that is female (INPUT)

= (FEMALE),

and PM_i = proportion of age group i that is mature (INPUT)

= (MATURE).

$B_o(t)$ = biomass of eggs produced at time t (kg)

= (EGGB)

$$= EGGW\ N_o(t)\ 0.001 \qquad (7.6)$$

where

EGGW = individual egg weight

= 0.0012 grams (based on estimated specific gravity of 1.47 and mean egg diameter of 1.16 mm),

$\bar{l}_{i+1}(t+1)$ = average total length (mm) of individuals of age group i+1 at time t+1

= (AVGTL)

$$= \bar{l}_i(t)\ e^{G_i(t)} \qquad (7.7)$$

where

$G_i(t)$ = instantaneous annual rate of growth in total length for age group i during time period t, t+1 (INPUT)

= (GTL)

$$= \log_e \left[\bar{l}_{i+1}(t+1)/\bar{l}_i(t) \right] . \quad (7.8)$$

$\bar{w}_{i+1}(t+1)$ = average weight (g) of individuals of age group i+1 at time t+1

= (AVGW)

$$= \bar{w}_i(t)\ e^{\,bG_i(t)} \quad (7.9)$$

where

b = exponent in the length weight relationship: $w = a\ l^{\,b}$ (INPUT)

= (BWTLEN), and

$bG_i(t)$ = instantaneous rate of growth in weight of age group i during time period t, t+1

= (GW).

$B_i(t)$ = biomass (kg) of age group i at time t

$$= N_i(t)\ \bar{w}_i(t)\ 0.001. \quad (7.10)$$

$\bar{N}_i(t)$ = average number of fish of age group i during time period t, t+1

= (AVGN)

$$= \int_t^{t+1} N_i(t)\ e^{-Z_i(t)} dt \quad (7.11)$$

$$= \frac{N_i(t)(1 - e^{-Z_i(t)})}{Z_i(t)} . \quad (7.12)$$

$\bar{B}_i(t)$ = average biomass (kg) of age group i during time period t, t+1

$= \text{(AVGB)}$

$$= \int_t^{t+1} B_i(t)\; e^{[bG_i(t) - Z_i(t)]t}\, dt \qquad (7.13)$$

$$= \frac{B_i(t)\left[1 - e^{-[Z_i(t) - bG_i(t)]}\right]}{Z_i(t) - bG_i(t)} \text{ when } bG < Z \qquad (7.14)$$

$$= B_i(t) \quad \text{when } bG = Z \qquad (7.15)$$

$$= \frac{B_i(t)\left[\; e^{[bG_i(t) - Z_i(t)]} - 1\right]}{bG_i(t) - Z_i(t)} \text{ when } bG > Z \qquad (7.16)$$

$C_i(t)$ = number of age group i harvested during time period t, t+1

$$= F_i(t)\; \bar{N}_i(t). \qquad (7.17)$$

$Y_i(t)$ = weight (kg) of age group i harvested during time period t, t+1

$$= F_i(t)\; \bar{B}_i(t). \qquad (7.18)$$

$GP_i(t)$ = gross production (kg) of age group i during time period t, t+1

$$= bG_i(t)\; \bar{B}_i(t).$$

$NP_i(t)$ = net production (kg) of age group i during time period t, t+1

$$= [bG_i(t) - Z_i(t)]\; \bar{B}_i(t). \qquad (7.20)$$

Numbers, biomass, production and yield are then summed over ages 1 to k to give the level of these state variables for the entire stock for each year of simulation. The instantaneous rates of growth and natural and fishing mortality, G, M, and F, respectively, are expressed here as time-varying coefficients but in most cases they will be constant for each simulation run. Program statements could be added to the computer program to make growth and mortality a function of population number, biomass or environmental factors. Output from Model III consists of number at start of year, mean number during year, mean total length, mean weight per fish, biomass at start of year, mean biomass during year, yield in weight and numbers, and gross and net production for each age group. In addition number at start of year, mean number during year, biomass at start of year, mean biomass during year, yield in weight and numbers and gross and net production for the entire stock is given. A computer program listing, sample output, and sample input data for Model III are included in Appendices E, F, and G, respectively. Derivations of the parameters to be used as input data are described in succeeding sections.

Fecundity

Although numerous studies on fecundity have been made, there are few investigations where sample size allows quantification of the relationship between fecundity and age or size. Part of the problem is that there is typically great variability in the number of eggs in fish of the same length, weight, and age because environmental factors, such as food supply, influence the amount of energy channeled into gonadal development. To avoid this problem most authors studying the fecundity of various fish species have plotted fecundity and length data as a scatter diagram and have concluded that the relationship is of the form

$$m = al^b \qquad (7.21)$$

where m = fecundity, l = fish length, and a and b are a constant and an exponent derived from the data respectively (Bagenal 1967). This curve can be transformed to a straight line by a logarithmic transformation:

$$\log m = \log a + b \log l \qquad (7.22)$$

and the logarithmic values analyzed by simple linear regression analysis.

Fecundity estimates and lengths are presented (Figure 14) for largemouth bass from a small infertile lake in northern Michigan (Clady 1970), large reservoirs in Tennessee (Coomer 1976) and Arkansas (Olmsted 1974), and a stream in Maine (Kelley 1962). These data were fitted to a line of the form in 7.22 by linear regression and the results of the analyses presented in Table 8.

Regressions for each author's data separately and the combined data were highly significant (Table 8) but some of the coefficients were different. Analysis of covariance (Snedecor and Cochran 1967:432-436) was employed to compare the regression lines. Since this analysis assumes homogeneity of variance, Bartlett's test (Snedecor and Cochran 1967:296-298) was applied to compare the residual mean squares from the four sets of data. The chi-square value, corrected for unequal sample size, was 8.86 (3 d.f.) which has an associated probability of a greater chi-square of 0.0312 (Table 9). This probability makes the assumption of equal variances invalid. One reason for the unequal variances could be the different length ranges sampled by the authors (Table 8). Variability in fecundity tends to increase with an increase in fish size (Bagenal 1967). There was a significant positive correlation (r=0.9531; P=0.0369) between the residual mean squares (Table 9) and mean total length of bass sampled (Table 8). Data from Clady (1970) included slow growing bass from a narrow length range (254-368 mm), with the largest of these being 10 years old. The fish may not display a typical length-fecundity relationship because of the relatively low variance in Clady's data.

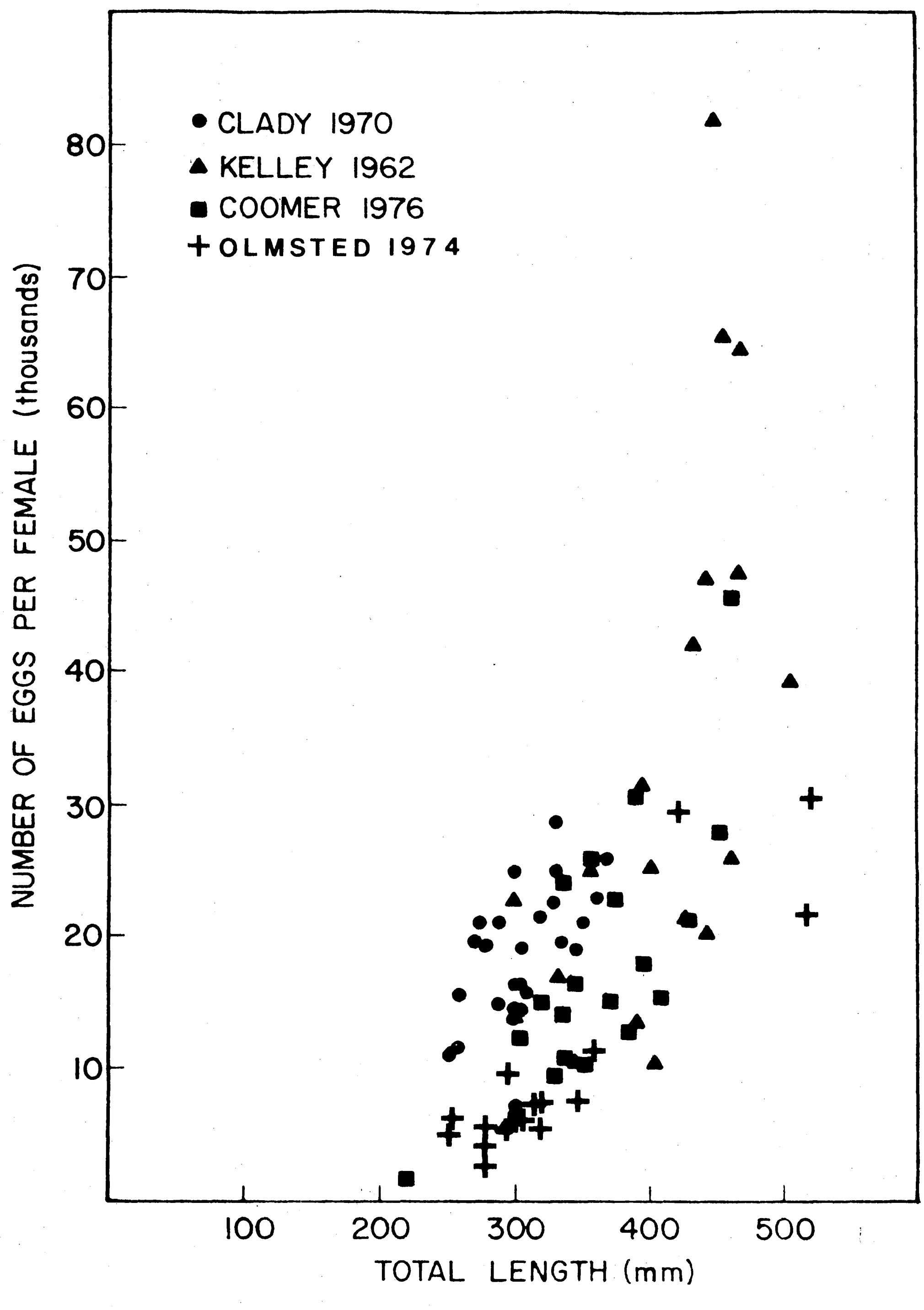

Figure 14. Scatter diagram of fecundity and total length for largemouth bass collected from a lake in Michigan (Clady 1970), reservoirs in Tennessee (Coomer 1976) and Arkansas (Olmsted 1974), and a stream in Maine (Kelley 1962).

Table 8. Results of regressions of log-transformed values of length and fecundity of largemouth bass from Michigan (Clady 1970), Tennessee (Coomer 1976), Maine (Kelley 1962), and Arkansas (Olmsted 1974).

Author	No. of fish	Total length (mm)		Fecundity		a	b	F[a]	P[b]
		$\bar{X}$	range	$\bar{X}$	range				
Clady 1970	26	306.6	(254-368)	18728.5	(7511-28536)	3.6608	1.4860	8.66	0.0071
Coomer 1976	20	359.6	(218-461)	17917.6	(2137-46128)	5.342×10^{5}	3.3149	47.55	0.0001
Kelley 1962	20	404.0	(295-503)	31564.8	(5549-81582)	3.642×10^{-4}	3.0162	19.19	0.0004
Olmsted 1974	16	334.9	(252-523)	10462.9	(2942-30709)	2.042×10^{-3}	2.6276	51.81	0.0001
Combined	82	348.8	(218-523)	20048.7	(2137-81582)	9.622×10^{-3}	2.4558	70.93	0.0001

[a]F ratio (Mean square due to regression divided by mean square due to residual variation) used to test the null hypothesis H_o: $b = 0$.

[b]Probability of a greater value of F.

Table 9. Comparison of residual mean squares of log-transformed fecundity data for largemouth bass from Michigan (Clady 1970), Tennessee (Coomer 1976), Maine (Kelley 1962), and Arkansas (Olmsted 1974) by Bartlett's test for unequal sample size.

Author	d.f. f_i	S.S. $f_i s_i^2$	M.S. s_i^2	$\log s_i^2$	$f_i \log s_i^2$	$1/f_i$
Clady 1970	24	0.313157	0.013048	-1.884456	-45.226945	0.041667
Coomer 1976	18	0.414454	0.023025	-1.637800	-29.480406	0.055555
Kelley 1962	18	0.841928	0.046774	-1.329995	-23.939919	0.055555
Olmsted 1974	14	0.266395	0.019028	-1.720601	-24.088414	0.071429
Totals:	74	1.835934	0.101875		-122.735684	0.224207

$a = 4$

$$M = (2.3026)\left[(\Sigma f_i)\log(\Sigma f_i s_i^2/\Sigma f_i) - \Sigma f_i \log s_i^2\right] = 9.067546$$

$$C = 1 + \frac{1}{3(a-1)}\left[\Sigma\frac{1}{f_i} - \frac{1}{\Sigma f_i}\right] = 1.023410$$

$\chi^2 = M/C = 8.8601$ with 3 d.f.

$P = 0.0312$

Bartlett's test was applied to compare the residual mean squares of the data from Coomer (1976), Kelley (1962) and Olmsted (1974), omitting that from Clady (1970). The analysis resulted in a non-significant chi-square value of 3.79 (2 d.f.) and thus equal variances. Covariance analysis (Table 10) indicated that the regression lines for these three data sets were parallel (F=0.16; 2 and 50 d.f.; P=0.8521). The F-test for adjusted means was significant (F=7.11; 2 and 52 d.f.; P=0.0019) indicating that if the mean logarithm of fecundity for each data set was adjusted to the same logarithm of total length the results would be significantly different. This difference was due primarily to the lower adjusted mean from Olmsted's data since the F-test for adjusted means from covariance analysis of Kelley's data and Coomer's data was non-significant (F=1.07; 1 and 37 d.f.; P=0.3072).

The analysis reported above removes the variation due to techniques, types of study areas and/or geographic location. Therefore the parameters derived in Table 10 should be fairly representative of the length-fecundity relationship for largemouth bass.

Growth Rates and Length-Weight Relationships

Model III requires parameters for the length-weight relationship and age-specific growth rates. There appeared to be an important, and possibly predictable, trend in growth rates of largemouth bass in Lake Carl Blackwell from 1962 through 1967 (Zweiacker et al. 1973). Therefore, 2384 largemouth bass collected from Fall 1972 through Spring 1977 plus an additional 64 bass collected in the spring of 1967 were weighed, measured and scale samples taken. Scale impressions were made on plastic slides, examined at 41.5 magnification with a 16 mm micro-

Table 10. Analysis of covariance and comparison of regression lines for log-transformed length-fecundity relationship for largemouth bass from Tennessee (Coomer 1976), Maine (Kelley 1962) and Arkansas (Olmsted 1974).

				Deviations from regression			
Author	d.f.	Σx^2	Σxy	Σy^2	d.f.	S.S.[a]	M.S.
Coomer 1976	19	0.099641	0.330303	1.509386	18	0.414454	0.023025
Kelley 1962	19	0.098648	0.297543	1.739380	18	0.841928	0.046774
Olmsted 1974	15	0.142793	0.375202	1.252266	14	0.266388	0.019028
					50	1.522770	0.088827
Pooled, W	53	0.341082	1.003048	4.501032	52	1.551286	0.029832
		Difference between slopes			2	0.028516	0.014258
Between, B	2	0.069150	0.380606	2.141083			
W + B	55	0.410232	1.383654	6.642115	54	1.975247	
	Difference between adjusted means				2	0.423961	0.211980

Comparison of slopes: $F = 0.014258/0.088827 = 0.16051$

2 and 50 d.f. $P = 0.8521$ N.S.

Comparison of adjusted means: $F = 0.211980/0.029832 = 7.106$

2 and 52 d.f. $P = 0.0019$

$$\log \text{Fecundity} = -3.345912 + 2.9407808 \log \text{Length}$$

$$\text{Fecundity} = 0.00045091\ \text{Length}^{2.941}$$

[a]S.S. $= \Sigma y^2 - [(\Sigma xy)^2/\Sigma x^2]$

tessar lens and lengths from scale focus to each annulus measured. Linear and curvilinear (5th degree polynomial) regressions were calculated for the total length-scale radius relationship and used to back-calculate the total length of bass at the time of formation of each annulus. These growth rate data were combined with that of Zweiacker et al. (1973) and analyzed by correlation and regression techniques to determine the relationships with environmental factors. Parameters for the length-weight relationships, $w = al^b$, were derived by linear regression using a logarithmic transformation of the data, $\log w = \log a + b \log l$.

The majority (8 of 12) of the total length-scale radius relationships used for back calculating length-at-annulus for various collection periods were linear (Table 11) and all regressions were highly significant ($P<0.005$). Back-calculated lengths at annulus and growth increments for largemouth bass from Lake Carl Blackwell are presented for years 1959 to 1976 in Table 12. In general, growth was above the Oklahoma average (Houser and Bross 1963) as also noted by Zweiacker et al. (1973). However, growth patterns since 1974 are unusual in that increments for bass in the second year of life are well below average for Lake Carl Blackwell. Growth increments for age 3 bass from the 1973 and 1974 year-classes were below average as were increments for age 4 bass from the 1971 and 1973 year-classes.

Correlation analysis was performed on growth increment data (Table 12) and average annual water level (AAWL), mean temperature from May through October (TEMP), mean annual turbidity (TURB), density of young-of-the-year bass on 13 August (YOYD), standing crop of all bass (LMBSC), density of gizzard shad (GSD), and standing crop of gizzard

Table 11. Total length-scale radius (X41.5) relationships used for back-calculating length at annulus for largemouth bass from Lake Carl Blackwell.

Time of collection	Total length-scale radius (X41.5) relationships	R^2
Spring 1977	$Y = 31.2586 + 1.6600\ X$	0.9331
Fall 1976	$Y = 13.6770 + 1.7152\ X$	0.9033
Fall 1975	$Y = 21.1284 + 1.6959\ X - (5.905 \times 10^{-4})\ X^2$	0.9429
Fall 1974	$Y = 44.9098 + 1.4382\ X - (3.977 \times 10^{-11})\ X^5$	0.7320
August 1974	$Y = 64.3382 + 1.2016\ X$	0.3767
Spring 1974	$Y = 31.5970 + 1.4797\ X + (2.1777 \times 10^{-6})\ X^3 - (2.1090 \times 10^{-11})\ X^5$	0.9264
Fall 1973	$Y = 35.2742 + 1.5032\ X - (5.2330 \times 10^{-12})\ X^5$	0.7714
Spring 1973	$Y = 33.0287 + 1.5485\ X$	0.9253
Fall 1972	$Y = 23.1977 + 1.5733\ X$	0.8264
1971 from Zweiacker et al. (1973)	$Y = 8.04 + 1.69\ X$	0.9025
1968 & 1969 Zweiacker et al. (1973)	$Y = 37.67 + 1.29\ X$	0.9409
Spring 1967	$Y = 19.1374 + 1.7615\ X$	0.9123

Table 12. Mean back-calculated total lengths (mm) and annual growth increments at end of each year of life for largemouth bass in Lake Carl Blackwell, 1959-1976 (sample sizes in parentheses).

Year Class	I T.L.	I Inc.	II T.L.	II Inc.	III T.L.	III Inc.	IV T.L.	IV Inc.	V T.L.	V Inc.	VI T.L.	VI Inc.	VII T.L.	VII Inc.	VIII T.L.	VIII Inc.
	Total lengths (T.L.) and growth increments (Inc.)															
1976	150.3 (21)	150.3														
1975	150.4 (189)	150.4	239.3 (53)	79.5												
1974	139.8 (388)	139.8	229.8 (185)	83.6	283.2 (96)	43.2										
1973	177.0 (1338)	177.0	231.3 (200)	82.4	295.2 (99)	41.3	343.1 (59)	38.8								
1972[a]																
1971	157.9 (196)	157.9	278.6 (99)	113.1	359.8 (44)	72.7	394.3 (34)	37.1	429.7 (30)	39.1	467.8 (23)	24.8				
1970	132.7 (99)	132.7	272.6 (90)	138.5	350.8 (39)	88.0	429.7 (15)	66.3	487.0 (9)	46.9	504.6 (9)	17.6	529.5 (8)	12.7		
1969	134.3 (92)	134.3	257.5 (92)	123.2	345.7 (76)	85.3	402.6 (36)	56.8	449.5 (7)	35.2	513.0 (2)	18.4	569.1 (1)	19.9	577.4 (1)	8.3
1968	128.8 (165)	128.8	251.1 (63)	128.9	341.9 (63)	88.1	398.8 (51)	51.7	437.1 (24)	44.5	450.0 (4)	26.5				
1967	129.1 (521)	129.1	266.5 (254)	136.4	336.6 (35)	87.8	391.9 (35)	55.2	436.4 (33)	39.2	474.9 (13)	30.1	501.8 (5)	16.5		
1966	146.7 (140)	146.7	284.1 (128)	136.3	360.6 (60)	75.2	380.7 (8)	67.8	420.4 (8)	39.7	442.5 (8)	22.0				
1965	151.2 (177)	151.2	288.0 (177)	137.7	373.4 (168)	85.0	424.0 (104)	50.9	437.0 (3)	55.8	465.4 (3)	28.4	485.0 (2)	33.8		
1964	158.2 (158)	158.2	283.4 (158)	126.2	365.1 (158)	81.7	428.1 (150)	58.9	460.0 (96)	35.8	486.2 (2)	22.1	515.9 (2)	29.7	534.5 (1)	15.7
1963	150.7 (98)	150.7	278.0 (98)	127.3	364.9 (98)	86.9	419.6 (98)	54.6	465.0 (82)	41.0	484.0 (47)	20.0	497.0 (1)	53.0		
1962	161.8 (26)	161.8	290.2 (26)	127.7	372.5 (26)	82.2	427.0 (26)	54.5	461.4 (26)	34.5	490.0 (20)	24.0	508.0 (10)	21.0		
1961	127.3 (5)	127.3	269.1 (5)	141.8	350.9 (5)	81.9	411.3 (5)	60.3	464.8 (5)	53.6	498.2 (5)	33.4	481.0 (2)	26.0		
1959	138.9 (1)	138.9	218.2 (1)	79.3	290.4 (1)	72.2	387.3 (1)	96.9	422.5 (1)	35.2	461.3 (1)	38.8	512.4 (1)	51.1	537.0 (1)	24.7
Number	3614		1629		968		622		324		137		32		3	
Weighted Means	154.9	154.9	263.5	118.0	346.1	75.2	409.4	53.0	453.8	39.2	479.6	23.3	511.5	21.8	549.6	16.2
Means	145.9	145.9	262.5	117.5	342.2	76.5	403.0	57.7	447.6	41.7	478.2	25.5	511.1	29.3	549.6	16.2

[a] Year-class failure

shad (GSSC) from Table 13. Results of this analysis appear in Table 14 with the first year growth increment denoted by GI01, second year GI12, and so on. For the 1972 year-class a first year growth increment of 143.0 mm (the mean length on 6 October 1972) was used since there were not enough native bass collected the following spring to allow calculation of actual growth of that year-class (Shirley 1975). The only complete data sets for the 17 years are for average annual water level (AAWL) and the first year growth increment (GI01). The correlation between these two variables is not significant (r=0.1530; P=0.5578) when all years are considered but the correlation for years 1962 through 1967 is significant (r=0.8456; P=0.0339). Zweiacker et al. (1973) found that in years 1962 through 1967 first year growth of largemouth bass in Lake Carl Blackwell was positively correlated with the average annual water level, whereas growth increments in the second, third and fourth years of life were negatively correlated with water level. These correlations were probably due to the influence that water level has on food availability. Low lake levels have a negative effect on the littoral zone invertebrates upon which age 0 bass feed but they also make forage fishes more vulnerable to predation by age I and older bass. From 1962 to 1967 there was a continuing decline in the lake water level but during some of the other years the water level was rising (Figure 3). Therefore, all years were classified as rising-water or falling-water years based on the difference in mean monthly water levels in January and December of each year. Based on this classification, years 1959, 1961, 1968, 1969, 1973, and 1974 were rising-water years and the remaining 11 were falling-water years. Correlation between GI01 and AAWL for the falling-water years was improved (r=

Table 13. Biological and physical parameters used in correlation analysis of growth increment data for largemouth bass in Lake Carl Blackwell, Oklahoma.

Year	AAWL[a]	TEMP[b]	TURB[c]	YOYD[d]	LMBSC[e]	GSD[f]	GSSC[g]
1976	286.6			88.9	5.87	2595.4	88.29
1975	287.9			266.4	16.16	5713.9	321.59
1974	287.8	23.18	28.72	200.5	24.54	7053.5	143.21
1973	285.4	23.23	67.76	447.4	6.49	15865.9	69.06
1972	282.9	23.52	46.09	0.13			
1971	283.5	23.32	42.58	5.5	3.17	2981.8	54.90
1970	284.4	23.42	35.23	7.4			
1969	284.0	23.61	47.34	141.9			
1968	284.1	22.90	40.82	87.8	3.16	1422.6	39.11
1967	283.9	22.37	30.28	95.2	28.86	3387.3	66.87
1966	284.6	22.82	22.20	24.8	12.34	47.5	1.03
1965	285.6	24.13	27.46	54.6			
1964	286.1		21.38				
1963	287.0		20.50				
1962	297.6		24.90				
1961	287.8		30.65				
1959	287.4		55.57				
Means	285.68	23.25	36.10	118.38	12.57	4883.48	98.01
Std. Dev.	1.7173	0.4828	13.7425	132.0018	9.8586	4953.6658	99.0427

[a]AAWL = average annual water level (m., M.S.L.).

[b]TEMP = mean temperature from May through October (C).

Table 13. (Continued).

[c]TURB = mean annual turbidity (JTU).

[d]YOYD = density of young-of-the-year bass on 13 August (no./ha).

[e]LMBSC = standing crop of largemouth bass (kg/ha).

[f]GSD = density of gizzard shad (no./ha).

[g]GSSC = standing crop of gizzard shad (kg/ha).

Table 14. Correlation coefficients (r) and probabilities for a greater value of r (in parentheses) for growth increments (GI) and biological and physical parameters. Variable names defined in text and Table 13.

	GI01	GI12	GI23	GI34	GI45	GI56	GI67	GI78
AAWL	0.1530 (0.5578)	-0.5892 (0.0208)	-0.6591 (0.0104)	0.0123 (0.9683)	-0.0132 (0.9676)	-0.3061 (0.3332)	-0.5205 (0.1509)	-0.7656 (0.4448)
TEMP	0.2836 (0.4271)	-0.2247 (0.5610)	0.3921 (0.2966)	0.0986 (0.7865)	0.6544 (0.0401)	0.4419 (0.2010)	0.2668 (0.5630)	-
TURB	0.1633 (0.5610)	0.0050 (0.9871)	-0.1441 (0.6549)	-0.0561 (0.8625)	-0.0060 (0.9859)	-0.2614 (0.4656)	-0.4525 (0.3080)	-
YOYD	0.5456 (0.0665)	-0.6213 (0.0413)	-0.4313 (0.1854)	0.2514 (0.4558)	-0.1507 (0.6582)	-0.3637 (0.2452)	-0.4104 (0.2726)	0.1189 (0.9241)
LMBSC	-0.4603 (0.2511)	-0.1834 (0.6939)	0.0940 (0.8412)	-0.0832 (0.8593)	0.6850 (0.0895)	-0.1590 (0.7068)	0.1256 (0.7884)	0.8456 (0.3585)
GSD	0.6924 (0.0570)	-0.6849 (0.0895)	-0.1009 (0.8296)	0.4057 (0.3665)	0.0396 (0.9329)	-0.1103 (0.7949)	-0.4801 (0.2756)	0.9982 (0.0270)
GSSC	0.0661 (0.8765)	-0.7009 (0.0793)	-0.7371 (0.0588)	-0.5582 (0.1928)	0.3786 (0.4023)	-0.6621 (0.0736)	-0.4184 (0.3502)	-0.5886 (0.5994)

0.0891; P=0.8667).

There were significant negative correlations between AAWL and the second and third year growth increments (r=-0.5892; P=0.0208) and (r= -0.6591; P=0.0104) respectively. Growth increments from the fourth through the eighth year of life were not significantly correlated with AAWL.

Mean temperature from May through October (TEMP) was not significantly correlated with growth increments for any age groups except age 4 fish (r=0.6544; P=0.0401). This correlation was most likely spurious. Mean annual turbidity (TURB) was not significantly correlated with growth increments for any age groups.

Correlation between first year growth increments (GI01) and young-of-the-year bass density (YOYD) was significant only at the 6.65% level (r=0.5456; P=0.0665). This correlation probably indicates that conditions which are favorable for survival of young-of-the-year bass are also favorable for growth. The significant correlation between second year growth increments (GI12) and YOYD (r=-0.6213; P=0.0413) was probably due to the correlation between YOYD and AAWL (r=0.5432; P=0.0680), since AAWL was also correlated with GI12.

Standing crop of largemouth bass (LMBSC) was not significantly correlated with growth increments for any age groups. Gizzard shad density (GSD) was not significantly correlated at the 5.0% level with growth increments for any age groups but age 7 (r=0.9982; P=0.0270), but this correlation involved only 3 pairs of data. Positive correlation between GI01 and GSD was significant, however, at the 5.7% level. Gizzard shad density (GSD) was also significantly correlated with YOYD (r=0.9365; P=0.0006), thereby confounding interpretation of these correlations. Gizzard shad standing crop (GSSC) was not correlated with growth increments for any age groups at the 5.0% level of significance. Correlations for the second (r=-0.7009; P=0.0793), third (r=-0.7371; P=0.0588), and sixth (r=-0.6621; P=0.0736) years of life did approach the 5.0% level of significance.

Lack of consistent significant correlations prevents any accurate predictions of growth increments based on these environmental factors. Multiple regression analysis was attempted but was unsuccessful because of the lack of a complete data set. It is questionable whether this type of analysis would be effective due to the interrelationships between turbidity, temperature, water level, water fluctuation, bass density, gizzard shad density, and the large variance associated with several of these variables.

Instantaneous rates of growth in length are required input for simulation of Model III. Instantaneous population growth rates (G_x) were computed from mean lengths of the surviving fish of successive ages (Table 15) and the individual growth rates (G) were computed from back-calculated lengths of individual fish (Table 16). Both types of growth rates were computed in order to detect any possible size-selective mortality or sampling bias (Ricker 1969). Ricker recommends that the best estimate of growth of individual fish (G) comes from the back-calculated lengths at the last two annuli on the scales since the estimate obtained from earlier annuli may not be representative of all fish that were alive at that time if there was any size-selective mortality. In this study the individual growth rates were not estimated in this way but differences still occurred. The population growth rates were slightly higher than individual growth rates in 38 of the 78

Table 15. Annual instantaneous population growth rates (G_x) for largemouth bass in Lake Carl Blackwell for year-classes 1959-1975.

Year class	Age Interval 1 - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8
1975	0.464420						
1974	0.496996	0.208944					
1973	0.267566	0.243938	0.150369				
1972[a]							
1971	0.567815	0.255771	0.091564	0.085975	0.084954		
1970	0.719915	0.252210	0.202871	0.125177	0.035502	0.048167	
1969	0.650944	0.294552	0.152372	0.110192	0.132140	0.103780	0.014479
1968	0.667590	0.308667	0.153942	0.091702	0.029086		
1967	0.724787	0.233521	0.152111	0.107552	0.084545	0.055097	
1966	0.660937	0.238443	0.054242	0.099195	0.051234		
1965	0.644357	0.259690	0.127083	0.030200	0.062964	0.041252	
1964	0.582999	0.253312	0.159186	0.071870	0.055394	0.059293	0.035419
1963	0.612330	0.272002	0.139678	0.104166	0.040048	0.026505	
1962	0.584209	0.249667	0.136547	0.077481	0.060140	0.036076	
1961	0.748536	0.265418	0.158822	0.122284	0.069394	-0.035134	
1959	0.451658	0.285847	0.287940	0.086990	0.087859	0.105057	0.046892
Means	0.589671	0.258713	0.151287	0.092732	0.066105	0.048899	0.032263
Std. Dev.	0.127193	0.025782	0.054303	0.025727	0.028456	0.041980	0.016435

[a]Year-class failure

Table 16. Mean annual instantaneous individual growth rates (G) for largemouth bass in Lake Carl Blackwell, 1959-1976 (sample sizes in parentheses).

Year class	Age Interval 1 - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8
1975	0.403795 (53)						
1974	0.452234 (185)	0.165514 (96)					
1973	0.440441 (200)	0.150713 (99)	0.120008 (59)				
1972[a]							
1971	0.520806 (99)	0.225718 (44)	0.098816 (34)	0.095403 (30)	0.054471 (23)		
1970	0.709420 (90)	0.288823 (39)	0.167583 (15)	0.101262 (9)	0.035502 (9)	0.024277 (8)	
1969	0.650944 (92)	0.283352 (76)	0.152083 (36)	0.081546 (7)	0.036526 (2)	0.035593 (1)	0.014479 (1)
1968	0.720192 (63)	0.297972 (63)	0.138847 (51)	0.107371 (24)	0.060694 (4)		
1967	0.717071 (254)	0.302246 (35)	0.151814 (35)	0.094119 (33)	0.065480 (13)	0.033434 (5)	
1966	0.653466 (128)	0.233878 (60)	0.196128 (8)	0.099195 (8)	0.050996 (8)		
1965	0.650327 (177)	0.258302 (168)	0.127887 (104)	0.136609 (3)	0.062964 (3)	0.072238 (2)	
1964	0.589340 (158)	0.253312 (158)	0.148018 (150)	0.081021 (96)	0.046520 (2)	0.059293 (2)	0.029813 (1)
1963	0.612330 (98)	0.272002 (98)	0.139404 (98)	0.092304 (82)	0.042200 (47)	0.112765 (1)	
1962	0.579892 (26)	0.249322 (26)	0.136547 (26)	0.077716 (26)	0.050220 (20)	0.042217 (10)	
1961	0.748536 (5)	0.265790 (5)	0.158537 (5)	0.122527 (5)	0.069394 (5)	0.055570 (2)	
1959	0.451658 (1)	0.285847 (1)	0.287940 (1)	0.086990 (1)	0.087859 (1)	0.105057 (1)	0.047088 (1)
Number	1629	968	622	324	137	32	3
Weighted Means	0.593678	0.242867	0.138566	0.090425	0.050015	0.044099	0.030460
Means	0.593363	0.252342	0.155662	0.098005	0.055236	0.060049	0.030460

[a]Year-class failure

estimates. Of the remaining 40 estimates, 20 were slightly less than individual growth rates and 20 were equal to individual growth rates. In most cases the differences were probably not significant except for the 1973 year-class during the interval 1 - 2 (Tables 15 and 16). During this interval the population growth rate was 0.267566 as opposed to an individual growth rate of 0.440441. This would probably indicate a size-selective mortality on the larger fish within this age group since these fish were approaching a size where they would begin to be exploited by anglers. Model III does not, however, accomodate size-selective mortality within age classes. Since size-selective mortality does not appear to occur consistently in the Lake Carl Blackwell bass population, the omission of this factor should not cause any major errors, but users should be cautious because the use of incorrect growth rates can cause rather large errors in estimates of production (Ricker 1969).

The weighted mean lengths (Table 12) were used to derive a von Bertalanffy curve (Figure 15 and 16) to describe the general growth pattern of largemouth bass in Lake Carl Blackwell using Beverton's method (Ricker 1975:225). Age-specific annual instantaneous growth rates to be used for Model III simulation were then computed from the fitted von Bertalanffy equation and are presented in Table 17.

Parameters and correlation coefficients (r) for length-weight relationships computed for collections of largemouth bass from Lake Carl Blackwell from 1967 to 1977 were very similar (Table 18). The parameters for the Fall 1975 collection were chosen to use in the simulation of Model III since these were derived from one of the larger collections with a fair representation of most size groups.

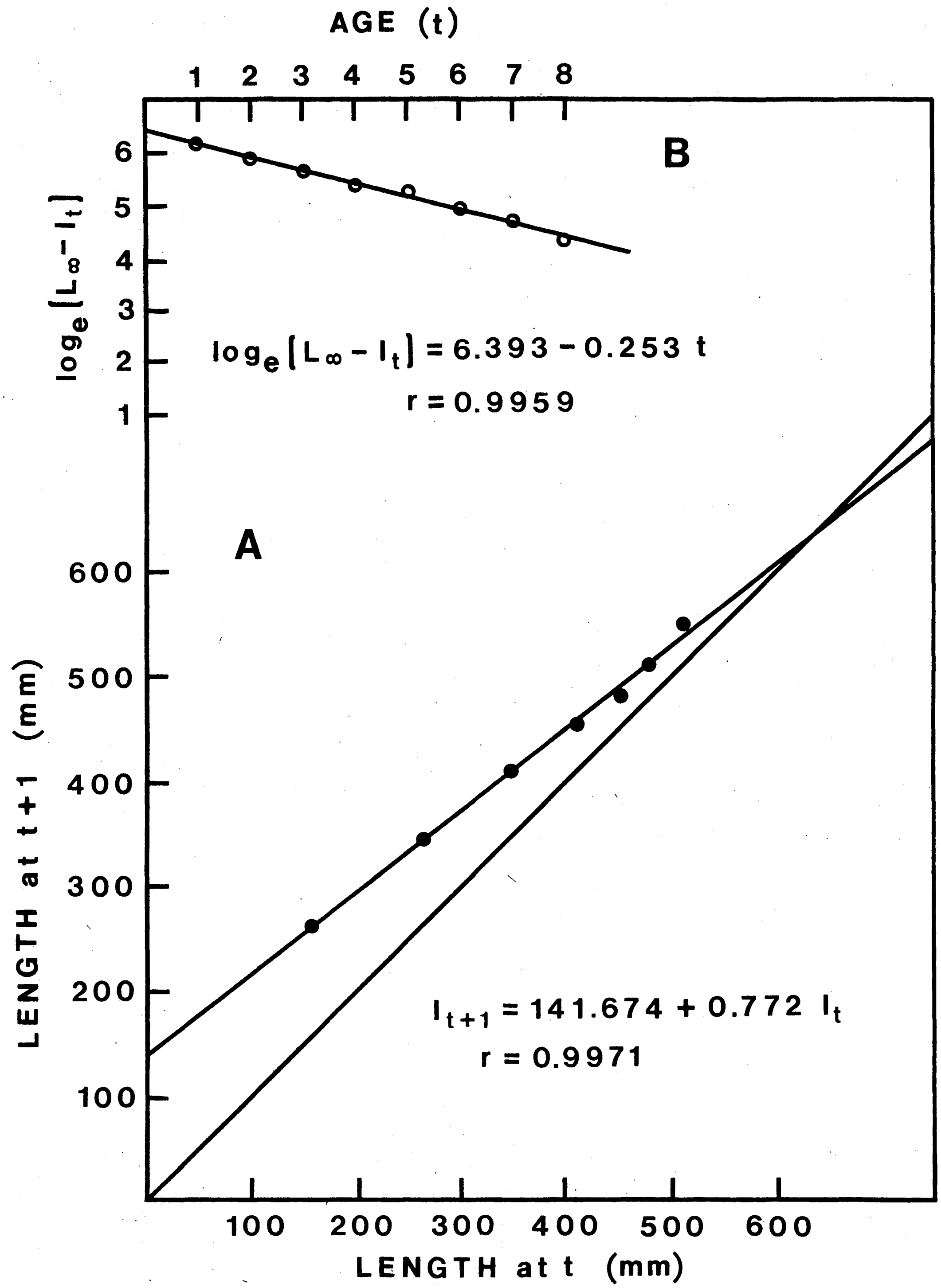

Figure 15. (A) Walford plot of length (mm) at age t+1 against length at age t and (B) $\log_e(L_\infty - l_t)$ plotted against age using L_∞ = 621.4 mm for largemouth bass from Lake Carl Blackwell, Oklahoma.

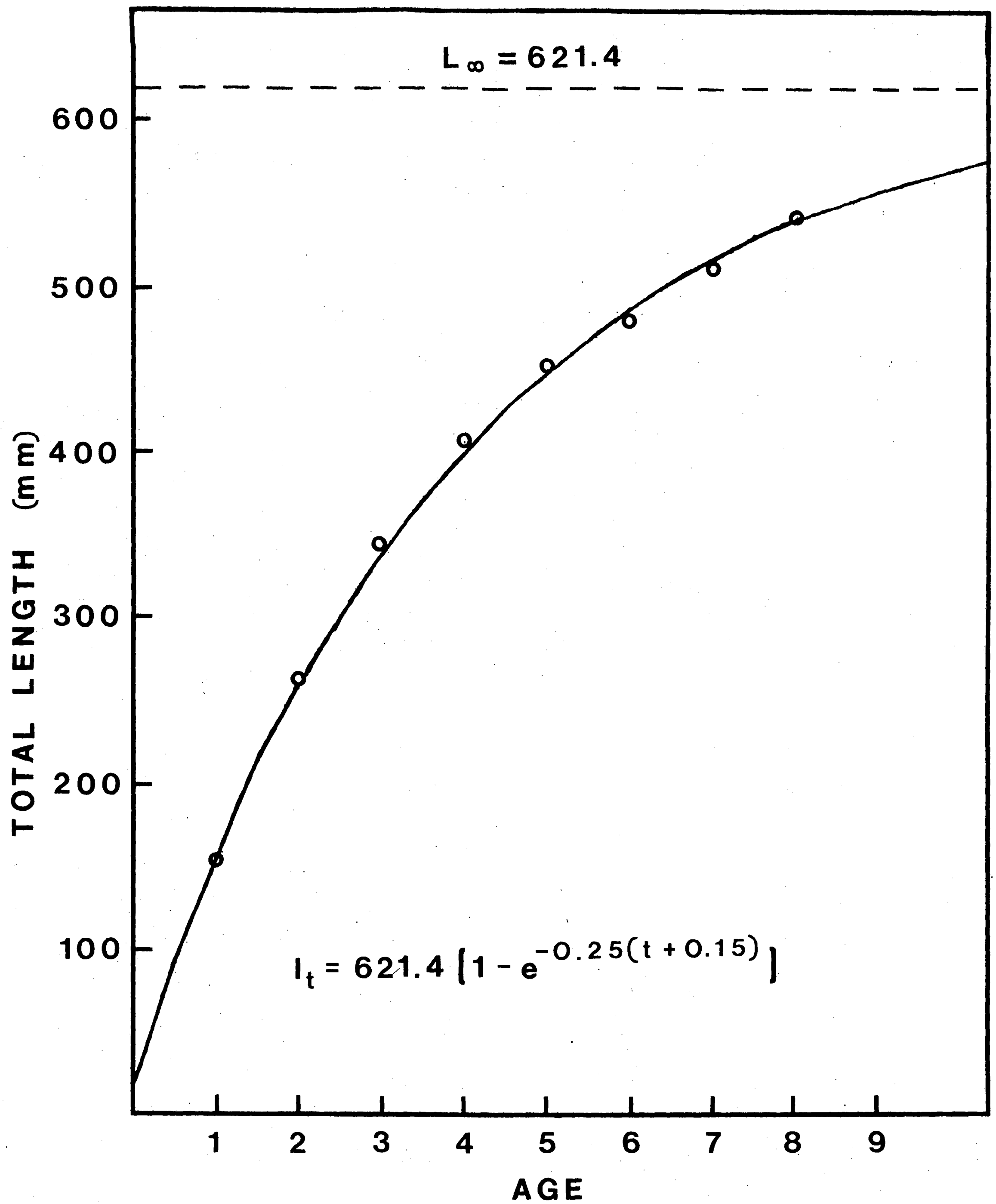

Figure 16. von Bertalanffy curve fitted to data for largemouth bass from Lake Carl Blackwell, Oklahoma. Open circles are weighted mean lengths from Table 12.

Table 17. Annual instantaneous rates of growth in total length (G) computed from the fitted von Bertalanffy equation in Figure 16.

Age interval	G
1 - 2	0.50927
2 - 3	0.27063
3 - 4	0.16947
4 - 5	0.11457
5 - 6	0.08094
6 - 7	0.05879
7 - 8	0.04351
8 - 9	0.03262

Table 18. Parameters and correlation coefficients (r) for length-weight relationships, log w = log a + b log l, computed for collections of largemouth bass from Lake Carl Blackwell, Oklahoma (1967-1977).

Collection period	No. of fish	a	b	r
Spring 1977	367	5.095×10^{-7}	3.5639	0.9901
Fall 1976	375	5.561×10^{-6}	3.1406	0.9858
Fall 1975	780	4.531×10^{-6}	3.1633	0.9884
Fall 1974	178	5.457×10^{-6}	3.1420	0.9862
August 1974	79	1.884×10^{-6}	3.3432	0.9907
Spring 1974	987	4.027×10^{-6}	3.2012	0.9811
Fall 1973	961	3.712×10^{-6}	3.2369	0.9860
Spring 1973	59	1.717×10^{-6}	3.3643	0.9919
Fall 1972	255	4.380×10^{-7}	3.6078	0.9862
Spring 1967	55	2.699×10^{-6}	3.2848	0.9944

Mortality Rates

Model III requires instantaneous annual rates of fishing mortality (F) and natural mortality (M) for each age group. Table 19 lists total (A), fishing (u), and natural (v) mortality rates that have been reported for largemouth bass from various lakes and reservoirs. These rates can be converted to instantaneous rates by the following relationships (Ricker 1975):

$$Z = -\log_e(1-A) \tag{7.23}$$

$$F = \frac{uZ}{A} \tag{7.24}$$

$$M = \frac{vZ}{A} \tag{7.25}$$

The assumption that mortality rates are constant after recruitment has been made for convenience in analyzing largemouth bass populations (Anderson 1974a, 1974b). Bennett (1969) presents data that shows that high natural mortality among small bass is usually followed by a period of low mortality until after the fish reaches age 7 or 8, at which time high mortality resumes. Age-specific mortality rates from Zweiacker (1972) and Clady (1970) also follow this general pattern.

Nominal simulation runs of Model III were made assuming 60% mortality (30% fishing, 30% natural) on all age groups except age 0. The corresponding instantaneous rates of fishing and natural mortality would be 0.458145, resulting in a total instantaneous mortality rate (Z) of 0.916291. Age-specific rates were also used for simulation of the largemouth bass population of Lake Carl Blackwell. Average age-specific mortality rates (A) from Zweiacker et al. (1973) were converted to instantaneous rates (Z) by equation 7.23. Instantaneous

Table 19. Reported annual rates of total (A), fishing (u), and natural (v) mortality for largemouth bass.

A	u	v	Location	Source
0.56	0.35	0.21	Ridge L, IL	Bennett et al. (1969)
–	0.416	–	Watauga Res., TN	Chance (1955)
–	0.412	–	S. Holston Res., TN	Chance (1955)
–	–	0.23	Cub L., MI	Clady (1970)
–	–	0.44	Cub L., MI	Clady (1970)
–	0.39	–	Center Hill Res., TN	Coomer (1976)
0.70	0.35	0.35	Sugarloaf L., MI	Cooper and Latta (1954)
0.42	0.22	0.20	Whitmore L., MI	Cooper and Schafer (1954)
0.37	–	–	Beaver L., AR	Houser and Rainwater (1975)
0.43	–	–	Beaver L., AR	Houser and Rainwater (1975)
0.74	–	–	Beaver L., AR	Houser and Rainwater (1975)
0.44	–	–	Beaver L., AR	Houser and Rainwater (1975)
0.34	–	–	Beaver L., AR	Houser and Rainwater (1975)
0.47	–	–	Bull Shoals L., AR&MO	Houser and Rainwater (1975)
0.74	–	–	Bull Shoals L., AR&MO	Houser and Rainwater (1975)
0.65	–	–	Bull Shoals L., AR&MO	Houser and Rainwater (1975)
0.31	–	–	Bull Shoals L., AR&MO	Houser and Rainwater (1975)
–	0.296	–	Spavinaw L., OK	Jackson (1966)
–	0.322	–	L. Eucha, OK	Jackson (1966)
0.56	0.20	0.36	Clear L., CA	Kimsey (1957)
0.68	0.20	0.48	Sutherland Res., CA	LaFaunce et al. (1964)
0.78	0.40	0.38	Sutherland Res., CA	LaFaunce et al. (1964)
0.73	0.47	0.26	Sutherland Res., CA	LaFaunce et al. (1964)

Table 19. (Continued).

A	v	v	Location	Source
0.55	0.35	0.20	Sutherland Res., CA	LaFaunce et al. (1964)
0.83	0.48	0.35	Sutherland Res., CA	LaFaunce et al. (1964)
0.62	0.15	0.47	Gladstone L., MN	Maloney et al. (1962)
0.24	0.12	0.12	Browns L., WI	Mraz and Threinen (1957)
0.89	0.40	0.49	Folsom L., CA	Rawstron (1967)
0.92	0.36	0.56	Merle Collins Res., CA	Rawstron and Hashagen (1972)
0.71	0.45	0.26	Merle Collins Res., CA	Rawstron and Hashagen (1972)
0.86	0.62	0.24	Merle Collins Res., CA	Rawstron and Hashagen (1972)
0.76	0.65	0.11	Merle Collins Res., CA	Rawstron and Hashagen (1972)
0.86	0.65	0.21	Merle Collins Res., CA	Rawstron and Hashagen (1972)
0.47	0.012	0.458	L. Carl Blackwell, OK	Zweiacker (1972)
0.40	0.012	0.388	L. Carl Blackwell, OK	Zweiacker (1972
0.608	0.345	0.322	Means	

age-specific fishing mortality rates (F) were obtained using 7.24 and the average u and A for the two years presented in Table 19 for Lake Carl Blackwell (Zweiacker 1972). Natural mortality rates (M) were then obtained by subtraction. The resulting age-specific rates appear in Table 20.

Results and Discussion

Simulation of the largemouth bass population of Lake Carl Blackwell with Model III resulted in estimates of year-class strength that were essentially the same as those for Model II. This result was expected since young-of-the-year survival was computed in the same manner. Thus Model III offers the same utility as Model II in quickly and easily predicting year-class strength. Predictions of production, yield and catch (Table 21) reflect the increase due to a large 1973 year-class that was produced during a year of rising water level. Production of largemouth bass (age I and older) in Lake Carl Blackwell in 1968 was estimated at 415.49 kg and yield at 6.83 kg by Zweiacker (1972). The difference between these estimates and Model III predictions was due to the use of slightly different population estimates, and different growth and mortality rates. Model III predictions of young-of-the-year production in 1973 (Table 22) compare favorably with the estimate made by Shirley (1975). Shirley's estimate was 5603.01 kg (5.77/ha) and a prediction by Model III was 4329.56 kg (4.46/ha).

It is unfortunate that we do not have more estimates of production and yield to compare with the Model III estimates. In general, I believe that Model III predictions are fairly accurate.

Table 20. Annual instantaneous rates of fishing (F), natural (M), and total (Z) mortality calculated for age groups of largemouth bass from Lake Carl Blackwell, Oklahoma.

Age	F	M	Z
I	0.01080	0.38076	0.39156
II	0.01338	0.47169	0.48507
III	0.01152	0.40611	0.41763
IV	0.01600	0.56382	0.57982
V	0.02706	0.95376	0.98082
VI	0.04481	1.57970	1.62451
VII	0.07297	2.57211	2.64508
VIII	0.07297	2.57211	2.64508[a]

[a]Assumed to be the same as age VII.

Table 21. Gross production, yield and catch of largemouth bass (age I and older) in Lake Carl Blackwell, 1968-1977, as predicted by Model III.

Year	Area ha	Production kg	Production kg/ha	Yield kg	Yield kg/ha	Catch no	Catch no/ha
1968	746.27	359.57	0.4818	13.37	0.0179	23	0.0308
1969	853.11	326.48	0.3827	11.13	0.0130	19	0.0223
1970	815.88	307.60	0.3770	9.25	0.0113	17	0.0208
1971	619.60	260.36	0.4202	8.94	0.0144	14	0.0226
1972	523.68	179.68	0.3431	8.34	0.0159	10	0.0191
1973	970.88	106.14	0.1093	6.55	0.0067	7	0.0072
1974	1373.55	8122.86	5.9138	58.59	0.0427	606	0.4412
1975	1384.07	9472.67	6.8441	146.20	0.1056	520	0.3757
1976	1203.17	7795.99	6.4795	163.74	0.1361	302	0.2410
1977	-	8445.51	-	236.79	-	493	-

Table 22. Predictions of gross and net production of young-of-the-year largemouth bass in Lake Carl Blackwell, 1968-1977, based on Model III.

Year	Mean biomass		Gross production		Net production	
	kg	kg/ha	kg	kg/ha	kg	kg/ha
1968	12.85	0.0172	133.16	0.1784	7.06	0.0095
1969	13.33	0.0156	138.11	0.1619	15.41	0.0181
1970	9.50	0.0116	98.41	0.1206	3.76	0.0046
1971	4.18	0.0067	43.27	0.0698	-5.22	-0.0084
1972	3.02	0.0058	31.28	0.0597	-6.15	-0.0117
1973	417.79	0.4303	4329.56	4.4594	2555.42	2.6321
1974	38.88	0.0283	402.91	0.2933	144.12	0.1049
1975	12.19	0.0088	126.33	0.0913	36.31	0.0262
1976	518.71	0.4311	5375.39	4.4677	835.57	0.6945
1977	415.53	-	4306.19	-	428.65	-

Sensitivity Analysis

Seventy-five 10-year simulations of Model III were run with various input parameters and initial state variables adjusted by a 10% increase or decrease to evaluate the sensitivity of Model III output to these changes. Nominal simulation of Model III, which served as a control, was run assuming 60% mortality (30% fishing, 30% natural), a stable age structure starting with 2000 age I bass, and constant survival of young-of-the-year. The data deck for nominal simulation is listed in Appendix G. Catch (numbers), yield (kg) and gross production (kg) of the stock (ages 1 through k) were summed over the 10-year period and the sensitivity of these outputs to variation in any given input was calculated by equation 5.4 Results of sensitivity analysis of catch, yield and gross production are presented in Tables 23, 24, and 25, respectively. Sensitivity to variations in maturity of age II and III was also evaluated (Table 26).

All three output responses were most sensitive to variations in Z_o, instantaneous mortality from egg to age I, and BFEC, the exponent of the length-fecundity relationship. Sensitivity to Z_o corroborates the results of sensitivity analysis of Model I. Accurate estimates of survival from egg to age I are necessary to predict not only population trends but also catch, yield and production. It is also important that we have accurate estimates of the exponent for the length-fecundity relationship although this may not be as critical as it appears from the sensitivity analysis. A change in the exponent accompanied by an appropriate change in the constant in this relationship may still give reasonable estimates of fecundity. In the sensitivity analysis the

Table 23. Sensitivity of cumulative catch (numbers) to variations in initial population size and input parameters for a 10-year simulation of Model III.

Adjusted parameter	+10% Catch	+10% Sensitivity	-10% Catch	-10% Sensitivity
Nominal	9706.5	-	9706.5	-
N_1	9966.0	0.0267	9447.0	-0.0267
N_2	9941.0	0.0245	9472.1	-0.0241
N_3	9940.2	0.0241	9472.7	-0.0241
N_4	9841.4	0.0139	9571.2	-0.0139
N_5	9770.8	0.0066	9641.5	-0.0067
N_6	9734.3	0.0029	9678.1	-0.0029
N_7	9721.1	0.0015	9691.3	-0.0016
N_8	9710.2	0.0004	9702.3	-0.0004
G_1	10785.8	0.1112	8840.8	-0.0892
G_2	10418.4	0.0733	9080.7	-0.0645
G_3	9968.1	0.0270	9460.4	-0.0254
G_4	9799.4	0.0096	9616.4	-0.0093
G_5	9737.5	0.0032	9675.6	-0.0032
G_6	9715.7	0.0009	9696.8	-0.0010
G_7	9708.6	0.0002	9703.9	-0.0003
G_8	9706.5	0.0000	9706.2	0.0000
F_1	9721.7	0.0016	9673.7	-0.0034
F_2	9457.5	-0.0256	9968.6	0.0270
F_3	9529.8	-0.0182	9892.3	0.0191
F_4	9605.4	-0.0104	9812.1	0.0109
F_5	9656.4	-0.0052	9758.4	0.0053
F_6	9685.3	-0.0022	9728.1	0.0022
F_7	9699.6	-0.0007	9713.0	0.0007
F_8	9707.0	0.0000	9705.4	-0.0001
M_1	9172.4	-0.0550	10286.6	0.0598
M_2	9236.1	-0.0485	10215.9	0.0525
M_3	9438.8	-0.0276	9990.1	0.0292
M_4	9568.4	-0.0142	9851.1	0.0149
M_5	9641.5	-0.0067	9773.8	0.0069
M_6	9679.3	-0.0028	9734.3	0.0029
M_7	9697.3	-0.0009	9715.6	0.0009
M_8	9705.9	-0.0001	9706.5	0.0000
Z_o	4259.1	-0.5612	34154.7	2.5187
AFEC	11052.5	0.1387	8473.5	-0.1270
BFEC	284395.6	28.2995	2445.0	-0.7481
AWTLEN	9706.3	0.0000	9706.2	0.0000
BWTLEN	9706.3	0.0000	9706.2	0.0000

Table 24. Sensitivity of cumulative yield (kg) to variations in initial population size and input parameters for a 10-year simulation of Model III.

Adjusted parameter	+10% Yield	+10% Sensitivity	-10% Yield	-10% Sensitivity
Nominal	2402.7	-	2402.7	-
N_1	2459.2	0.0235	2346.1	-0.0236
N_2	2463.8	0.0254	2341.4	-0.0255
N_3	2462.2	0.0248	2343.1	-0.0248
N_4	2437.6	0.0145	2367.7	-0.0146
N_5	2419.5	0.0070	2385.8	-0.0070
N_6	2409.9	0.0030	2395.4	-0.0030
N_7	2406.5	0.0016	2398.4	-0.0016
N_8	2403.6	0.0004	2401.7	-0.0004
G_1	2920.2	0.2154	2011.3	-0.1629
G_2	2656.9	0.1058	2183.1	-0.0914
G_3	2497.4	0.0394	2314.1	-0.0369
G_4	2436.9	0.0142	2369.6	-0.0138
G_5	2414.4	0.0049	2391.2	-0.0048
G_6	2406.3	0.0015	2399.0	-0.0015
G_7	2403.7	0.0004	2401.7	-0.0004
G_8	2402.7	0.0000	2402.5	-0.0001
F_1	2322.6	-0.0333	2487.6	0.0353
F_2	2339.4	-0.0263	2468.9	0.0276
F_3	2376.3	-0.0110	2429.7	0.0112
F_4	2393.7	-0.0037	2411.9	0.0038
F_5	2400.5	-0.0009	2404.9	0.0009
F_6	2403.0	0.0001	2402.3	-0.0002
F_7	2403.8	0.0004	2401.4	-0.0005
F_8	2404.3	0.0007	2400.9	-0.0007
M_1	2276.8	-0.0524	2539.3	0.0568
M_2	2276.6	-0.0525	2539.5	0.0569
M_3	2323.7	-0.0329	2486.4	0.0348
M_4	2359.6	-0.0179	2447.9	0.0188
M_5	2381.6	-0.0088	2424.6	0.0091
M_6	2393.6	-0.0038	2412.1	0.0039
M_7	2399.4	-0.0014	2406.1	0.0014
M_8	2402.2	-0.0002	2403.1	0.0002
Z_o	1300.1	-0.4589	6829.4	1.8424
AFEC	2663.0	0.1083	2160.8	-0.1007
BFEC	45960.7	18.1288	902.3	-0.6245
AWTLEN	2402.6	0.0000	2402.6	0.0000
BWTLEN	2921.6	0.2160	1997.7	-0.1686

Table 25. Sensitivity of cumulative gross production (kg) to variations in initial population size and input parameters for a 10-year simulation of Model III.

Adjusted parameter	+10% Gross production	+10% Sensitivity	-10% Gross production	-10% Sensitivity
Nominal	4032.9	-	4032.9	-
N_1	4136.6	0.0257	3929.2	-0.0257
N_2	4135.0	0.0253	3930.8	-0.0253
N_3	4130.9	0.0243	3934.9	-0.0243
N_4	4088.7	0.0138	3977.1	-0.0138
N_5	4059.2	0.0065	4006.6	-0.0065
N_6	4044.2	0.0028	4021.6	-0.0028
N_7	4038.8	0.0015	4026.9	-0.0015
N_8	4034.5	0.0004	4031.0	-0.0005
G_1	5195.9	0.2884	3177.3	-0.2122
G_2	4584.1	0.1367	3563.3	-0.1164
G_3	4236.9	0.0506	3843.0	-0.0471
G_4	4106.6	0.0183	3962.0	-0.0176
G_5	4058.3	0.0063	4008.1	-0.0061
G_6	4041.1	0.0020	4024.8	-0.0020
G_7	4035.3	0.0006	4030.5	-0.0006
G_8	4033.4	0.0001	4032.1	-0.0002
F_1	3801.5	-0.0574	4284.7	0.0624
F_2	3825.8	-0.0514	4257.6	0.0557
F_3	3916.5	-0.0289	4156.3	0.0306
F_4	3974.5	-0.0145	4094.2	0.0152
F_5	4006.2	-0.0066	4060.8	0.0069
F_6	4022.0	-0.0027	4044.3	0.0028
F_7	4029.3	-0.0009	4036.6	0.0009
F_8	4032.8	0.0000	4032.7	0.0000
M_1	3801.5	-0.0574	4284.7	0.0624
M_2	3825.8	-0.0514	4257.6	0.0557
M_3	3916.5	-0.0289	4156.3	0.0306
M_4	3974.5	-0.0145	4094.2	0.0152
M_5	4006.2	-0.0066	4060.8	0.0069
M_6	4022.0	-0.0027	4044.3	0.0028
M_7	4029.3	-0.0009	4036.6	0.0009
M_8	4032.8	0.0000	4032.7	0.0000
Z_0	1900.7	-0.5287	13278.8	2.2926
AFEC	4552.5	0.1288	3554.9	-0.1185
BFEC	103749.9	24.7259	1173.2	-0.7091
AWTLEN	4032.6	-0.0001	4032.6	-0.0001
BWTLEN	5213.8	0.2928	3114.0	-0.2278

Table 26. Sensitivity of cumulative catch (numbers), yield (kg) and gross production (kg) to variation in maturity for a 10-year simulation of Model III.

Adjusted maturity	Catch	Sensitivity	Yield	Sensitivity	Gross production	Sensitivity
Nominal	9706.5	-	2402.7	-	4032.9	-
20% Age II	11020.9	0.1354	2646.8	0.1058	4540.3	0.1258
40% Age II	12559.0	0.2939	2949.6	0.2276	5131.2	0.2723
60% Age II	14359.1	0.4793	3287.1	0.3681	5819.5	0.4430
80% Age II	16464.3	0.6962	3675.5	0.5297	6620.5	0.6416
0% Age II and 20% Age III	6146.8	-0.3667	1690.6	-0.2964	2644.8	-0.3442
40% Age III	6895.8	-0.2896	1844.0	-0.2325	2939.0	-0.2712
60% Age III	7733.5	-0.2033	2013.0	-0.1622	3266.5	-0.1900
80% Age III	8667.5	-0.1070	2198.8	-0.0849	3630.2	-0.0998

exponents were adjusted without any change in the constant and appeared to yield unreasonable fecundity estimates. To test this hypothesis, four 10-year simulations were run using the parameters derived for each author's fecundity data individually (Table 8). None of the sensitivity values exceeded 0.01 and thus there was little difference in the predictions of catch, yield and production based on the different parameter values for the length-fecundity relationship (Table 27).

In general, the three output responses were most sensitive to variations in growth rates, fishing and natural mortality rates, and initial population sizes of the younger age groups. Catch was more sensitive to variations in growth rates than to variations in mortality rates or initial population size, presumably because of increased fecundity. Yield and production were much more sensitive to variations in growth rates and BWTLEN, the exponent in the length-weight relationship, than to variations in mortality rates or initial population size. Sensitivity to variation in maturity of age II and III (Table 26) indicates the importance of accurate estimates of maturity in predicting catch, yield and production. Further research is needed to determine the variability of these parameters that Model III is most sensitive to and to understand the mechanisms controlling this variation within largemouth bass populations.

In addition to evaluating the robustness of the model, sensitivity analysis can aid in management of the system by determining the response of the system to changes in those parameters amenable to management. Of the parameters tested, fishing mortality is the only one over which we have some control. Based on the sensitivity analysis,

Table 27. Sensitivity (S) of cumulative catch (numbers), yield (kg) and gross production (kg) to the use of different parameters for the length-fecundity relationship derived for data from Clady (1970), Coomer (1976), Kelley (1962) and Olmsted (1974).

Author	Catch	S	Yield	S	Gross production	S
Nominal	9706.5	-	2402.7	-	4032.9	
Clady (1970)	9803.3	0.0100	2419.1	0.0068	4069.0	0.0090
Coomer (1976)	9695.0	-0.0012	2401.0	-0.0007	4028.8	-0.0010
Kelley (1962)	9703.8	-0.0003	2402.2	-0.0002	4031.9	-0.0002
Olmsted (1974)	9720.5	0.0014	2404.9	0.0009	4038.1	0.0013

generally a reduction in the fishing mortality should result in an increase in catch, yield and production. These outputs are more responsive to changes in the fishing mortality rate of the younger age groups. For example, a 10% decrease in the fishing mortality rate of age group I resulted in a slight decrease (0.34%) in the cumulative catch and increases in cumulative yield and production of 3.53 and 6.24%, respectively. A 10% decrease in the fishing mortality rate of age group II resulted in increases in cumulative catch, yield and production of 2.70, 2.76 and 5.57%, respectively.

Management Applications

Model III was developed for the purpose of evaluating alternative management strategies. In this section the utility of Model III is demonstrated by evaluating the effects of implementation of a 14-inch minimum length limit.

Using the average growth rates used in nominal simulation of Model III and assuming a standard deviation (σ) of 25 (a reasonable value based on data for largemouth bass from Lake Carl Blackwell), a 14-inch (355.6 mm) minimum length limit would effectively eliminate all fishing mortality on age groups I and II. At the start of the simulation year the mean length of age group III is 346 mm (13.6 in) and therefore includes some members under the limit and some over. The mean length of this age group during the year as determined by integration of the exponential growth function would be 377.04 mm. Based on a normal curve with σ = 25, an average of 80.44% of the age group would be above the minimum size limit during the year. The fishing mortality rate (F) for this age group would be (0.8044) x (0.45814) =

0.36853. It is assumed that under-sized fish that are caught and released do not suffer any additional mortality.

A 10-year simulation of the implementation of a 14-inch minimum length limit was run using the same parameters used in nominal simulation (Appendix G) except for altered fishing mortality rates for age groups I, II, and III. The implementation of this regulation resulted in a 37.6% decrease in the number of fish removed over the 10 years when compared with the nominal simulation. However, the cumulative yield in weight and gross production increased 89.9 and 340.1%, respectively, over the nominal simulation. The numbers of under-sized fish that were caught and released during the 10-year simulation were 22181, 11101, and 919, for age groups I, II, and III, respectively. Total weights of these fish were 1975.0, 3241.6, and 527.7 kg, for age groups I, II, and III, respectively.

This example has been simplified by leaving all other parameters constant to show the effect of the length limit. In a more realistic application, the fishery biologist would input population parameters for largemouth bass populations under his jurisdiction, water level and water level fluctuation data for predicting year-class strength, and could program relationships between density, water level and growth. Several simulation trials could then be made with and without various minimum length limits to determine which length limit would produce the optimum yield. In the same manner, Model III can be used to evaluate different management schemes for water level manipulation, or supplemental stocking of fingerling bass.

A possible deficiency of Model III is the lack of compensatory mechanisms for population control. At the low levels of biomass of largemouth bass in Lake Carl Blackwell these compensatory mechanisms may be inoperable. However, at extremely high levels of biomass, I would hypothesize that the population is constrained by decreased growth rates or fecundity or by increased natural or fishing mortality. These relationships need to be quantified and programmed into Model III so that it will become even more generally applicable.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

Management of largemouth bass fisheries in large reservoirs is complicated by reservoir size, multispecies interactions and a fluctuating environment. The objective of this research was to develop a computer simulation model of the largemouth bass population of Lake Carl Blackwell which would predict year-class strength, production and yield and serve as a tool for management of largemouth bass fisheries in large reservoirs.

Model I was developed to simulate population trends based on an equilibrium (stable) population. Model I is an age-structured deterministic model with numbers as the only state vector, and is similar to the Leslie matrix model (Leslie 1945). Constant age-specific fecundities and survival rates are required input. Young-of-the-year survival is estimated indirectly assuming an equilibrium population and using age-specific fecundity and survival data. Sensitivity analysis of this model indicates that density of bass is most sensitive to variations in survival from egg to age I.

Since Model I output was most sensitive to variations in survival from egg to age I, data on year-class strength of largemouth bass in Lake Carl Blackwell was analyzed by simple linear and multiple linear regression to develop a predictive equation to incorporate into Model II. 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 86.76% of the variation in mortality rate from egg to age I of largemouth bass in Lake Carl Blackwell. Model II predictions of number of age I recruits agree closely with population estimates from Lake Carl Blackwell. This model 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, future population size and structure.

Model III is an extension of the previous models to allow prediction of production and yield. Survival from egg to age I is calculated as in Model II. Instantaneous rates of growth, fishing and natural mortality by age group, and exponents and constants in exponential length-fecundity and length-weight relationships are required input as well as proportion of each age group that are mature and female. Output from the computer simulation, presented by age group, consists of number at start of year, mean number during year, mean total length, mean weight per fish, biomass at start of year, mean biomass during year, yield in weight and numbers, and gross and net production.

Parameters to be used in Model III are derived for the length-fecundity relationship using data from a small lake in northern Michigan (Clady 1970), large reservoirs in Tennessee (Coomer 1976) and Arkansas (Olmsted 1974), and a stream in Maine (Kelley 1962). The resulting predictive equation was: $\text{Fecundity} = 0.00045091\ \text{Length}^{2.941}$ where length is in millimeters.

Growth increment data was compiled for largemouth bass from Lake Carl Blackwell for 1959 through 1976. Correlation analysis was performed with several physical and biological parameters. There were significant negative correlations between average annual water levels and the second and third year growth increments. Lack of consistent significant correlations, however, prevented the incorporation of these findings into the computer simulation model.

A von Bertalanffy equation was fitted to data for largemouth bass from Lake Carl Blackwell and annual instantaneous rates of growth computed from the fitted equation.

Model III predictions of year-class strength also agree closely with population estimates. Predictions of production and yield compare favorably with estimates by Zweiacker (1972) and Shirley (1975). Sensitivity analysis of Model III indicates that production, yield and catch (numbers) are most sensitive to variation in mortality rate from egg to age I. Catch was more sensitive to variations in growth rate than to variations in mortality rates or initial population size of age I and older bass, presumably because of increased fecundity. Yield and production were much more sensitive to variations in growth rates and the exponent in the length-weight relationship than to variations in mortality rates or initial population size of age I and older bass.

The management potential of Model III is demonstrated by simulating the population and fishery with a 14-inch minimum length limit. Model III should also be useful for evaluating different management schemes for water level manipulation or supplemental stockings of fingerling bass.

This research was intended to be a beginning rather than an end of an attempt to develop a methodology for predicting the consequences of proposed management strategies prior to implementation. I recommend that three areas need to be investigated if we are to continue to build on our predictive capabilities.

(1) The relationships between density, growth and fishing and natural mortality.

(2) The dynamics of prey populations in reservoirs and their relationships with the predator stocks. Simultaneous simulations of predator and prey populations in reservoirs would be extremely useful in the management and understanding of these ecological systems.

(3) Testing the validity of Model III predictions of year-class strength, production and yield of largemouth bass populations in other reservoirs.

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APPENDICES

APPENDIX A

MODEL I COMPUTER PROGRAM LISTING

```
      C*****************************************************************************
      C
      C  SIMULATION MODEL OF LARGEMOUTH BASS POPULATION DYNAMICS
      C
      C*****************************************************************************
      C
      C  PROGRAMMER..
      C     DONALD J ORTH          OCTOBER 1976
      C
      C  PROGRAM DESCRIPTION..
      C      THIS PROGRAM SIMULATES THE POPULATION DYNAMICS OF LARGEMOUTH
      C      BASS BASED UPON A DETERMINISTIC AGE-STRUCTURED MODEL
      C      AGE-SPECIFIC FECUNDITY AND SURVIVAL RATES ARE REQUIRED
      C      YOUNG-OF-THE-YEAR SURVIVAL IS ESTIMATED BY THE METHOD OF
      C      VAUGHAN AND SAILA (1976) TRANS AM FISH SOC
      C
      C  PROGRAM INPUT..
      C      A SINGLE SIMULATION RUN REQUIRES 5 DATA CARDS AND SEVERAL
      C      OF THESE DATA SETS MAY BE PROCESSED AT THE SAME TIME
      C      DATA IS ARRANGED ON CARDS AS FOLLOWS:
      C        CARD 1  K       INTEGER  COLS 1-2
      C                NOYR    INTEGER  COLS 3-4
      C                IYEAR   INTEGER  COLS 5-8
      C        CARD 2  FECND   REAL  ARRANGED IN 6-COLUMN FIELDS
      C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
      C        CARD 3  S       REAL  ARRANGED IN 6-COLUMN FIELDS
      C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
      C        CARD 4  N       REAL  ARRANGED IN 6-COLUMN FIELDS
      C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
      C        CARD 5  MORE  INTEGER  COL 1   0 IF END OF DATA
      C                                       1 IF ANOTHER DATA SET TO PROCESS
      C
      C  PROGRAM OUTPUT..
      C      THE PROGRAM WILL LIST THE INPUT DATA ALONG WITH THE YOY SURVIVAL
      C      RATE COMPUTED BY THE PROGRAM.  FOR EACH YEAR OF SIMULATION THE
      C      PROGRAM WILL LIST TOTAL POPULATION NUMBER, NUMBER OF EGGS PRODUCED,
      C      AND NUMBER OF FISH IN EACH AGE GROUP.
      C
      C  DESCRIPTION OF VARIABLES..
      C      FECND  - ARRAY CONTAINING ESTIMATE OF NUMBER OF EGGS
      C               PRODUCED PER INDIVIDUAL OF EACH AGE GROUP
      C      I      - SUBSCRIPT DENOTING AGE GROUP
      C      IYEAR  - LABEL FOR YEAR OF SIMULATION
      C      K      - NUMBER OF AGE GROUPS TO BE CARRIED IN SIMULATION
      C               NOT COUNTING AGE 0     MAXIMUM IS 13
      C      LAST   - LAST YEAR THE SIMULATION WILL RUN
      C      MORE   - INTEGER READ FROM DATA CARD 5 TO DENOTE END OF DATA SET
      C      N      - ARRAY CONTAINING ESTIMATE OF NUMBER OF FISH
      C               IN EACH AGE GROUP
      C      NOYR   - NUMBER OF YEARS THE SIMULATION WILL RUN
      C               MAXIMUM IS 99
      C      NTOT   - TOTAL NUMBER OF FISH IN AGE GROUPS 1 TO K
      C      S      - ARRAY CONTAINING AGE-SPECIFIC SURVIVAL RATES
      C
      C  SUBROUTINES..
      C      EGG
      C      YOYSRV
      C
      C
0001        COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG
0002        DIMENSION LSTYRN(13)
0003        REAL N, NTOT
0004        DATA IN, LP / 5, 6 /
      C
      C          READ INPUT DATA
0005      1 READ (IN, 1000) K, NOYR, IYEAR
0006   1000 FORMAT (2I2, I4)
0007        LAST = IYEAR + NOYR
0008        READ (IN, 1010) FECND, S, N
0009   1010 FORMAT (13F6.0)
      C          WRITE HEADINGS
0010        WRITE (LP, 1020)
0011   1020 FORMAT (1H1, 129('*'),/,130('*'),/,46('*'),38X,46('*'),/,
           $            46('*'),' LARGEMOUTH BASS POPULATION SIMULATOR ',
           $            46('*'),/,46('*'),38X,46('*'),/,130('*'),/,
           $            130('*'))
0012        WRITE (LP, 1025) NOYR, K
0013   1025 FORMAT(1H0,'SIMULATION WILL RUN FOR ',I2,' YEARS ',
           $            'AND WILL CARRY ',I2,' AGE GROUPS NOT INCLUDING AGE 0')
      C          CALL SUBROUTINE TO COMPUTE SURVIVAL OF YOY
0014        CALL YOYSRV(SURV)
```

```
          WRITE (LP, 1030) FECND, S, N, SURV
     1030 FORMAT (1H0,'AGE-SPECIFIC',/,1X,'FECUNDITY',1X,13F8.0,//,
     $              1X,'AGE-SPECIFIC',/,1X,'SURVIVAL RATES',1X,13F8.5,//,
     $              1X,'INITIAL',/,1X,'AGE STRUCTURE',1X,13F8.0,//,
     $              1X,'YOUNG OF YEAR SURVIVAL = ',F8.6,//,1X, 130('='))
          WRITE (LP, 2000)
     2000 FORMAT(1H0,7X,'TOTAL',9X,'NUMBER',42X,'NUMBER PER AGE GROUP',/,
     $          7X,'POPULATION',4X,'OF EGGS',/,
     $          1X,'YEAR',2X,'NUMBER',8X,'PRODUCED',6X,'N1',8X,'N2',
     $          6X,'N3',5X,'N4',5X,'N5',5X,'N6',5X,'N7',
     $          5X,'N8',5X,'N9',4X,'N10',4X,'N11',4X,'N12',
     $          4X,'N13',/,1X,4('='),2X,10('='),4X,8('='),6X,2('='),
     $          8X,2('='),6X,2('='),6(5X,2('=')),4(4X,3('=')))
C
C          CALCULATE TOTAL POPULATION
        5 NTOT=0.0
          DO 10 I=1,K
            NTOT=NTOT+N(I)
       10 CONTINUE
C          CALL SUBROUTINE TO COMPUTE TOTAL EGG PRODUCTION
          CALL EGG
C          PRINT OUTPUT FOR START OF YEAR
          WRITE (LP, 2010) IYEAR, NTOT, TOTEGG, (N(I),I=1,K)
     2010 FORMAT(1H0, I4, F12.0, F12.0, F10.0, F9.0, F8.0, 10F7.0)
C          CHECK FOR END OF SIMULATION
          IF (IYEAR .GE. LAST) GO TO 30
C          GENERATE NEW AGE DISTRIBUTION FOR IYEAR+1
          DO 15 I=1,K
            LSTYRN(I) = N(I)
       15 CONTINUE
          DO 20 I=1,K
            N(I+1) = LSTYRN(I)*S(I)
       20 CONTINUE
          N(1) = TOTEGG*SURV
          IYEAR = IYEAR + 1
          GO TO 5
       30 WRITE (LP, 3000)
     3000 FORMAT (1H0,56('*'),' END OF SIMULATION ',54('*'))
          READ (IN, 4000) MORE
     4000 FORMAT (I1)
          IF (MORE .EQ. 1) GO TO 1
          STOP
          END

C
C##############################################################################
C
          SUBROUTINE EGG
C
C##############################################################################
C
          COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG
          REAL N
          TOTEGG=0.0
          DO 99 I=1,K
            TOTEGG = TOTEGG + (FECND(I)*N(I))
       99 CONTINUE
          RETURN
          END
C
C##############################################################################
C
          SUBROUTINE YOYSRV(SURV)
C
C##############################################################################
C
C          THIS SUBROUTINE CALCULATES SURVIVAL RATE FOR AGE 0
C          BY THE METHOD OF VAUGHAN AND SAILA (1976) TRANS AM FISH SOC
C
          COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG
          SUM=0.0
          PROD=1.0
          L=K-1
C          ENTER DO LOOP TO CALCULATE SUM OF FECUNDITY TIMES
C          CUMULATIVE SURVIVAL
          DO 10 I=1,L
            PROD = PROD*S(I)
            SUM = SUM + FECND(I+1)*PROD
       10 CONTINUE
          SURV = 1.0/SUM
          RETURN
          END
C
C******************************************************************************
```

APPENDIX B

MODEL I SAMPLE OUTPUT

LARGEMOUTH BASS POPULATION SIMULATOR

SIMULATION WILL RUN FOR 40 YEARS AND WILL CARRY 8 AGE GROUPS NOT INCLUDING AGE 0

AGE-SPECIFIC FECUNDITY	0.	0.	9335.	4350.	5750.	13610.	13610.	13610.	0.	0.	0.	0.	0.
AGE-SPECIFIC SURVIVAL RATES	0.67600	0.61600	0.65900	0.56000	0.37500	0.19700	0.07100	0.0	0.0	0.0	0.0	0.0	0.0
INITIAL AGE STRUCTURE	10000.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.

YOUNG OF YEAR SURVIVAL = 0.000145

YEAR	TOTAL POPULATION NUMBER	NUMBER OF EGGS PRODUCED	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	N13
2000	10000.	0.	10000.	0.	0.	0.	0.	0.	0.	0.					
2001	6760.	0.	0.	6760.	0.	0.	0.	0.	0.	0.					
2002	4164.	38866672.	0.	0.	4164.	0.	0.	0.	0.	0.					
2003	8365.	11933862.	5621.	0.	0.	2743.	0.	0.	0.	0.					
2004	7062.	8832459.	1726.	3800.	0.	0.	1536.	0.	0.	0.					
2005	5360.	29684976.	1277.	1166.	2340.	0.	0.	576.	0.	0.					
2006	7530.	14957232.	4293.	863.	718.	1542.	0.	0.	113.	0.					
2007	6942.	12095243.	2163.	2902.	532.	473.	864.	0.	0.	8.					
2008	5938.	24137312.	1749.	1462.	1788.	350.	265.	324.	0.	0.					
2009	7110.	16866912.	3491.	1182.	901.	1178.	195.	99.	64.	0.					
2010	6876.	14488389.	2439.	2359.	728.	593.	659.	73.	20.	4.					
2011	6272.	21138896.	2095.	1649.	1453.	480.	332.	247.	14.	1.					
2012	6889.	17554416.	3057.	1416.	1015.	958.	268.	125.	49.	1.					
2013	6811.	15880346.	2539.	2067.	872.	669.	536.	101.	24.	3.					
2014	6456.	19552720.	2297.	1716.	1273.	575.	374.	201.	20.	2.					
2015	6777.	17819888.	2828.	1552.	1056.	838.	321.	140.	39.	1.					
2016	6760.	16701449.	2577.	1911.	956.	696.	469.	120.	28.	3.					
2017	6555.	18708816.	2415.	1742.	1177.	630.	389.	176.	24.	2.					
2018	6722.	17896544.	2706.	1633.	1073.	776.	353.	146.	34.	2.					
2019	6726.	17174128.	2588.	1829.	1005.	707.	434.	132.	29.	2.					
2020	6608.	18265152.	2484.	1749.	1126.	662.	396.	163.	26.	2.					
2021	6692.	17892288.	2642.	1679.	1077.	742.	371.	148.	32.	2.					
2022	6702.	17440848.	2588.	1785.	1034.	710.	416.	139.	29.	2.					
2023	6633.	18024688.	2522.	1749.	1100.	681.	397.	156.	27.	2.					
2024	6675.	17859504.	2607.	1705.	1077.	724.	381.	149.	31.	2.					
2025	6683.	17579600.	2583.	1762.	1050.	709.	405.	143.	29.	2.					
2026	6643.	17892224.	2542.	1745.	1085.	691.	397.	152.	28.	2.					
2027	6663.	17823952.	2588.	1718.	1075.	714.	387.	149.	30.	2.					
2028	6668.	17651840.	2578.	1749.	1058.	708.	400.	145.	29.	2.					
2029	6645.	17811568.	2553.	1742.	1077.	697.	396.	150.	28.	2.					
2030	6653.	17788496.	2576.	1725.	1073.	709.	390.	148.	29.	2.					
2031	6658.	17693536.	2573.	1741.	1063.	707.	397.	146.	29.	2.					
2032	6646.	17777936.	2559.	1739.	1072.	700.	396.	149.	29.	2.					
2033	6648.	17757776.	2571.	1729.	1071.	706.	391.	148.	29.	2.					
2034	6650.	17703376.	2568.	1738.	1065.	705.	395.	147.	29.	2.					
2035	6642.	17746880.	2560.	1736.	1070.	702.	395.	148.	29.	2.					
2036	6642.	17733264.	2567.	1731.	1069.	704.	393.	148.	29.	2.					
2037	6641.	17699392.	2565.	1735.	1066.	704.	394.	147.	29.	2.					
2038	6635.	17719824.	2560.	1733.	1068.	702.	394.	148.	29.	2.					
2039	6635.	17711120.	2563.	1730.	1068.	704.	393.	147.	29.	2.					
2040	6633.	17686592.	2561.	1732.	1065.	703.	394.	147.	29.	2.					

END OF SIMULATION

APPENDIX C

MODEL II COMPUTER PROGRAM LISTING

```
C*********************************************************************
C
C   SIMULATION MODEL OF LARGEMOUTH BASS POPULATION DYNAMICS - MODEL II
C
C*********************************************************************
C
C   PROGRAMMER..
C      DONALD J ORTH              FEBRUARY 1977
C
C   PROGRAM DESCRIPTION..
C      THIS PROGRAM SIMULATES THE POPULATION DYNAMICS OF LARGEMOUTH
C      BASS BASED UPON A DETERMINISTIC AGE-STRUCTURED MODEL.
C      AGE-SPECIFIC FECUNDITY AND SURVIVAL RATES ARE REQUIRED.
C      YOUNG-OF-THE-YEAR SURVIVAL IS ESTIMATED BY A MULTIPLE
C      REGRESSION EQUATION USING WATER LEVEL DURING SPAWNING
C      AND WATER LEVEL FLUCTUATION SINCE THE END OF THE PREVIOUS
C      GROWING SEASON.
C
C   PROGRAM INPUT..
C      A SIMULATION RUN REQUIRES 8 DATA CARDS PLUS A DATA CARD FOR EACH
C      YEAR OF THE SIMULATION.  SEVERAL DATA SETS MAY BE PROCESSED AT
C      THE SAME TIME.  DATA IS ARRANGED ON CARDS AS FOLLOWS:
C        CARD 1  K       INTEGER  COLS 1-2
C                NOYR    INTEGER  COLS 3-4
C        CARD 2  TITLE   ALPHANUMERIC  COLS 1-80
C        CARD 3  FECND   REAL  ARRANGED IN 6-COLUMN FIELDS
C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
C        CARD 4  MATURE REAL ARRANGED IN 5-COLUMN FIELDS
C                        PUNCHED WITH DECIMAL
C        CARD 5  PERFEM REAL  ARRANGED IN 5-COLUMN FIELDS
C                        PUNCHED WITH DECIMALS
C        CARD 6  S       REAL  ARRANGED IN 6-COLUMN FIELDS
C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
C        CARD 7  N       REAL  ARRANGED IN 5-COLUMN FIELDS
C                        RIGHT-JUSTIFIED OR PUNCHED WITH DECIMALS
C        CARD 8  IYEAR   INTEGER  COLS 1-4
C                FLUCT   REAL      COLS 6-11   IF UNAVAILABLE ENTER BLANKS
C                        AND AVERAGE YOY SURVIVAL WILL BE USED
C                WATLEV REAL      COLS 13-18  IF UNAVAILABLE ENTER BLANKS
C                        AND AVERAGE YOY SURVIVAL WILL BE USED
C                MUST HAVE AS MANY CARD 8'S AS YOU HAVE YEARS OF SIMULATION
C                LAST CARD 8 MUST HAVE ZERO'S IN COLS 1-4
C        CARD 9  MORE    INTEGER  COL 1    0 IF END OF DATA
C                                           1 IF ANOTHER DATA SET TO PROCESS
C
C   PROGRAM OUTPUT..
C      THE PROGRAM WILL LIST THE INPUT DATA ALONG WITH THE YOY SURVIVAL
C      RATE COMPUTED BY THE PROGRAM.  FOR EACH YEAR OF SIMULATION THE
C      PROGRAM WILL LIST TOTAL POPULATION NUMBER, NUMBER OF EGGS PRODUCED,
C      AND NUMBER OF FISH IN EACH AGE GROUP.
C
C   DESCRIPTION OF VARIABLES..
C      AVGSO  - AVERAGE SURVIVAL RATE OF AGE 0
C      AVGZO  - AVERAGE INSTANTANEOUS MORTALITY RATE OF AGE 0
C      FECND  - ARRAY CONTAINING ESTIMATE OF NUMBER OF EGGS
C               PRODUCED PER FEMALE OF EACH AGE GROUP
C      FLUCT  - WATER LEVEL FLUCTUATION FROM END OF PREVIOUS GROWING
C               SEASON TO SPAWNING SEASON OF IYEAR (FEET)
C      I      - SUBSCRIPT DENOTING AGE GROUP
C      IN     - I/O UNIT NUMBER FOR CARD READER
C      IYEAR  - LABEL FOR YEAR OF SIMULATION
C      K      - NUMBER OF AGE GROUPS TO BE CARRIED IN SIMULATION
C               NOT COUNTING AGE 0     MAXIMUM IS 13
C      LSTYRN - ARRAY CONTAINING NUMBER OF FISH AT START OF LAST YEAR IN
C               EACH AGE GROUP
C      LP     - I/O UNIT NUMBER FOR LINE PRINTER
C      MATURE - ARRAY CONTAINING PERCENT THAT ARE MATURE BY AGE GROUP
C      MORE   - INTEGER READ FROM DATA CARD 5 TO DENOTE END OF DATA SET
C      N      - ARRAY CONTAINING ESTIMATE OF NUMBER OF FISH
C               IN EACH AGE GROUP
C      NOYR   - NUMBER OF YEARS THE SIMULATION WILL RUN
C               MAXIMUM IS 99
C      NTOT   - TOTAL NUMBER OF FISH IN AGE GROUPS 1 TO K
C      PERFEM - ARRAY CONTAINING PERCENT THAT ARE FEMALE BY AGE GROUP
C      S      - ARRAY CONTAINING AGE-SPECIFIC SURVIVAL RATES
C      SURV   - SURVIVAL OF AGE 0 BASED ON ENVIRONMENTAL CONDITIONS FOR
C               SIMULATION YEAR
C      TITLE  - TITLE FOR SIMULATION YEAR
C      TOTEGG - TOTAL NUMBER OF EGGS PRODUCED AT START OF SIMULATION YEAR
C      WATLEV - MEAN WATER LEVEL DURING SPAWNING (FEET ABOVE MSL)
C
C   SUBROUTINES..
C      EGG
C      YOYSRV
C      EQUILS
C
C
```

```
      COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG,
     $           MATURE(13), PERFEM(13)
      DIMENSION LSTYRN(13), TITLE(20)
      REAL N, NTOT, MATURE
      DATA IN, LP / 5, 6 /
C
C          READ INPUT DATA
    1 READ (IN, 1000) K, NOYR, TITLE
 1000 FORMAT (2I2,/,20A4)
      READ (IN, 1010) FECND, MATURE, PERFEM, S, N
 1010 FORMAT (13F6.0)
C
C          WRITE HEADINGS AND TITLE
      WRITE (LP, 1020) TITLE
 1020 FORMAT (1H1, 129('*'),/,130('*'),/,46('*'),38X,46('*'),/,
     $           46('*'),' LARGEMOUTH BASS POPULATION SIMULATOR ',
     $           46('*'),/,46('*'),38X,46('*'),/,130('*'),/,
     $           130('*'),//,1X,24('*'),1X,20A4,1X,23('*'))
      WRITE (LP, 1025) NOYR, K
 1025 FORMAT(1H0,35X,'SIMULATION WILL RUN FOR ',I2,' YEARS ',
     $          'AND WILL CARRY ',I2,' AGE GROUPS')
C
C          CALCULATE AVERAGE MORTALITY OF AGE ZERO FISH
      CALL EQUILS (AVGZO)
      AVGSO = EXP(-AVGZO)
C
C          WRITE POPULATION PARAMETERS AND HEADINGS
      WRITE (LP, 1030) FECND, MATURE, PERFEM, S, AVGSO, N
 1030 FORMAT (1H0,'AGE-SPECIFIC',/,1X,'FECUNDITY',1X,13F8.0,//,
     $           1X,'PROPORTION',/,1X,'MATURE',7X,13F8.3,//,
     $           1X,'PROPORTION',/,1X,'FEMALE',7X,13F8.3,//,
     $            1X,'AGE-SPECIFIC',/,1X,'SURVIVAL RATES',1X,13F8.5,//,
     $            1X,'EQUILIBRIUM',/,1X,'YOY SURVIVAL = ',F10.8,//,
     $            1X,'INITIAL',/,1X,'AGE STRUCTURE',1X,13F8.0,//,
     $            130('='))
      WRITE (LP, 2000)
 2000 FORMAT (1H0,7X,'TOTAL',9X,'NUMBER',42X,'NUMBER PER AGE GROUP',/,
     $         7X,'POPULATION',4X,'OF EGGS',/,
     $         1X,'YEAR',2X,'NUMBER',8X,'PRODUCED',6X,'N1',8X,'N2',
     $         6X,'N3',5X,'N4',5X,'N5',5X,'N6',5X,'N7',
     $         5X,'N8',5X,'N9',4X,'N10',4X,'N11',4X,'N12',
     $         4X,'N13',/,1X,4('='),2X,10('='),4X,8('='),5X,2('='),
     $         8X,2('='),6X,2('='),6(5X,2('=')),4(4X,3('=')))
C
C          CALCULATE TOTAL POPULATION
    5 NTOT=0.0
      DO 10 I=1,K
        NTOT=NTOT+N(I)
   10 CONTINUE
C
C          CALL SUBROUTINE TO COMPUTE TOTAL EGG PRODUCTION
      CALL EGG
C
C          CHECK FOR END OF SIMULATION
      READ (IN, 2015) IYEAR, FLUCT, WATLEV
 2015 FORMAT (I4,1X,F6.0,1X,F6.0)
      IF (IYEAR .EQ. 0 ) GO TO 30
C
C          PRINT OUTPUT FOR START OF YEAR
      WRITE (LP, 2010) IYEAR, NTOT, TOTEGG, (N(I),I=1,K)
 2010 FORMAT(1H0, I4, F12.0, F12.0, F10.0, F9.0, F8.0, 10F7.0)
C
C          CALL SUBROUTINE TO COMPUTE SURVIVAL OF YOY
      CALL YOYSRV (FLUCT, WATLEV, SURV, AVGZO)
      WRITE (LP, 2020) SURV
 2020 FORMAT (105X,'YOY SURVIVAL = ',F10.3)
C
C          GENERATE NEW AGE DISTRIBUTION FOR IYEAR+1
      DO 15 I=1,K
        LSTYRN(I) = N(I)
   15 CONTINUE
      DO 20 I=1,K
        N(I+1) = LSTYRN(I)*S(I)
   20 CONTINUE
      N(1) = TOTEGG*SURV
      GO TO 5
   30 WRITE (LP, 3000)
 3000 FORMAT (1H0,56('*'),' END OF SIMULATION ',54('*'))
      READ (IN, 4000) MORE
 4000 FORMAT (I1)
      IF (MORE .EQ. 1) GO TO 1
      STOP
      END
```

```
C
C###############################################################################
      SUBROUTINE EGG
C
C###############################################################################
C
C           THIS SUBROUTINE CALCULATES TOTAL EGG PRODUCTION FOR SIMULATION YEAR
C
      COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG,
     $               MATURE(13), PERFEM(13)
      REAL N, MATURE
      TOTEGG=0.0
      DO 99 I=1,K
        TOTEGG = TOTEGG + (FECND(I)*N(I)*MATURE(I)*PERFEM(I))
   99 CONTINUE
      RETURN
      END

C
C###############################################################################
      SUBROUTINE EQUILS (AVGZO)
C
C###############################################################################
C
C           THIS SUBROUTINE CALCULATES SURVIVAL RATE FOR AGE 0 BASED ON
C           THE METHOD OF VAUGHAN AND SAILA 1976 TRANS. AM. FISH. SOC.
C
      COMMON / YOY / K, N(13), NTOT, S(13), IYEAR, FECND(13), TOTEGG,
     $               MATURE(13), PERFEM(13)
      REAL N, NTOT, MATURE
      SUM = 0.0
      PROD = 1.0
      L = K - 1
C
C  ENTER DO LOOP TO CALCULATE SUM OF FECUNDITY TIMES CUMULATIVE SURVIVAL
      DO 10 I=1,L
        PROD = PROD * S(I)
        SUM = SUM + FECND(I+1)*MATURE(I+1)*PERFEM(I+1)*PROD
   10 CONTINUE
      AVGZO = -(ALOG(1.0/SUM))
      RETURN
      END

C
C###############################################################################
      SUBROUTINE YOYSRV (FLUCT, WATLEV, SURV, AVGZO)
C
C###############################################################################
C
C           THIS SUBROUTINE CALCULATES YOY SURVIVAL BASED ON
C           ENVIRONMENTAL CONDITIONS DURING IYEAR
C
      IF (WATLEV .EQ. 0.0) Z = AVGZO
      IF(WATLEV .NE. 0.0) Z = AVGZO + 221.86241513
     $                              -   0.29531602 * FLUCT
     $                              -   0.23642939 * WATLEV
      SURV = EXP(-Z)
      RETURN
      END
C
C*******************************************************************************
```

APPENDIX D

MODEL II SAMPLE OUTPUT

LARGEMOUTH BASS POPULATION SIMULATOR

LAKE CARL BLACKWELL LARGEMOUTH BASS POPULATION 1968 - 1992 ** MODEL II

SIMULATION WILL RUN FOR 25 YEARS AND WILL CARRY 8 AGE GROUPS

AGE-SPECIFIC FECUNDITY	0.	7628.	18487.	28917.	37665.	43929.	49613.	58527.	0.	0.	0.	0.	0.
PROPORTION MATURE	0.0	0.0	1.000	1.000	1.000	1.000	1.000	1.000	0.0	0.0	0.0	0.0	0.0
PROPORTION FEMALE	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.0	0.0	0.0	0.0	0.0
AGE-SPECIFIC SURVIVAL RATES	0.67600	0.61600	0.65900	0.56000	0.37500	0.19700	0.07100	0.0	0.0	0.0	0.0	0.0	0.0

EQUILIBRIUM YOY SURVIVAL = 0.00008142

INITIAL AGE STRUCTURE	1151.	305.	192.	175.	206.	78.	24.	0.	0.	0.	0.	0.	0.

YEAR	TOTAL POPULATION NUMBER	NUMBER OF EGGS PRODUCED	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	N13	
1968	2131.	10493071.	1151.	305.	192.	175.	206.	78.	24.	0.						YOY SURVIVAL = 0.00004105
1969	1716.	7539454.	431.	778.	188.	127.	98.	77.	15.	2.						YOY SURVIVAL = 0.00007535
1970	1585.	8755161.	568.	291.	479.	123.	71.	37.	15.	1.						YOY SURVIVAL = 0.00003523
1971	1290.	8296082.	308.	384.	179.	316.	65.	26.	7.	1.						YOY SURVIVAL = 0.00000680
1972	825.	7900557.	56.	208.	236.	117.	176.	26.	5.	0.						YOY SURVIVAL = 0.00000309
1973	482.	6235566.	24.	38.	128.	155.	66.	66.	5.	0.						YOY SURVIVAL = 0.01074390
1974	67285.	3920622.	67038.	16.	23.	84.	86.	24.	13.	0.						YOY SURVIVAL = 0.00096530
1975	49211.	2039253.	3785.	45317.	10.	14.	47.	32.	5.	1.						YOY SURVIVAL = 0.00046601
1976	31462.	258819856.	950.	2558.	27915.	6.	8.	18.	6.	0.						YOY SURVIVAL = 0.00011868
1977	51339.	280742912.	30717.	642.	1575.	18396.	3.	3.	3.	0.						YOY SURVIVAL = 0.00003389
1978	42013.	212692128.	9513.	20764.	395.	1038.	10301.	1.	0.	0.						YOY SURVIVAL = 0.00008142
1979	41243.	217776224.	17318.	6431.	12751.	260.	581.	3863.	0.	0.						YOY SURVIVAL = 0.00008142
1980	42951.	184869808.	17732.	11706.	3961.	8429.	146.	218.	761.	0.						YOY SURVIVAL 0.00008142
1981	41730.	157102528.	15052.	11986.	7211.	2610.	4720.	54.	43.	54.						YOY SURVIVAL = 0.00008142
1982	41602.	203681232.	16048.	10175.	7383.	4751.	1461.	1770.	11.	3.						YOY SURVIVAL = 0.00008142
1983	42123.	199087104.	16584.	10848.	6268.	4865.	2661.	548.	348.	1.						YOY SURVIVAL = 0.00008142
1984	42087.	198094304.	16210.	11210.	6682.	4130.	2724.	998.	108.	25.						YOY SURVIVAL = 0.00008142
1985	41533.	198573264.	16129.	10557.	6905.	4403.	2312.	1022.	196.	8.						YOY SURVIVAL = 0.00008142
1986	41519.	199055824.	16168.	10903.	6750.	4550.	2466.	867.	201.	14.						YOY SURVIVAL = 0.00008142
1987	41958.	199330240.	16207.	10930.	6716.	4448.	2548.	924.	171.	14.						YOY SURVIVAL = 0.00008142
1988	41984.	198975392.	16230.	10956.	6732.	4426.	2490.	956.	182.	12.						YOY SURVIVAL = 0.00008142
1989	41965.	198742544.	16201.	10971.	6748.	4436.	2478.	934.	188.	13.						YOY SURVIVAL = 0.00008142
1990	41948.	198902528.	16182.	10951.	6758.	4447.	2484.	929.	184.	13.						YOY SURVIVAL = 0.00008142
1991	41949.	199005008.	16195.	10936.	6746.	4453.	2490.	932.	183.	13.						YOY SURVIVAL = 0.00008142
1992	41956.	198930912.	16203.	10947.	6738.	4445.	2453.	933.	183.	13.						YOY SURVIVAL = 0.00008142

END OF SIMULATION

APPENDIX E

MODEL III COMPUTER PROGRAM LISTING

```
C*****************************************************************************
C                                                                            *
C  SIMULATION MODEL OF LARGEMOUTH BASS POPULATION DYNAMICS - MODEL III       *
C                                                                            *
C*****************************************************************************
C                                                                            *
C  PROGRAMMER..  DONALD J. ORTH                        MARCH 1977            *
C                OKLA. COOP. FISH. RES. UNIT                                 *
C                STILLWATER, OK  74074                                       *
C                                                                            *
C  PROGRAM DESCRIPTION..                                                     *
C    THIS PROGRAM SIMULATES THE POPULATION, PRODUCTION AND YIELD DYNAMICS    *
C    OF LARGEMOUTH BASS BASED UPON A DETERMINISTIC AGE-STRUCTURED MODEL.     *
C    YOUNG-OF-THE-YEAR SURVIVAL IS ESTIMATED BY A MULTIPLE REGRESSION        *
C    EQUATION USING WATER LEVEL DURING SPAWNING AND WATER LEVEL FLUCTUA-     *
C    TION SINCE THE END OF THE PREVIOUS GROWING SEASON.                      *
C                                                                            *
C  PROGRAM INPUT..                                                           *
C    A SIMULATION RUN REQUIRES 12 DATA CARDS PLUS ONE DATA CARD FOR EACH     *
C    YEAR OF SIMULATION AND ONE TO DENOTE END OF SIMULATION.                 *
C    SEVERAL DATA SETS MAY BE PROCESSED AT THE SAME TIME.                    *
C    DATA IS ARRANGED ON CARDS AS FOLLOWS:                                   *
C     CARD 1   K        COLS 1-2   INTEGER   RIGHT-JUSTIFIED                 *
C              NOYR     COLS 3-4   INTEGER   RIGHT-JUSTIFIED                 *
C     CARD 2   TITLE    COLS 1-80  ALPHANUMERIC                              *
C     CARD 3   AVGTL    6-COLUMN FIELDS BY AGE GROUP, RIGHT-JUSTIFIED OR     *
C                       PUNCHED WITH DECIMALS                                *
C     CARD 4   AVGW     6-COLUMN FIELDS BY AGE GROUP, RIGHT-JUSTIFIED OR     *
C                       PUNCHED WITH DECIMALS                                *
C     CARD 5   N        6-COLUMN FIELDS BY AGE GROUP, RIGHT-JUSTIFIED OR     *
C                       PUNCHED WITH DECIMALS                                *
C     CARD 6   GTL      6-COLUMN FIELDS BY AGE GROUP, PUNCHED WITH DECIMALS *
C     CARD 7   F        6-COLUMN FIELDS BY AGE GROUP, PUNCHED WITH DECIMALS *
C     CARD 8   M        6-COLUMN FIELDS BY AGE GROUP, PUNCHED WITH DECIMALS *
C     CARD 9   FEMALE   6-COLUMN FIELDS BY AGE GROUP, PUNCHED WITH DECIMALS *
C     CARD 10  MATURE   6-COLUMN FIELDS BY AGE GROUP, PUNCHED WITH DECIMALS *
C     CARD 11  AFEC     COLS 1-10  PUNCHED WITH DECIMAL                      *
C              BFEC     COLS 11-20 PUNCHED WITH DECIMAL                      *
C              AWTLEN   COLS 21-30 PUNCHED WITH DECIMAL                      *
C              BWTLEN   COLS 31-40 PUNCHED WITH DECIMAL                      *
C     CARD 12  SIMYR    COLS 1-4   INTEGER                                   *
C              FLUCT    COLS 6-11  PUNCHED WITH DECIMAL.  IF UNAVAILABLE     *
C                       ENTER BLANKS AND AVERAGE RATES WILL BE USED          *
C              WATLEV   COLS 13-18 PUNCHED WITH DECIMAL.  IF UNAVAILABLE     *
C                       ENTER BLANKS AND AVERAGE RATES WILL BE USED          *
C              MUST HAVE AS MANY CARD 12'S AS YOU HAVE YEARS OF SIMULATION *
C              LAST CARD 12 MUST HAVE ZERO'S IN COLS 1-4 TO DENOTE END       *
C              OF SIMULATION                                                 *
C     CARD 13  MORE     COL 1    0 IF END OF DATA                            *
C                                1 IF ANOTHER DATA SET TO PROCESS            *
C                                                                            *
C  PROGRAM OUTPUT..                                                          *
C    THE PROGRAM WILL LIST THE INPUT DATA ALONG WITH THE POPULATION          *
C    PARAMETERS COMPUTED BY THE PROGRAM.  FOR EACH YEAR OF SIMULATION THE    *
C    PROGRAM WILL LIST BY AGE GROUP THE NUMBER AT START OF YEAR, MEAN        *
C    NUMBER DURING YEAR, MEAN TOTAL LENGTH, MEAN WEIGHT PER FISH, BIOMASS    *
C    AT START OF YEAR, MEAN BIOMASS DURING YEAR, YIELD IN WEIGHT AND         *
C    NUMBERS, AND GROSS AND NET PRODUCTION.                                  *
```

```
C                                                                               *
C  DESCRIPTION OF VARIABLES..                                                   *
C     A      = VECTOR OF TOTAL ANNUAL MORTALITY RATES BY AGE GROUP              *
C     AFEC   = PARAMETER 'A' IN FECUNDITY ESTIMATION EQUATION:                  *
C              FECUNDITY = A*(LENGTH**B)                                        *
C     AVGB   = VECTOR OF MEAN BIOMASS DURING YEAR BY AGE GROUP (KG)             *
C     AVGBO  = MEAN BIOMASS OF AGE 0 DURING YEAR                                *
C     AVGN   = VECTOR OF AVERAGE NUMBER OF FISH DURING YEAR BY AGE GROUP        *
C     AVGSO  = EQUILIBRIUM SURVIVAL RATE FOR AGE 0                              *
C     AVGTL  = VECTOR OF AVERAGE TOTAL LENGTH AT START OF YEAR BY               *
C              AGE GROUP (MM)                                                   *
C     AVGZO  = EQUILIBRIUM INSTANTANEOUS MORTALITY RATE FOR AGE 0               *
C     AVGW   = VECTOR OF AVERAGE INIVIDUAL WEIGHTS AT START OF YEAR BY          *
C              AGE GROUP (GRAMS)                                                *
C     AWTLEN = PARAMETER 'A' IN WEIGHT-LENGTH PREDICTION EQUATION:              *
C              WEIGHT = A*(LENGTH**B)                                           *
C     B      = VECTOR OF BIOMASS AT START OF YEAR BY AGE GROUP (KG)             *
C     BFEC   = PARAMETER 'B' IN FECUNDITY ESTIMATION EQUATION:                  *
C              FECUNDITY = A*(LENGTH**B)                                        *
C     BWTLEN = PARAMETER 'B' IN WEIGHT-LENGTH PREDICTION EQUATION:              *
C              WEIGHT = A*(LENGTH**B)                                           *
C     C      = VECTOR OF CATCH IN NUMBERS BY AGE GROUP                          *
C     EGGW   = WEIGHT OF A SINGLE EGG (GRAMS)                                   *
C     EGGB   = TOTAL BIOMASS OF EGGS PRODUCED                                   *
C     F      = VECTOR OF INSTANTANEOUS FISHING MORTALITY RATES BY AGE           *
C              GROUP                                                            *
C     FECND  = VECTOR OF NUMBER OF EGGS PER FEMALE BY AGE GROUP                 *
C     FEMALE = VECTOR OF PROPORTION OF FISH THAT ARE FEMALE BY AGE GROUP        *
C     FLUCT  = WATER LEVEL FLUCTUATION FROM END OF PREVIOUS GROWING             *
C              SEASON TO SPAWNING SEASON OF SIMYR (FEET)                        *
C     GP     = VECTOR OF GROSS PRODUCTION DURING YEAR BY AGE GROUP (KG)         *
C     GTL    = VECTOR OF INSTANTANEOUS RATE OF GROWTH IN LENGTH BY AGE          *
C              GROUP                                                            *
C     GW     = VECTOR OF INSTANTANEOUS RATE OF GROWTH IN WEIGHT BY AGE          *
C              GROUP                                                            *
C     I      = SUBSCRIPT DENOTING AGE GROUP                                     *
C     IN     = I/O UNIT NUMBER FOR CARD READER                                  *
C     K      = NUMBER OF AGE GROUPS TO BE CARRIED IN SIMULATION NOT             *
C              COUNTING AGE 0.  MAXIMUM IS 13.                                  *
C     LP     = I/O UNIT NUMBER FOR LINE PRINTER                                 *
C     LSTYRL = VECTOR OF AVERAGE TOTAL LENGTH BY AGE GROUP FOR START            *
C              OF PREVIOUS YEAR                                                 *
C     LSTYRN = VECTOR OF NUMBER OF FISH BY AGE GROUP FOR START OF               *
C              PREVIOUS YEAR                                                    *
C     LSTYRW = VECTOR OF AVERAGE INDIVIDUAL WEIGHTS BY AGE GROUP FOR            *
C              START OF PREVIOUS YEAR                                           *
C     M      = VECTOR OF INSTANTANEOUS NATURAL MORTALITY RATES BY AGE           *
C              GROUP                                                            *
C     MATURE = VECTOR OF PROPORTION OF INDIVIDUALS THAT ARE SEXUALLY            *
C              MATURE BY AGE GROUP                                              *
C     MORE   = INTEGER READ FROM LAST DATA CARD TO DENOTE END OF DATA SET       *
C              OR NEW DATA SET TO PROCESS                                       *
C     N      = VECTOR OF NUMBER OF FISH AT START OF YEAR BY AGE GROUP           *
C     NOYR   = NUMBER OF YEARS THE SIMULATION WILL RUN.  MAXIMUM IS 99.         *
C     NP     = VECTOR OF NET INCREASE IN BIOMASS BY AGE GROUP DURING YEAR       *
C              (KG)                                                             *
C     SIMYR  = LABEL FOR YEAR OF SIMULATION                                     *
C     TITLE  = TITLE FOR SIMULATION RUN                                         *
```

```
C       TL2     = VECTOR OF AVERAGE TOTAL LENGTHS AT END OF YEAR BY AGE GROUP *
C       TOTAVB = AVERAGE BIOMASS OF STOCK DURING YEAR (KG)                    *
C       TOTAVN = AVERAGE NUMBER IN STOCK DURING YEAR                          *
C       TOTB    = BIOMASS OF STOCK AT START OF YEAR (KG)                      *
C       TOTC    = TOTAL CATCH IN NUMBERS DURING YEAR                          *
C       TOTEGG = TOTAL NUMBER OF EGGS PRODUCED AT START OF YEAR               *
C       TOTGP   = GROSS PRODUCTION OF STOCK DURING YEAR (KG)                  *
C       TOTN    = TOTAL NUMBER IN STOCK AT START OF YEAR                      *
C       TOTNP   = NET INCREASE IN BIOMASS OF STOCK DURING YEAR (KG)           *
C       TOTY    = TOTAL CATCH BY WEIGHT DURING YEAR (KG)                      *
C       WATLEV = MEAN WATER LEVEL DURING SPAWNING (FEET ABOVE MSL)            *
C       W2      = VECTOR OF AVERAGE INDIVIDUAL WEIGHTS AT END OF YEAR         *
C                 BY AGE GROUP                                                *
C       Y       = VECTOR OF CATCH BY WEIGHT DURING YEAR BY AGE GROUP (KG)     *
C       YOYGW  = INSTANTANEOUS RATE OF GROWTH IN WEIGHT OF AGE 0 FROM EGG     *
C                 STAGE TO AGE 1                                              *
C       YOYNP   = NET INCREASE IN BIOMASS OF YOUNG-OF-THE-YEAR FROM EGG       *
C                 STAGE TO AGE 1 (KG)                                         *
C       YOYGP   = GROSS PRODUCTION OF YOUNG-OF-THE-YEAR FROM EGG STAGE TO     *
C                 AGE 1 (KG)                                                  *
C       YOYSRV = SURVIVAL RATE FOR AGE 0 FROM EGG STAGE TO AGE 1              *
C       Z0      = INSTANTANEOUS MORTALITY RATE FOR AGE 0 FROM EGG STAGE TO    *
C                 AGE 1                                                       *
C       Z       = VECTOR OF INSTANTANEOUS TOTAL MORTALITY RATE BY AGE GROUP   *
C                                                                             *
C   SUBROUTINES..                                                             *
C       SUMMUP                                                                *
C       YOYSUB
C                                                                             *
C******************************************************************************
C
C   START
C
      COMMON / YOY / AVGS0, AVGZ0, FECND(13), FEMALE(13), FLUCT, K,
     1               MATURE(13), WATLEV, YOYSRV, Z(13), Z0, IFLAG
      DIMENSION A(13), AVGB(13), AVGN(13), AVGTL(13), AVGW(13), B(13),
     1          C(13), F(13), GP(13), GTL(13), GW(13), LSTYRL(13),
     2          LSTYRN(13), LSTYRW(13), M(13), N(13), NP(13), Y(13),
     3          TITLE(20), TL2(13), W2(13)
      REAL LSTYRL, LSTYRN, LSTYRW, M, MATURE, N, NP
      INTEGER SIMYR
      DATA IN, LP / 5, 6 /
C
C   READ # AGE GROUPS, # SIMULATION YEARS, AND TITLE
C
    1 READ (IN,1010) K, NOYR, TITLE
 1010 FORMAT (2I2,/,20A4)
      IFLAG = 0
C
C   HEADINGS FOR OUTPUT
C
      WRITE (LP,1020) TITLE, NOYR, K
 1020 FORMAT (1H1,129('*'),/,130('*'),/,35('*'),61X,34('*'),/,35('*'),
     1        ' LARGEMOUTH BASS POPULATION, PRODUCTION, AND YIELD',
     2        ' SIMULATOR ',34('*'),/,35('*'),61X,34('*'),/,130('*'),/,
     3        130('*'),//,1X,24('*'),1X,20A4,1X,23('*'),//,39X,
     4        'SIMULATION WILL RUN ',I2,' YEARS AND CARRY ',I2,
     5        ' AGE GROUPS')
```

```
C   READ POPULATION PARAMETERS
C
        READ (IN,1030) AVGTL, AVGW, N, GTL, F, M, FEMALE, MATURE
 1030 FORMAT (13F6.0)
        READ (IN, 1040) AFEC, BFEC, AWTLEN, BWTLEN
 1040 FORMAT (4F10.0)
C
C   READ ENVIRONMENTAL CONDITIONS FOR SIMULATION YEAR
C
      2 READ (IN, 1050) SIMYR, FLUCT, WATLEV
 1050 FORMAT (I4,1X,F6.0,1X,F6.0)
C
C   CHECK FOR END OF SIMULATION
C
        IF (SIMYR .EQ. 0) GO TO 90
C
C   COMPUTE INSTANTANEOUS RATE OF GROWTH IN WEIGHT
C
        DO 10 I=1,K
          GW(I) = BWTLEN*GTL(I)
     10 CONTINUE
C
C   COMPUTE INSTANTANEOUS TOTAL MORTALITY RATES, AVERAGE NUMBER PER AGE
C   GROUP AND BIOMASS PER AGE GROUP
C
        DO 20 I=1,K
          Z(I) = F(I)+M(I)
          A(I) = 1-EXP(-Z(I))
          AVGN(I) = N(I)*A(I)/Z(I)
          B(I) = N(I)*AVGW(I)*0.001
     20 CONTINUE
C
C   COMPUTE FECUNDITY
C
        DO 30 I=1,K
          FECND(I) = AFEC*(AVGTL(I)**BFEC)
     30 CONTINUE
C
C   COMPUTE TOTAL EGG PRODUCTION
C
        TOTEGG = 0.0
        DO 40 I=1,K
          TOTEGG = TOTEGG + (N(I)*FECND(I)*MATURE(I)*FEMALE(I))
     40 CONTINUE
C
C   COMPUTE GROSS AND NET PRODUCTION OF YOUNG-OF-THE-YEAR
C
        EGGW = 0.0012
        EGGB = EGGW*TOTEGG*0.001
        CALL YOYSUB
        YOYGW = ALOG(AVGW(1)/EGGW)
C
C   COMPUTE AVERAGE BIOMASS OF AGE 0 DURING YEAR
C
        IF (YOYGW - Z0) 41,42,43
     41 AVGB0 = EGGB*(1-EXP(-(Z0-YOYGW)))/(Z0-YOYGW)
        GO TO 44
     42 AVGB0 = EGGB
```

```
          GO TO 44
       43 AVGBO = EGGB*(EXP(YOYGW-ZO)-1)/(YOYGW-ZO)
C
C  COMPUTE PRODUCTION OF YOUNG-OF-THE-YEAR
C
       44 YOYGP = YOYGW*AVGBO
          YOYNP = (YOYGW-ZO)*AVGBO
C
C  COMPUTE AVERAGE BIOMASS PER AGE GROUP DURING YEAR
C
          DO 50 I=1,K
            IF (GW(I)-Z(I))51,52,53
       51     AVGB(I) = B(I)*(1-EXP(-(Z(I)-GW(I))))/(Z(I)-GW(I))
              GO TO 50
       52     AVGB(I) = B(I)
              GO TO 50
       53     AVGB(I) = B(I)*(EXP(GW(I)-Z(I))-1)/(GW(I)-Z(I))
       50 CONTINUE
C
C  COMPUTE PRODUCTION AND YIELD PER AGE GROUP
C
          DO 60 I=1,K
            C(I) = F(I)*AVGN(I)
            Y(I) = F(I)*AVGB(I)
            GP(I) = GW(I)*AVGB(I)
            NP(I) = (GW(I)-Z(I))*AVGB(I)
       60 CONTINUE
C
C  COMPUTE TOTAL POPULATION, BIOMASS, PRODUCTION AND YIELD
C
          CALL SUMMUP (N, K, TOTN)
          CALL SUMMUP (AVGN, K, TOTAVN)
          CALL SUMMUP (B, K, TOTB)
          CALL SUMMUP (AVGB, K, TOTAVB)
          CALL SUMMUP (Y, K, TOTY)
          CALL SUMMUP (C, K, TOTC)
          CALL SUMMUP (GP, K, TOTGP)
          CALL SUMMUP (NP, K, TOTNP)
C
C  WRITE POPULATION PARAMETERS AND HEADINGS FOR SIMYR
C
          WRITE (LP,1070) SIMYR
     1070 FORMAT (1H0,129('*'),//,58X,14('*'),/,58X,'*',12X,'*',/,58X,'*',
         1        ' YEAR: ',I4,' *',/,58X,'*',12X,'*',/,58X,14('*'),//,
         2        130('='),//,55X,'POPULATION PARAMETERS',//,60X,
         3        'BY AGE GROUP',//,17X,'0',7X,'1',7X,'2',7X,'3',7X,'4',7X,
         4        '5',7X,'6',7X,'7',7X,'8',7X,'9',6X,'10',6X,'11',6X,'12',
         5        6X,'13',/,14X,6('='),13(2X,6('=')))
          WRITE (LP,1080) (F(I),I=1,K)
     1080 FORMAT (1H0,'F',19X,13F8.5)
          WRITE (LP,1081) ZO, (M(I),I=1,K)
     1081 FORMAT (1H0,'M',11X,14F8.5)
          WRITE (LP,1082) ZO, (Z(I),I=1,K)
     1082 FORMAT (1H0,'Z',11X,14F8.5)
          WRITE (LP,1083) (GTL(I),I=1,K)
     1083 FORMAT (1H0,'GTL',17X,13F8.5)
          WRITE (LP,1084) YOYGW, (GW(I),I=1,K)
     1084 FORMAT(1H0,'GW',10X,14F8.5)
```

```
      WRITE (LP,1085) (FECND(I),I=1,K)
 1085 FORMAT (1H0,'FECUNDITY',11X,13F8.1)
      WRITE (LP,1086) (MATURE(I),I=1,K)
 1086 FORMAT (1H0,'MATURITY',12X,13F8.5)
      WRITE (LP,1087) (FEMALE(I),I=1,K)
 1087 FORMAT (1H0,'FEMALE',14X,13F8.5)
      WRITE (LP,1088) AFEC, BFEC, AWTLEN, BWTLEN
 1088 FORMAT (1H0,'AFEC = ',F10.8,5X,'BFEC = ',F10.8,5X,'AWTLEN = ',
     1        F10.8,5X,'BWTLEN = ',F10.8)
      WRITE (LP,1089) AVGZO, AVGSO, YOYSRV, FLUCT, WATLEV
 1089 FORMAT (1H0,'AVGZO = ',F11.8,5X,'AVGSO = ',F11.9,5X,'YOYSRV = ',
     1        F11.9,//,' FLUCT = ',F6.2,5X,'WATLEV = ',F6.2,//,130('='))
C
C  WRITE HEADINGS AND SIMULATION RESULTS
C
      WRITE (LP,1090)
 1090 FORMAT (1H0,33X,'MEAN',13X,'MEAN',15X,'MEAN',/,24X,'NUMBER',4X,
     1       'NUMBER',4X,'MEAN',3X,'WEIGHT',2X,'BIOMASS',3X,'BIOMASS',4X,
     2       'YIELD',5X,'YIELD',8X,'PRODUCTION',/,23X,'AT START',3X,
     3       'DURING',3X,'TOTAL',4X,'PER',4X,'AT START',3X,'DURING',5X,
     4       'IN',8X,'IN',9X,'DURING YEAR',/,17X,'AGE',3X,'OF YEAR',5X,
     5       'YEAR',4X,'LENGTH',3X,'FISH',3X,'OF YEAR',5X,'YEAR',5X,
     6       'WEIGHT',3X,'NUMBERS',4X,'GROSS',6X,'NET',/,17X,'===',3X,
     7       2(8('='),2X),2(6('='),2X),6(8('='),2X))
      WRITE (LP,1100) TOTEGG, EGGW, EGGB, AVGBO, YOYGP, YOYNP,
     1                (I,N(I),AVGN(I),AVGTL(I),AVGW(I),B(I),AVGB(I),Y(I),
     2                C(I),GP(I),NP(I), I=1,K)
 1100 FORMAT (1H0,17X,'0',3X,F10.0,20X,F6.4,2F10.2,20X,2F10.2,//,
     1       (17X,I2,2X,2F10.0,2X,F5.0,4X,F5.0,1X,3F10.2,F10.0,2F10.2,
     2       //))
      WRITE (LP,1110) K,TOTN,TOTAVN,TOTB,TOTAVB,TOTY,TOTC,TOTGP,TOTNP
 1110 FORMAT (1H0,15X,'1-',I2,F11.0,F10.0,17X,3F10.2,F10.0,2F10.2,//,
     1       130('='))
C
C  GENERATE AGE DISTRIBUTION, AGE-SPECIFIC LENGTHS AND WEIGHTS FOR SIMYR+1
C
      DO 70 I=1,K
        LSTYRN(I) = N(I)
        LSTYRL(I) = AVGTL(I)
        LSTYRW(I) = AVGW(I)
   70 CONTINUE
      DO 80 I=1,K
        N(I+1) = LSTYRN(I)*EXP(-Z(I))
        AVGTL(I+1) = LSTYRL(I)*EXP(GTL(I))
        AVGW(I+1) = LSTYRW(I)*EXP(GW(I))
   80 CONTINUE
      N(1) = TOTEGG*YOYSRV
      GO TO 2
C
C  WRITE 'END OF SIMULATION'
C
   90 WRITE (LP,1120)
 1120 FORMAT (1H0,//,130('*'),/,56('*'),' END OF SIMULATION ',55('*'),/,
     1       130('*'))
      READ (IN, 1130) MORE
 1130 FORMAT (I1)
      IF (MORE .EQ. 1) GO TO 1
      STOP
      END
```

```
C
C
C*****************************************************************************
      SUBROUTINE SUMMUP (X, K, TOT)
C                                                                            *
C*****************************************************************************
C  SUBROUTINE SUMMUP COMPUTES THE SUM OF A K-DIMENSIONED ARRAY               *
C                                                                            *
C  VARIABLES..                                                               *
C     K   = INTEGER REPRESENTING DIMENSION OF ARRAY TO BE SUMMED             *
C     TOT = SUM OF ARRAY X                                                   *
C     X   = ARRAY TO BE SUMMED                                               *
C                                                                            *
      DIMENSION X(K)
      TOT = 0.0
      DO 10 I=1,K
        TOT = TOT + X(I)
   10 CONTINUE
      RETURN
      END
```

```
C
C
C*****************************************************************************
      SUBROUTINE YOYSUB
C                                                                            *
C*****************************************************************************
C                                                                            *
C  SUBROUTINE YOY COMPUTES EQUILIBRIUM SURVIVAL RATE OF AGE 0 (AVGZO)        *
C  BASED ON THE METHOD OF VAUGHAN AND SAILA 1976 TRANS. AM. FISH. SOC. AND   *
C  THE SURVIVAL RATE OF AGE 0 FOR SIMULATION YEAR (ZO) BASED ON A MULTIPLE   *
C  REGRESSION EQUATION USING WATER LEVEL DURING SPAWNING AND WATER LEVEL     *
C  FLUCTUATION FROM PREVIOUS GROWING SEASON AS INDEPENDENT VARIABLES         *
C                                                                            *
C                                                                            *
      COMMON / YOY / AVGSO, AVGZO, FECND(13), FEMALE(13), FLUCT, K,
     1               MATURE(13), WATLEV, YOYSRV, Z(13), ZO, IFLAG
      REAL MATURE
      IF (IFLAG .NE. 0) GO TO 20
      SUM = 0.0
      PROD = 1.0
      L = K-1
C  ENTER DO LOOP TO CALCULATE SUM OF FECUNDITY TIMES CUMULATIVE SURVIVAL
C
      DO 10 I=1,L
        PROD = PROD*EXP(-Z(I))
        SUM = SUM + FECND(I+1)*MATURE(I+1)*FEMALE(I+1)*PROD
   10 CONTINUE
      AVGSO = 1.0/SUM
      AVGZO = -(ALOG(AVGSO))
C
   20 IF (WATLEV .EQ. 0.0) ZO = AVGZO
      IF (WATLEV .NE. 0.0) ZO = AVGZO+221.86241513-0.29531602*FLUCT
     1                                       -0.23642989*WATLEV
      YOYSRV = EXP(-ZO)
      IFLAG = 1
      RETURN
      END

C*****************************************************************************
```

APPENDIX F

MODEL III SAMPLE OUTPUT

LARGEMOUTH BASS POPULATION, PRODUCTION, AND YIELD SIMULATOR

SAMPLE SIMULATION OUTPUT FOR APPENDIX F

SIMULATION WILL RUN 1 YEAR AND CARRY 8 AGE GROUPS

YEAR: 1968

POPULATION PARAMETERS

BY AGE GROUP

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
F		0.12080	0.12674	0.07460	0.13177	0.15693	0.20231	0.30648	0.69147					
M	9.75769	0.27076	0.35833	0.34303	0.44805	0.82389	1.42220	2.33860	6.21630					
Z	9.75769	0.39156	0.48507	0.41763	0.57982	0.98082	1.62451	2.64508	6.90777					
GTL		0.50927	0.27063	0.16947	0.11457	0.08094	0.05879	0.04351	0.03262					
GW	10.71442	1.55837	0.82813	0.51858	0.35058	0.24768	0.17990	0.13314	0.09982					
FECUNDITY		1245.6	5963.3	13211.5	21606.9	29370.1	34596.4	41826.8	51628.7					
MATURITY		0.0	0.0	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000					
FEMALE		0.50000	0.50000	0.50000	0.50000	0.50000	0.50000	0.50000	0.50000					

AFEC = 0.00045091 BFEC = 2.94078064 AWTLEN = 0.00001071 BWTLEN = 3.06000042

AVGZO = 9.12893200 AVGSO = 0.000108481 YOYSRV = 0.000057848

FLUCT = 1.97 WATLEV = 933.03

AGE	NUMBER AT START, OF YEAR	MEAN NUMBER DURING YEAR	MEAN TOTAL LENGTH	MEAN WEIGHT PER FISH	BIOMASS AT START OF YEAR	MEAN BIOMASS DURING YEAR	YIELD IN WEIGHT	YIELD IN NUMBERS	PRODUCTION DURING YEAR GROSS	PRODUCTION DURING YEAR NET
0	5201536.			0.0012	6.24	10.46			112.07	10.01
1	960.	794.	155.	54.	51.84	98.26	11.87	96.	153.13	114.66
2	244.	193.	264.	275.	67.10	80.05	10.15	25.	66.29	27.46
3	158.	129.	346.	630.	99.54	104.74	7.81	10.	54.31	10.57
4	134.	102.	409.	1051.	140.83	125.86	16.58	13.	44.12	-28.85
5	131.	83.	454.	1447.	189.56	134.35	21.08	13.	33.27	-98.49
6	37.	18.	480.	1715.	63.45	33.57	6.79	4.	6.04	-48.49
7	7.	2.	512.	2090.	14.63	5.35	1.64	1.	0.71	-13.44
8	0.	0.	550.	2602.	0.0	0.0	0.0	0.	0.0	0.0
1- 8	1671.	1323.			626.96	582.17	75.93	161.	357.88	-36.59

END OF SIMULATION

APPENDIX G

INPUT DATA FOR NOMINAL SIMULATION OF MODEL III

```
         00000000011111111112222222222333333333344444444445555555555666666666677777777778
         12345678901234567890123456789012345678901234567890123456789012345678901234567890
CARD
0001      810
0002                NOMINAL SIMULATION WITH STABLE AGE STRUCTURE  **  MODEL III
0003        155    264    346    409    454    480    512    550
0004         38    207    488    828   1151   1373   1684   2112
0005       2000    800    320    128     51     20      8      3
0006     .50927.27063.16947.11457.08094.05879.04351.03262
0007     .45814.45814.45814.45814.45814.45814.45814.45814
0008     .45814.45814.45814.45814.45814.45814.45814.45814
0009     .50000.50000.50000.50000.50000.50000.50000.50000
0010     0.00000.00001.00001.00001.00001.00001.00001.0000
0011     0.00045091 2.9407808.000004531 3.1633000
0012     1968
0013     1969
0014     1970
0015     1971
0016     1972
0017     1973
0018     1974
0019     1975
0020     1976
0021     1977
0022     0000
0023     0
```

VITA

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Candidate for the Degree of

Master of Science

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