

A GENERAL POPULATION DYNAMICS THEORY  
FOR LARGEMOUTH BASS FISHERIES

by

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Thesis submitted to the Graduate Faculty of the  
Virginia Polytechnic Institute and State University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Fisheries Science

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ACKNOWLEDGMENTS

The problem of modeling largemouth bass populations was conceived and proposed by . encouraged, reviewed, and commented on the model through much of its evolution.

, and broadened my perspectives through their teaching and also reviewed the thesis.

My wife, , and parents, encouraged and supported my work in innumerable ways. Thanks are due to each for his contribution.

This research was financed by the Bass Research Foundation, Starkville, Mississippi.

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## INTRODUCTION

Largemouth bass, Micropterus salmoides (Lacépède), are the most widely distributed warm-water predatory fish in North America. They are extremely popular among some sport anglers and, in addition, significantly influence the dynamics of other sport fish populations; bass are consequently the object of much management effort. Yet, despite--or perhaps because of--widespread interest in largemouth bass management and extensive research on bass, there is little agreement on the objectives or methods to be used in managing largemouth bass populations.

One means of clarifying these issues is to develop a concrete, precise theory of the dynamics of largemouth bass populations which provides adequate tools for choosing optimal management strategies when the desired results are specified. Such a theory would also help to clarify the normative issues of management by focusing attention on the range of alternatives that are available. My intent in this thesis is to describe a general model relating life history to population structure in biological populations and to illustrate its use in studying several issues in largemouth bass management.

The model was motivated by the nature of largemouth bass populations but is proposed here as a general population model. The applications are intended as illustrations only and are not sufficiently specific for direct management use. Direct application with the hope of resolving some management issues will require extensive modeling of specific life history processes which may then be

incorporated in the theory described below.

### Issues in Largemouth Bass Management

1. Sport and prestige seem to be major factors making bass popular among anglers. Anderson (1975a) has argued that the quality of bass fishing is best measured by an index incorporating catch rate, size of fish caught, species combination creeled, and positive value from fish caught and released.

Bass become catchable between 250 mm and 300 mm in length, but angling technique and angler preferences are size selective so that catchability generally increases as bass grow to 375-400 mm. Beyond this size catchability declines (Bennett, et al. 1968). The observations of Bennett (194), Lagler and De Roth (1953), and Anderson and Heman (1969) suggest that this decline is a consequence of exploitation rather than growth. These authors attribute the decline in catchability to learning by bass, though the possibility that declining catchability is due to removal of inherently more catchable individuals from the population apparently was not considered.

Data presented by Redmond (1974) indicate that catchability varies seasonally with very low rates in winter and peaks of catchability in spring and fall. Holbrook (1975) gave evidence that relative catchability of females as compared to males is high in early spring, declines before spawning season, then increases again. Overall, a significantly larger percentage of harvested bass is female. The causes and implications of this difference in catchability have not been studied.

2. A common consequence of exploiting biological populations is a decline in average age of individuals in the exploited population (Usher 1963). When organisms are harvested before reaching maximum size, as with most fish, this leads to a decline in average size of harvested individuals. The effect of exploitation on size distribution is magnified when exploitation rate is higher on smaller fish than on larger ones. Thus, under significant exploitation, quality of bass fishing generally declines. This has led many managers to impose fishing regulations to limit harvest or change the pattern of exploitation. Fox (1975) summarized the history and present status of bass fishing regulations in the United States.

Because fishing seasons and creel limits have not generally altered the level of bass harvest or size-selectivity of angling, size limits are the principal regulation in current use. Ricker (1945) presented a mathematical model showing that yield can be increased by use of minimum size limits. Anderson (1974, 1975a, 1975b) has emphasized the use of size limits in maintaining a desirable size structure and balance between bass and bluegill, Lepomis macrochirus Rafinesque. His concern with management of predator-prey relations led to consideration of protecting certain size ranges of bass while allowing fishing for bass smaller or larger than the protected ones.

Bennett (1974) and Rasmussen and Michaelson (1974), on the other hand, found slower growth of bass smaller than minimum size limits and a 'piling up' of fish just below legal size. Sanderson (1958) found that a lowered minimum size limit in the Potomac River Basin



resulted in higher yield and increased average size of fish kept by anglers because of increased growth.

3. The concept of balance was developed by Swingle (1950) to describe the range of satisfactory size and species distributions in bass-bluegill ponds. This concept has been used extensively to define the objectives for managing fish communities in ponds and small lakes. The management strategies required to establish and maintain balance vary widely from region to region (see, e.g., Dillard and Novinger 1975). Although acceptable strategies for achieving balance in different regions have been found by trial and error, the functional causes of variation are not understood.

Jenkins and Morais (1977) have greatly extended the concept of predator-prey balance by comparing the size distribution of predators to the size distribution of available prey. Lawrence (1958) showed that maximum prey size available to largemouth bass was limited by bass mouth size. Jenkins and Morais found similar relationships for other predatory fishes, then compared cumulative (by size) biomass of predators to available prey abundance. Using this approach, they found 9 of 23 study reservoirs to be deficient in available prey in some size range.

4. The dynamics of size structure in bass populations are complicated by wide fluctuations in year-class strength. Fluctuations in production corresponding to fluctuations in year-class strength (Houser and Rainwater 1975) suggest that potential yield from larger lakes is strongly dependent on recruitment. Clady (1977), however,

found that production and biomass remained relatively constant despite year-class fluctuations. Clady suggested that this constancy was due to density-dependence both within and between cohorts. It is not known whether density-dependent variation in growth rates acts to stabilize size structure despite fluctuations in year-class strength.

#### Desiderata for a Theory of Largemouth Bass Management

The management issues described above suggest the need for a fairly general theory of the dynamics of largemouth bass populations, especially their size structure and production. The traditional models used in the describing fish populations are deficient in two respects: most are either unstructured (Shaefer 1954) or age-structured (Beverton and Holt 1957) and are therefore difficult to use in the analysis of populations in which many organism characteristics are size specific and they fail to incorporate stochastic variation in growth rates, mortality rates, or other life history functions. It is therefore desirable to construct a general population model which explicitly incorporates population size-structure and variation in life history and which permits calculation of production, yield, and the size structure of harvest.

In this thesis, I will develop such a model based on the relationship between life history and population dynamics, show its relationship to various other models, and illustrate its application to largemouth bass in a few simple problems.

## LIFE HISTORY

Life history has been defined as the history of the changes through which an organism passes in its development from the egg, spore, or other primary stage until its natural death (Webster 1959), but in common usage life history also refers to certain fixed traits which influence the course of an organism's life. This usage is formalized in the following definitions.

Definition: A trait is an attribute of an organism that can, at least potentially, be observed (either instantaneously or through repeated or continuous monitoring) without reference to the environment, community, or population in which the organism lives.

This definition excludes those characteristics which can only be observed in the context of the organism's surroundings, such as habitat preferences and food preferences. However, spatial location, stomach contents or food habits, age, length, weight, sex, and physiological state are included in this definition.

Definition: The particular values of a set of traits, taken together, will be referred to as a phenotype.

A life history can now be defined as the changes in phenotype that occur through an organism's life. This would require, however, that a life history describe each change of phenotype rather than describe the ontogenic processes leading to the changes. Therefore,

Definition: A life history is a description of the processes by which an organism's phenotype changes in time from the organism's origin through its death.

Definition: The specific sequence of development of a particular organism resulting from a life history will be called a life.

Suppose that the dynamics of a particular finite list of traits is to be described by a life history. Let a unique numerical representation be associated with every possible state of each trait. This will be done most conveniently using positive real numbers for continuous traits and positive integers for traits with discrete states. At any moment, an organism may now be described by a vector-variate in which each position is associated with one trait. Such a vector will be called a trait vector or phenotype and will be denoted by  $\underline{T} = (T_1, \dots, T_n)'$ . The set of all possible trait vectors will be denoted by  $\mathcal{T}$  and called a trait space.

Trait vectors will generally change with time from an organism's origin at some time  $t_b$  to its death at a later time  $t_d$ . Since any time  $t \in [t_b, t_d)$  can be written as  $t = t_b + a$  where  $a$  is the organism's age, trait vectors may be viewed as depending on age and the time of birth  $t_b$ . This dependence will be denoted by writing  $\underline{T}(a; t_b)$  with  $a \in [0, t_d - t_b)$ . The function  $\underline{T}(a; t_b)$  now represents the life of an organism.

It is implicit in the distinction between a life and a life history that the particular life is not determined by life history.

In particular, a life is a random function of time taken from the set of all possible lives according to a probability law generated by the life history, which is a stochastic process. Thus a particular life of an organism will generally be denoted by  $\underline{T}(a; t_b, \omega)$  for  $\omega \in \Omega$  a parameter specifying the particular outcome of the stochastic life history. Clearly, a life in this context is a sample path from the life history. Correspondingly, the life history is equivalent to a probability distribution on the space of possible lives and can be denoted by  $\{\underline{T}(a; t_b, \omega) : \omega \in \Omega\}$  or simply  $\{\underline{T}(a; t_b)\}$ .

It is desirable, however, to represent life history as a stochastic process in which the particular path taken at any point in time is a consequence of the phenotype of the organism and the state of its surroundings at that time. The remainder of this section deals with such representations.

Traits of organisms generally change in two ways: continuous processes and event processes. In a continuous process, a trait will change in a smooth fashion. Spatial movement and growth in length are continuous processes. Event processes, on the other hand, entail sudden jumps in the value of a trait. Reproduction and death are characteristically event processes. Some traits will change in a mixed fashion. Stomach contents of bass, for example, will take significant positive jumps when the bass feeds then decline in a continuous fashion as digestion proceeds.

Continuous stochastic processes are generally either differentiable or non-differentiable as appropriate rate functions either

exist or fail to exist. Since most life histories will have reasonable rate functions, e.g., swimming velocity or metabolic rates, I shall assume that all continuous processes in the life history are differentiable, except at isolated points. If a non-differentiable process were appropriate, the methods of Itô (Itô 1950, 1951, Itô and McKean 1965) could be used in place of the following arguments.

Event processes are specified by a rate function which describes the temporal occurrence of events and a jump function which describes the magnitudes of changes in traits which occur at each event. I will assume that the rate functions of both continuous and event processes and the jump function of the event process will depend only on the present state of the organism and its environment and not its past life. This assumption, known as the Markov property, is essentially an assumption that the organism lacks memory other than through some trait included in the phenotype. The Markov assumption can be circumvented by assuming that there is a trait that functions as a memory in the trait vector. Indeed, it seems likely that for most life history phenomena some real trait will in fact function in this capacity whenever such a model is necessary.

Since virtually all traits will be bounded by biological possibility, the entire life history process may be assumed to be of second order, i.e.  $E_{\Omega}[\underline{T}(a; t_b) \cdot \underline{T}'(a; t_b)]$  finite for all  $a \in [0, t_d - t_b)$ .

Under the above assumptions, the following notation will be used (also see Appendix III):

1) Let  $\underline{g}(\underline{T}, a; t_b) \equiv \frac{\partial}{\partial a} \{\underline{T}(a; t_b)\}$  be the derivative of the continuous part of the life history.  $\underline{g}$  is well-defined except at times when discrete events occur.

2) Let  $r(\underline{T}, a; t_b)$  be the rate function of the event process.

3) Denote the phenotype resulting from a jump by  $\underline{j}$ . Assume  $\underline{j}$  is taken from a distribution  $H(\underline{j}; \underline{T}, a, t_b)$ . If the distribution has a density, it will be denoted by  $h(\underline{j}; \underline{T}, a, t_b)$ .

4) Denote the rate function of the death process by  $\mu(\underline{T}, a; t_b)$ . The probability that an organism born at time  $t_b$  will survive to age  $a$  will then be given by  $\lambda(a; t_b) \equiv E_{\Omega}[\exp(-\int_0^a \mu(\underline{T}(t, \omega), t; t_b, \omega))]$ .

5) Summarize the probability that an organism survives to age  $a$  and has phenotype  $\underline{P}$  with  $P_i \leq T_i$ ,  $i = 1, \dots, n$ , for arbitrary  $\underline{T}$  by the function  $F(\underline{T}; a, t_b)$ . Clearly,  $F(\underline{0}; a, t_b) = 0$  and  $F(\underline{\infty}; a, t_b) = \lambda(a; t_b) \leq 1.0$ . The function  $F$  is similar to a distribution function except that its least upper bound is less than 1.0. If there is a function analagous to a density for  $F$ , it will be denoted by  $f(\underline{T}; a, t_b)$ .

Now suppose that  $h$  and  $f$  both exist. The time-dependent "density" function  $f(\underline{T}; a, t_b)$  is a summary of the likelihood of the phenotypes  $\underline{T}$  in  $\tau$  for an organism of age  $a$  but born at time  $t_b$ . Any information concerning the relationship between phenotype at one age and phenotype at another is lost. Nonetheless, the temporal dynamics of  $f$  is an important problem with repercussions in population dynamics.

Theorem 2: Given the assumptions and notation stated above, the density functional  $f$  must satisfy the differential form:

$$\frac{\partial f(\underline{T}; a, t_b)}{\partial a} = \int_{\tau} \dots \int f(\underline{x}; a, t_b) r(\underline{x}, a; t_b) h(\underline{T}; \underline{x}, a, t_b) dx_1 \dots dx_n - f(\underline{T}; a, t_b) r(\underline{T}, a; t_b) + \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 [\sigma_{ij}(\underline{T}, a; t_b) f(\underline{T}; a, t_b)]}{\partial T_i \partial T_j} - \sum_{i=1}^n \frac{\partial [m_i(\underline{T}, a; t_b) f(\underline{T}; a, t_b)]}{\partial T_i} - \mu(\underline{T}, a; t_b) f(\underline{T}; a, t_b) \quad (1)$$

where  $m_i$  and  $\sigma_{ij}$  are the instantaneous means and covariances of the changes in traits  $T_i$  and  $T_j$ .

Interpretation: The differential form (1) may be interpreted as follows: any change in the likelihood of an organism having phenotype I with a change in age must be due to changes in the probability of survival to that age or flux in the likelihood of the phenotype due to continuous or jump processes. The first term on the right hand side (RHS) of (1) is the likelihood of a jump from another phenotype ending at phenotype I, while the second RHS term is the likelihood of a jump from phenotype I to some other phenotype. The next two terms describe flux in the density due to the continuous process  $g$ . The final term is the likelihood of death occurring at age  $a$  with phenotype I.

Derivation: See Appendix I.

The integro-differential operator for phenotype density functions will hereafter be referred to as the life history operator and will be



denoted

$$Lf = \frac{\partial f}{\partial a} + \sum_{i=1}^n \frac{\partial (m_i f)}{\partial T_i} - \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 (\sigma_{ij} f)}{\partial T_i \partial T_j} + \mu f + r f - \int_{\tau} \dots \int f r h d\tau .$$

In the above analysis, dependence on  $a$ ,  $t_b$ . To simplify notation in later analysis, this will hereafter be denoted by  $a$ ,  $t$  where  $t - a = t_b$ .

### POPULATIONS

Biological populations have been described in various ways. Wright (1931) defined a population as the collection of organisms in a gene pool. Odum (1971), on the other hand, referred to a population as "a collective group of organisms of the same species occupying a particular space". The essential aspects of a population are that it is a group of organisms which through reproduction is persistent for periods longer than the life-length of its members and which is genetically or reproductively integrated. The following definitions provide an operational interpretation of the population concept.

Definition: A group of organisms is closed with respect to reproduction, or reproductively closed, if every offspring of a member of the group is a member of the group at its birth and every organism born as a member of the group is an offspring of members of the group. For example, consider the group of immature bass in a lake. This group is not reproductively closed since larval bass which are members of the group are not offspring of members of the group. The group of

mature bass in a lake is not reproductively closed for the opposite reason.

Definition: A group of organisms is self-renewing if it is reproductivity closed and if every organism in the group having a positive probability of reproducing during the remainder of its life has a positive probability of reproducing while it is a member of the group.

Definition: A group of organisms is a population if it is self-renewing and cannot be partitioned on the basis of life history into disjoint groups that are reproductively closed.

The self-renewing nature of populations is the key to dynamics of populations.

Suppose that every individual in a population is characterized by values of a set of traits which includes age. To simplify later notation, I will write  $\underline{P}$  for  $(a, \underline{T})'$  where explicit use of age is not required. Define a population structure function,  $N(\underline{P}, t)$ , as the number of individuals in the population at time  $t$  with phenotype  $\underline{x} \leq \underline{P}$ . If the population is sufficiently large,  $N(\underline{P}, t)$  will be essentially continuous in the continuous variates of  $\underline{P}$ . The corresponding 'density' function  $n(\underline{P}, t)$  will then have expected value  $\eta(\underline{P}, t) = \sum f_i(\underline{P}, t)$  where the summation is over all members of the population.  $\eta(\underline{P}, t)$  divided by population size would then be the likelihood of a randomly selected member of the population at time  $t$  having phenotype  $\underline{P}$ . The function  $\eta$  is then subject to a functional

equation similar to the life history operator equation (1), namely,

$$\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial a} + \sum_{i=1}^n \frac{\partial (m_i \eta)}{\partial T_i} - \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 (\sigma_{ij} \eta)}{\partial T_i \partial T_j} + \mu \eta + r \eta - \int \dots \int \eta r h d \tau = 0. \quad (2)$$

In addition, we have the boundary condition at  $a = 0$

$$\eta(0, I; t) = \beta(I, t) \quad (3)$$

where  $\beta(\underline{T}, t)$  is the expected number of births of organisms with traits  $\underline{T}$  at time  $t$ . The system of equations (2) and (3) is essentially a generalization of the model proposed by Sinko and Streifer (1967) to include more than one trait other than age, jumps in phenotype rather than only continuous alternation, and stochastic continuous processes as well as deterministic ones.

The system (2) and (3), However, has two major faults: it is comparatively intractable in the general form and cannot be used to predict statistical properties of the population. Under very restrictive assumptions generally involving the absence of temporal variation in life history parameters, and thereby excluding density dependence and environmental variation, the equations can be solved analytically for  $\eta$ . In principle, the equations can be solved numerically under more general assumptions. The standard centered-difference and grid techniques, however, require extremely large numbers of grid points to achieve reasonable solutions for problems in large dimensions. Furthermore, the equations only allow prediction of the expected density function and do not account for the effects of statistical fluctuations in finite populations.

A more fruitful approach to solving these differential equations is to use stochastic integral equations corresponding to (2) and (3). When applied to the density  $\eta$  the equations will be deterministic and entirely equivalent to (2) and (3). When applied to the actual density  $n$ , the integral form will be stochastic. Unfortunately, in the absence of restrictive assumptions the equations developed below are nonlinear and only slightly more tractable than the differential form. Current work by mathematicians on stochastic integral equations, however, holds some promise for analytical solution (see e.g., Bharucha-Reid 1972).

In the discussion of life history, the initial phenotype of a neonate was not explicitly discussed. The initial value of the density  $f$  at time  $t_b$  ( $a = 0$ ), if taken for an arbitrary individual born at time  $t_b$ , would be a result of parental influence and environmental conditions. This may be made explicit as follows: let  $b(\underline{P}_n, t; \underline{P}_p)$  be the actual rate of production of neonates with phenotype  $\underline{P}_n$  by parents with phenotype  $\underline{P}_p$  at time  $t$ , expressed as offspring per parent. Then  $B(\underline{P}_n, t)$ , the net rate of production of neonates with phenotype  $\underline{P}_n$  at time  $t$  by the population is given by

$$B(\underline{P}_n, t) = \frac{1}{p} \int \dots \int b(\underline{P}_n, t; \underline{P}_p) n(\underline{P}_p; t) d\underline{P}_p \quad (4)$$

where  $p$  is the number of parents for which each offspring is counted in the integral. If only one sex is included  $p$  will be 1; if both sexes are counted,  $p$  will be 2.

Assuming  $B(\underline{P}, t)$  is sufficiently large for all times  $t$ ,  $n(\underline{P}, t)$  can be approximated by

$$n(\underline{P}, t) \doteq \int_0^t \int \dots \int B(\underline{T}, \tau) f(\underline{P}, t; \underline{T}, \tau) d\underline{T} d\tau \quad (5)$$

where  $f(\underline{P}, t; \underline{P}_n, \tau)$  is the likelihood an organism born at time  $\tau$  with phenotype  $\underline{P}_n$  will survive to time  $t$  and have phenotype  $\underline{P}$ . If, however, the population description is begun at time  $t = 0$  with initial density  $n(\underline{P}; 0)$ , some of the population density at later times may be attributed to original members of the population. In particular, if  $k(\underline{P}_2, t_2; \underline{P}_1, t_1)$  is the likelihood that an organism with phenotype  $\underline{P}_1$  at time  $t_1$  will survive to time  $t_2$  and have phenotype  $\underline{P}_2$ , then

$$n(\underline{P}, t) = \int \dots \int [k(\underline{P}, t; \underline{P}_n, 0) + \int_0^t B(\underline{P}_n, \tau) f(\underline{P}, t; \underline{P}_n, \tau) d\tau] d\underline{P}_n. \quad (6)$$

Now define an expected fertility function  $\phi(t, \tau)$  equivalent to the standard demographic fertility function (e.g., Keyfitz 1968) by

$$\phi(t, \tau) = \int \dots \int \int \dots \int \int \dots \int b(\underline{P}_n, t; \underline{P}_p) f(\underline{P}_p, t; \underline{P}_n, \tau) d\underline{P}_n d\underline{P}_p d\underline{P}. \quad (6)$$

$\phi(t, \tau)$  is then the expected number of offspring produced at time  $t$  by an individual born at time  $\tau$  in the absence of other information on the individual's life. Then using  $\phi$  and substituting (6) in (4), we have the expected birth rate at time  $t$  as

$$B(t) = q(t) + \frac{1}{p} \int_0^t \phi(t, \tau) B(\tau) d\tau \quad (7)$$

where  $q(t)$ , the contribution of the initial population

$$q(t) = \frac{1}{p} \int_t^A \phi(t, a - t) n(a - t, 0) da.$$

where  $A$  is the maximum age of reproducing individuals. This is essentially the model of Lotka (1925) and Feller (1941).

In the present context, an analogous argument leads to a stochastic version of this equation, namely

$$B(t, \omega) = q(t, \omega) + \frac{1}{p} \int_0^t \phi(t, \tau; \omega) B(\tau, \omega) d\tau \quad \omega \in \Omega \quad (8)$$

where  $\omega$  indexes the particular outcome of the process. It is shown in Appendix II that this equation has a unique solution subject to conditions which follow from our earlier assumptions, except that it is also assumed that the maximum reproductive rate over all phenotypes may not exceed the greatest lower bound of the temporal average of mortality rate up to any age. In the case that the death rate  $\mu(a, t)$  is constant, this condition guarantees that the population is expected to become extinct in finite time.

Heretofore, few assumptions have been made about the fertility function  $\phi(t; \omega)$ . In the remainder of this thesis, it will be assumed that  $\phi(t; \omega)$  is density independent and that equation (8) is linear. The model as developed above is more general than those of Sinko and Streifer (1967) or Lotka (1925). It is well known that the Lotka age-structured model is the limiting version of the Leslie matrix model as the time step  $\Delta t$  approaches 0. Sinko and Streifer showed that their model was a generalization of the models of Von Foerster (1959), Oldfield (1966), Trucco (1965), Bailey (1931), Hoyle (1963),

Verhulst (1838), and Pearl and Reed (192). The assumption of linearity reduces this generality, but serves to make the model more tractable.

Before illustrating the application of the model, two further results will be demonstrated. First, under the assumption that survival, reproduction, and abundance are stochastically independent, the expected number of births follows the Lotka integral equation in the expected reproduction and survival rates. Although it will not be established here, these independence conditions also appear to be necessary. Secondly, I will show that under the linearity assumption, the model implies an asymptotically stable density function over the entire set of traits.

Theorem 2: If the processes  $B(t; \omega)$  and  $\phi(t, \tau; \omega)$  are uncorrelated, then

$$E_{\Omega}[B(t; \omega)] = E_{\Omega}[q(t; \omega)] + \int_0^t E_{\Omega}[\phi(t, \tau; \omega)] E_{\Omega}[B(\tau; \omega)] d\tau .$$

If the processes  $\lambda(t, \tau; \omega)$  and  $b(t, \tau; \omega)$  are also uncorrelated, then

$$E_{\Omega}[B(t; \omega)] = E_{\Omega}[q(t; \omega)] + \int_0^t E_{\Omega}[\lambda(t, \tau; \omega)] E_{\Omega}[b(t, \tau; \omega)] E_{\Omega}[B(\tau; \omega)] d\tau .$$

Proof: Since  $\lambda(t, \tau; \omega)$ ,  $b(t, \tau; \omega)$ , and  $B(t, \tau; \omega)$  are nonnegative we may interchange the integral and expectation. Hence,

$$\begin{aligned} E_{\Omega}[B(t; \omega)] &= E_{\Omega}[q(t; \omega)] + E_{\Omega}\left[\int_0^t \phi(t, \tau; \omega) B(\tau; \omega) d\tau\right] \\ &= E_{\Omega}[q(t; \omega)] + \int_0^t E_{\Omega}[\phi(t, \tau; \omega) B(\tau; \omega)] d\tau \end{aligned}$$

$$= E_{\Omega}[q(t; \omega)] + \int_0^t E_{\Omega}[\phi(t, \tau; \omega)] E[B(\tau; \omega)] d\tau$$

by the assumption that  $\phi(t, \tau; \omega)$  and  $B(\tau; \omega)$  are uncorrelated. Then since  $\lambda(t, \tau; \omega)$  and  $b(t, \tau; \omega)$  are uncorrelated,  $E_{\Omega}[\phi(t, \tau; \omega)] = E_{\Omega}[\lambda(t, \tau; \omega)] E_{\Omega}[b(t, \tau; \omega)]$ . Q E D

When the assumptions of this theorem are not met, the expectation will not hold and the deterministic models will be inaccurate.

It is well known that the deterministic age-structured model is asymptotically ergodic for any non-zero initial population (Lopez 1964): since the expected value of the birth process, in the usual models, obeys a law similar to the law governing the stochastic birth process, it is reasonable to expect that the asymptotic population structures will be similar. In particular, it is obvious that

$$E_{\Omega}[n(a, t; \omega)] = E_{\Omega}[\lambda(t, t-a; \omega) B(t-a; \omega)] = E_{\Omega}[\lambda(t, t-a; \omega)] E_{\Omega}[B(t-a, \omega)]$$

under the assumption of independence of  $\lambda$ ,  $B$ . Hence, under the assumptions of the last theorem, the expected value of  $n(a, t)$  will be identical to its value in the expected value model. It is unknown at this point whether the randomness of the various processes will lead to any particular fluctuations in population structure or density.

Theorem 3: A population of organisms having time and density independent life histories will have an asymptotically stable expected density function.



Proof: By the argument given above, the population will have an asymptotically stable expected age structure  $\eta(a, t)$ . But the expected distribution of phenotypes at a given age is  $f(\underline{T}; a, t)$  so we have expected structure function  $\eta(a, \underline{T}; t) = \eta(a, t) f(\underline{T}; a, t)$ .

Lopez (1967) has shown rigorously that the age structure predicted by the Lotka model is of the form  $\eta(a, t) = N e^{r(t-a)} \lambda(a)$ , where  $r$  is the asymptotic growth rate of the population and  $N$  is the initial abundance. For example, if we assume that the population has approximately constant abundance. then  $r = 0$  and  $\eta(a, t)$  is proportional to  $\lambda(a)$  so that  $\eta(a, \underline{T}, t) = N \lambda(a) f(\underline{T}; a, t)$  for  $t$  sufficiently large.

One special case is of particular interest here: namely, where a trait  $T_i$  is determined by age with  $T_i = m_i(a)$ . Then the distribution  $\eta_i(T_i)$  is obtained by a standard change of variables and we have  $\eta_i(T_i, t) = \sum_j \eta_a(m_{ij}^{-1}(T_i), t) \cdot |m_{ij}^{-1}'(T_i, t)|$  where the summation runs over all solutions of  $m_i(a) = T_i$ , provided there are at most countably many such solutions for any  $T_i$  (Harris 1966). In the case that  $m_i(a)$  is monotone, this trait distribution and the corresponding differential equation reduce to the model of "physiological age distributions" studied by Van Sickle (1976).

## APPLICATIONS

The four issues in largemouth bass management discussed in the Introduction were the principal motivation for the model developed above. None of these issues can be resolved here because of an absence of empirical information on which to base specific models. My purposes in this section, then, are to illustrate the use of the model and outline possible directions to their solution. First, I shall attempt to illustrate how some of the effects of exploitation can be described. Second, a possible approach to the selection of size limits will be presented. Third, the information necessary for a theoretical investigation of the ideas of Jenkins and Morais (1977) will be outlined. Finally, the differential equation form of the model will be used to derive formulae for production and yield using a size-structured model.

### Effects of Exploitation

Two potential effects of exploitation will be illustrated here: the possible impact of fishing on average catchability and the usual effect of fishing on population size structure.

Suppose that a population of bass is to be exploited over a short period during which no reproduction occurs. Further, suppose that during this period the catchability of each individual fish is fixed at some value  $c$  having a distribution  $f(c; t)$  in the population at time  $t$ . If all individuals have a common, invariant natural mortality rate  $\mu$  and if effort  $E$  is constant over the period, then  $f(c; t)$  obeys the differential equation:

$$\frac{\partial f(c; t)}{\partial t} = -(c E + \mu) f(c; t)$$

with the initial density  $f(c; 0) = g(c)$ . Now

$$\frac{1}{f(c; t)} = \frac{\partial f(c; t)}{\partial t} = \frac{\partial \ln f(c; t)}{\partial t} = -(c E + \mu)$$

so that

$$f(c; t) = \exp[\ln f(c; t)] = \exp[-(c E + \mu)t] f(c; 0) .$$

The expected catch rate at time  $t$  will then be

$$c(t) = \int_0^{\infty} c f(c; t) dc = \int_0^{\infty} c e^{-(cE+\mu)t} f(c; 0) dc .$$

As an example, suppose  $g(c)$  is a gamma density with parameters  $\alpha, n$ .

Then

$$\begin{aligned} c(t) &= \int_0^{\infty} c e^{-(cE+\mu)t} \frac{1}{\Gamma(n)} \alpha^n e^{-\alpha c} c^{n-1} dc \\ &= \frac{e^{-\mu t}}{\Gamma(n)} \frac{\alpha^n}{(\alpha+Et)^n} \int_0^{\infty} c (\alpha + Et)^n e^{-(\alpha+Et)c} c^{n-1} dc \\ &= \frac{n \alpha^n e^{-\mu t}}{(\alpha+Et)^{n-1}} . \end{aligned}$$

Since the abundance of the population is declining with time, mean catchability will be  $\frac{c(t)}{F(\infty; t)}$ , or  $\frac{n}{(\alpha+Et)}$ . The variance of catchability will be  $\frac{n}{(\alpha+Et)^2}$ . A graph of catchability under these assumptions is shown in Figure 1.

The second aspect of exploitation to be discussed here is its effect on population size structure. Again, a simple model will illustrate the point. Suppose that bass grow in weight,  $z$ , according

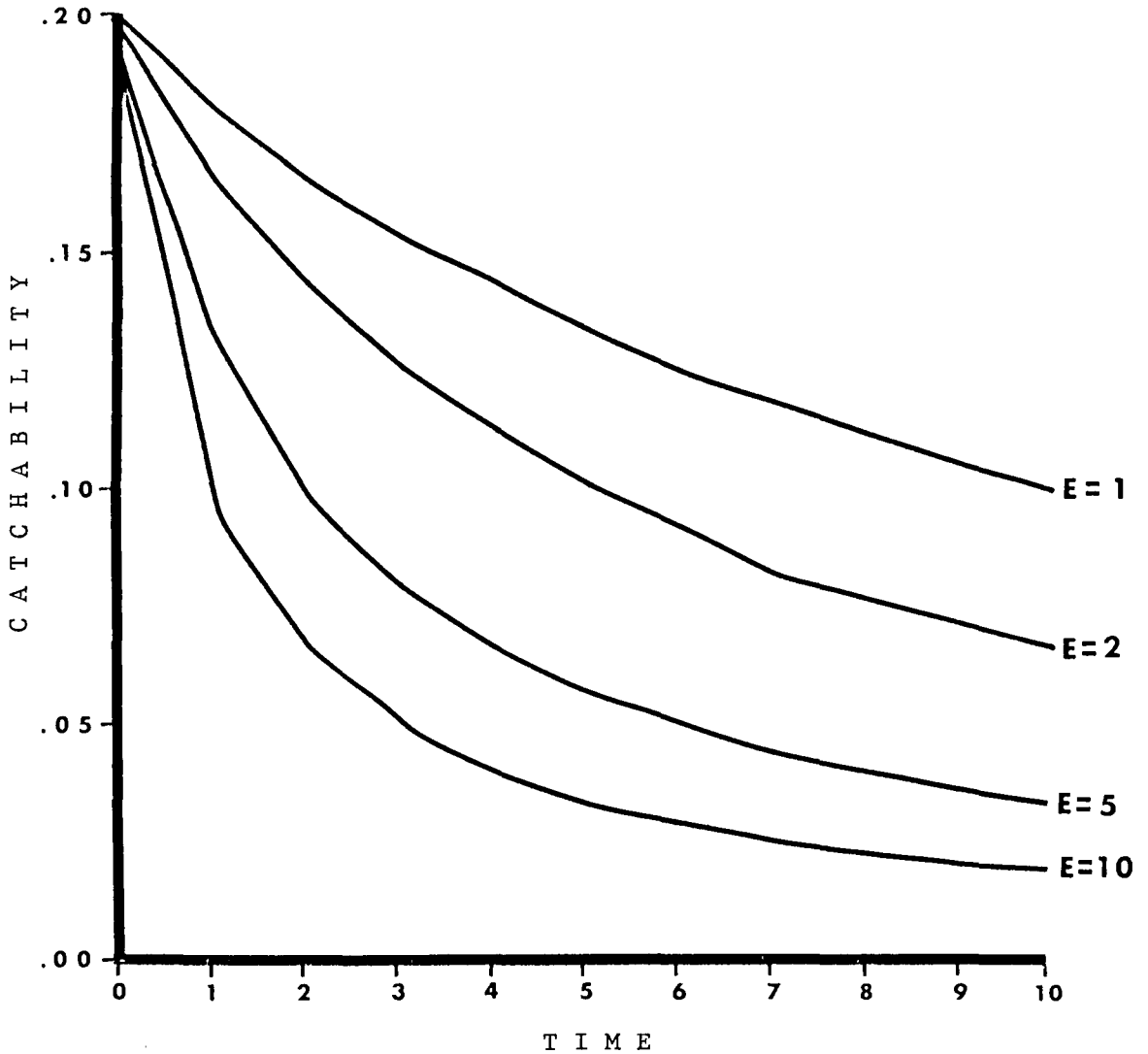


Fig. 1. Change in average population catchability resulting from removal of more catchable individuals. Graph based on an initial gamma distribution of catchability with parameters  $\alpha = 10$ ,  $n = 2$ .  $E$  is effort per unit time.

to the von Bertalanffy equation:

$$g(z) = 3k[z_{\infty}^{1/3} z^{2/3} - z] ,$$

or

$$z(a) = z_{\infty}(1 - e^{-ka})^3 .$$

Also assume that bass are subject to a constant natural mortality rate over all sizes beyond the size of recruitment and that through some mechanism recruitment is constant. Then Theorem 3 implies that the asymptotic size structure of the population is given by

$$\eta(z) = \exp[-\mu a(z)]/g(z) .$$

If we now impose a fishing mortality rate  $f$  on all sizes, the resulting stationary size structure will be given by

$$\eta_1(z) = \exp[-(\mu + f)a(z)]/g(z) .$$

These size structures are illustrated in Figure 2 for the case  $z_{\infty} = 500$ ,  $k = .3$ ,  $\mu = .4$ ,  $f = .4$ . The effects of exploitation are obvious.

#### Selection of Size Limits

Once again, assume a simple population having von Bertalanffy growth and constant natural mortality. Assume that fishing mortality rate  $f$  is constant for all fish that are legally subject to capture and zero elsewhere. Also, suppose that  $f$  is not affected by changes in size limits. Size limits might then be chosen as follows:

Principle: It should be required that a fish which has been caught be released if and only if its expected value through subsequent

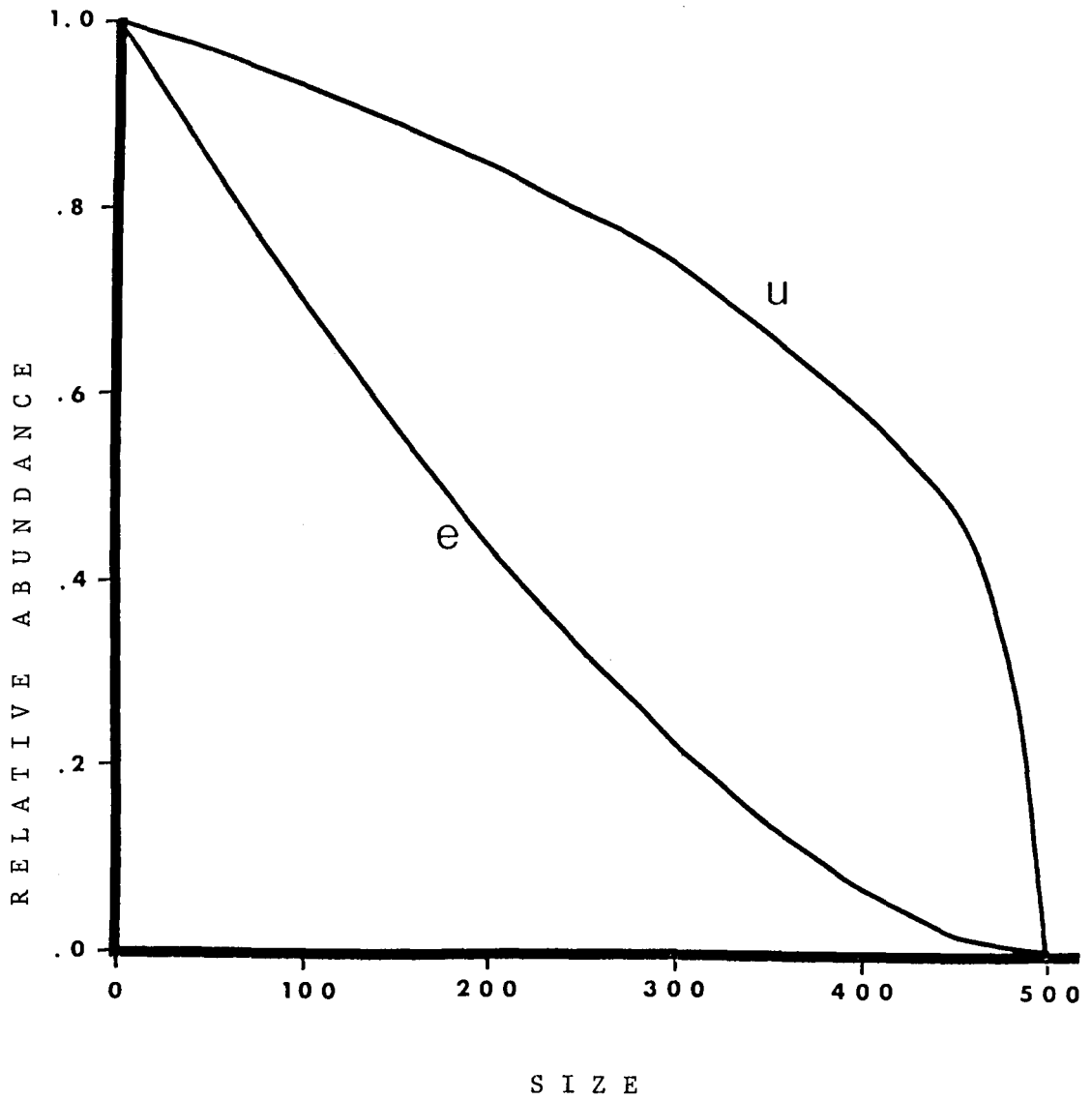


Fig. 2. Size structure of an artificial population with asymptotic individual size  $z_{\infty} = 500$ , instantaneous growth rate  $K = 0.3$ , and natural mortality rate  $\mu = 0.4$  without exploitation (u) and with a fishing mortality rate of  $f = 0.4$  (e).

capture or prey consumption when released exceeds its present value.

A number of measures of value may be appropriate in various situations. I shall assume for simplicity that value corresponds to biomass yield. In the absence of regulations, the expected value of a fish known to be alive with body weight  $z_0$  at some time may be calculated as follows:

1) Under the assumptions, the distribution of age at death is given by  $(f + \mu)e^{-(\mu+f)(a-a(z_0))}$ . The distribution of age at death given that death is due to capture is identical and the probability of death due to capture is  $\frac{f}{f+\mu}$ .

2) The distribution of size at capture will then be given by  $(f + \mu)\exp[-(\mu + f)(a(z) - a(z_0))] \frac{1}{g(z)}$ .

3) Expected value is then given by

$$Ev(z_0) = \frac{f}{f+\mu} \int_{z_0}^{z_\infty} \frac{z}{g(z)} (f+\mu) e^{-(f+\mu)(a(z)-a(z_0))} dz .$$

4) Substituting for  $g(z)$  and  $a(z)$ , we have

$$\begin{aligned} Ev(z_0) &= f e^{(f+\mu)a(z_0)} \int_{z_0}^{z_\infty} \frac{z}{g(z)} e^{-(f+\mu)a(z)} dz \\ &= \frac{f}{3k} e^{(f+\mu)a(z_0)} \int_{z_0}^{z_\infty} z [z_\infty^{1/3} z^{2/3} - z]^{-1} [1 - (\frac{z}{z_\infty})^{1/3}]^{(f+\mu)/k} \\ &= \frac{f}{3k} e^{(f+\mu)a(z_0)} \int_{z_0}^{z_\infty} (\frac{z}{z_\infty})^{1/3} [1 - (\frac{z}{z_\infty})^{1/3}]^{(f+\mu)/k-1} dz \\ &= z_\infty [1 + \frac{3k}{\mu+f+k} e^{-ka(z_0)} - \frac{6k}{\mu+f+k} e^{-2k a(z_0)} + \frac{3k}{\mu+f+k} e^{-3k a(z_0)} \\ &\quad + \frac{2k}{\mu+f+3k} e^{-(\mu+f+3k)a(z_0)} - \frac{2k}{\mu+f+2k} e^{-(\mu+f+k)a(z_0)}] . \end{aligned}$$

Thus the maximum of  $Ev(z_0)$  occurs at

$$z_0 = z \left( 1 - \exp \left[ -k \ln \left\{ \left( \frac{\mu+f+k}{3} \right)^{1/(\mu+f+k)} \right\} \right] \right)^3 .$$

Thus any range of protected sizes should contain the point  $z_0$ . Under more general assumptions, the calculations are naturally more complex but can be done numerically. Searches for optimal limits are also possible.

#### Predator-Prey Relationships

At present, it is not possible to predict the response of a bass population to the size structure of available prey. Such predictions require an understanding of the functional responses of bass to prey size distribution in terms of feeding behavior, energetics, and mortality.

Resolution of this issue will require further investigation of prey selection by bass, the influence of size of prey on digestion rate, feeding frequency, and energetic efficiency, and the response of bass growth and mortality rates to net energy availability.

#### Production and Yield

Production over a time interval  $[t_1, t_2]$  is defined as the total biomass elaborated by a population during the interval. Thus, production during  $[t_1, t_2]$  is equivalent to the net change in standing crop, plus the total weight of fish dying during the interval (Chapman 1967).



Once again, suppose a size structured model with  $z$  representing body weight. Then population biomass is given by  $\int_0^{z_\infty} z \eta(z; t) dz = \omega(t)$ . Now using Liebzniz rule,

$$\frac{\partial \omega(t)}{\partial t} = \int_0^{z_\infty} z \frac{\partial \eta(z; t)}{\partial t} dz$$

which according to this model, if growth is continuous and deterministic is

$$\frac{\partial \omega(t)}{\partial t} = -\int_0^{z_\infty} \left[ \frac{\partial (g(z)\eta(z; t))}{\partial z} \right] z dz - \int_0^{z_\infty} z\mu(z; t)\eta(z; t) dz .$$

On integration by parts this becomes

$$\frac{\partial \omega(t)}{\partial t} = \int_0^{z_\infty} g(z; t)\eta(z; t) dz - \int_0^{z_\infty} z\mu(z; t)\eta(z; t) dz ,$$

assuming no individuals survive to  $z_\infty$  and no reproduction occurs.

Since production is typically computed over times not including spawning this will often be appropriate. Now since production is change in biomass plus biomass lost through death, instantaneous production is given by

$$\begin{aligned} P'(t) &= \frac{\partial \omega(t)}{\partial t} + \int_0^{z_\infty} z\mu(z; t)\eta(z; t) dz \\ &= \int_0^{z_\infty} g(z; t)\eta(z; t) dz . \end{aligned}$$

Production over the interval  $[t_1, t_2]$  is therefore given by

$$P(t_1, t_2) = \int_{t_1}^{t_2} \int_0^{z_\infty} g(z, t)\eta(z, t) dz dt .$$

Yield is the biomass removed from the population by fishing. The instantaneous yield from a population may therefore be computed as

$$Y'(t) = \int_0^{z_{\infty}} zf(z;t)\eta(z;t) dz ,$$

and yield over a period of time will be given by

$$Y(t_1, t_2) = \int_{t_1}^{t_2} \int_0^{z_{\infty}} zf(z;t)\eta(z;t) dz dt .$$

Van Sickle (1976) has shown these yield and production equations to be equivalent to traditional equations for estimating production under certain assumptions.

The more interesting problems of production and yield in bass populations must await further empirical investigation of the patterns of variation in bass growth.

## SUMMARY

In this thesis, I have developed a general theory of the relationship between life history and population structure. In its most usable form the model is represented by a stochastic integral equation that is analagous to the classical Lotka model for age structure of populations. The corresponding differential equations can also be used successfully when closed-form solutions are available or when the phenotype dimension is low enough to permit numerical solution.

Although they were not discussed above, three other approaches could be used as substitutes for this theory. The first is to develop the model equations in terms of the structure function  $F(\underline{T}, t)$  rather than the corresponding "density"  $f(\underline{T}, t)$ . Although this requires somewhat fewer assumptions, the results are more complicated and more tedious to prove. The second approach is to apply a Fourier transform to derive a differential equation for the "characteristic function" of population structure. This approach is even more tedious than using the structure function and is less intuitive but leads to equations that are more susceptible to numerical solution. The third approach is one of strict simulation of life history phenomena with an appropriate summary of population structure. This technique would be very useful for studying applied problems but is also limited by lack of generality in the resulting predictions unless considerable computation is done with a variety of assumptions. Each of the five approaches summarized here should be developed further.

Three general conclusions can be found in the theory described in this thesis. The first is that population dynamics may be appropriately viewed as a consequence of life history phenomena. This view suggests that, at least where prediction of population structure or where explanation of the phenomena is desired, such phenomena as density-dependence may be most appropriately described by analyzing the effects of population structure and density on life history in the population. The second conclusion is that variation in life history may be important in determining population structure. Terms describing the effects of variation are explicitly included in the model equations. The magnitude of these terms, however, is completely unknown for any life histories with which I am familiar. The third conclusion to be drawn is that population structure, at least averaged over time, should be fairly stable in large populations. The effects of variation in small populations, on the other hand, have not been analyzed and might be important.

The applications to largemouth bass populations described in the last section are not conclusive for any realistic management problems. They are intended to illustrate some possible uses of the model. Some conclusions may be drawn from these, however. The application to the effects of exploitation on catchability makes plausible the hypothesis that declining catchability under exploitation is due to removal of more catchable fish. The other applications provide some justification for using size-structured models rather than more conventional age-structured population models.

As often occurs, the work contained in this thesis has led to more questions than it has answered. I recommend further research to

1) develop all of the alternative forms of this theory, preferably in the context of specific problems;

2) develop methods for solving the model equations under fairly general assumptions;

3) determine in more detail the statistical properties that the models predict;

4) relate the size structure and abundance of prey to food consumption, growth, and mortality of bass, especially as they lead to density-dependence; and

5) determine the effects of year-class fluctuations on production and yield of bass fisheries.

#### LITERATURE CITED

- Anderson, R. O. 1974. Influence of mortality rates on production and potential sustained harvest of largemouth bass populations. Page 18-28 in J. L. Funk, ed. Symposium on overharvest and management of largemouth bass in small impoundments. North Central Div., Am. Fish. Soc., Spec. Publ. No. 3. 116 pp.
- Anderson, R. O. 1975a. Factor influencing the quality of largemouth bass fishing. Page 183-194 in H. Clepper, ed. Black bass biology and management. Sport Fishing Institute, Washington, D.C. 534 pp.
- Anderson, R. O. 1975b. Optimum sustainable yield in inland recreational fisheries management. Page 29-38 in P. M. Roedel, ed. Optimum sustainable yield as a concept in fisheries management. Amer. Fish. Soc., Spec. Publ. No. 9. 89 pp.
- Anderson, R. O. and M. L. Heman. 1969. Angling as a factor influencing catchability of largemouth bass. Trans. Amer. Fish. Soc. 98 (2): 317-320.
- Bailey, V. A. 1931. The interaction between hosts and parasites. Quart. J. Math. 2: 68-77.
- Bennett, G. W. 1949. Training school for bass. Ill. Wildlife 3 (3): 6-7.
- Bennett, G. W. 1974. Ecology and management of largemouth bass, Micropterus salmoides (Lac.). Pages 10-17 in J. L. Funk, ed. Symposium on overharvest and management of largemouth bass in small impoundments. North. Central Div., Am. Fish. Soc., Spec. Publ. No. 3. 116 pp.
- Bennett, G. W., H. W. Adkins, and W. F. Childers. 1963. The largemouth bass and other fishes in Ridge Lake, Illinois, 1941-1963. Ill. Nat. Hist. Survey Bull. 30 (1), 1-67.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. (London) 19: 1-533.
- Bharucha-Reid, A. T. 1972. Random integral equations. Academic Press, New York. 267 pp.
- Chapman, D. W. 1967. Production in fish populations. Pages in S. D. Gerking, ed. The biological basis of freshwater fish production. John Wiley and Sons, New York.

- Clady, M. 1977. Abundance and production of young largemouth bass, smallmouth bass, and yellow perch in two infertile Michigan Lakes. *Trans. Amer. Fish. Soc.* 106 (1): 57-63.
- Dillard, J. G. and G. Novinger. 1975. Stocking largemouth bass in small impoundments. Page 459-474 in H. Clepper, ed. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C. 534 pp.
- Feller, W. 1941. On the integral equation of renewal theory. *Annals of Math. Stat.* 12: 243.
- Fox, A. C. 1975. Effects of traditional harvest regulations on bass populations and fishing. Pages 392-398 in H. Clepper, ed. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C. 534 pp.
- Harris, B. 1966. *Theory of probability*. Addison-Wesley Publishing Company, Reading, Mass. 294 pp.
- Holbrook, J., II. 1975. Bass fishing tournaments. Page 408-415 in H. Clepper, ed. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C. 534 pp.
- Houser, A. and W. C. Rainwater. 1975. Production of largemouth bass in Beaver and Bull Shoals Lakes. Page 310-316 in H. Clepper, ed. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C. 534 pp.
- Hoyle, F. 1963. A contradiction in the argument of Malthus. *Univ. of Hull Pub.*, Hull. 22 pp.
- Itô, K. 1950. Stochastic differential equations in a differentiable manifold. *Nagoya Math. J.* 1: 35-47.
- Itô, K. 1951. On stochastic differential equations. *Mem. Amer. Math. Soc.* No. 4.
- Itô, K. and H. P. McKean. 1965. *Diffusion processes and their sample paths*. Springer-Verlag, Berlin and New York.
- Jenkins, R. M. and D. I. Morais. 1977. Prey-predator relationships in the Predator-Stocking-Evaluation reservoirs. *Proc. South-eastern Assoc. Game and Fish Comm.* (in press).
- Keyfitz, N. 1968. *Introduction to the mathematics of populations*. Addison-Wesley Publ. Co., Reading, Mass. 450 pp.
- Lagler, K. F. and G. C. DeRoth. 1953. Populations and yield to anglers in a fishery for largemouth bass. *Mich. Acad. Sci., Arts and Letters (Papers)* 38: 235-253.

- Lawrence, J. M. 1958. Mouth size of largemouth bass in relationship to size of forage fishes. Ph.D. Thesis, Iowa State College.
- Lopez, A. 1967. Asymptotic properties of a human age distribution under a continuous net maternity function. *Demography* 4: 680-687.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore. Republished by Dover Publications, 1956.
- Odum, E. P. 1971. *Fundamentals of ecology*, 3rd ed. W. B. Saunders Company, Philadelphia. 574 pp.
- Oldfield, D. G. 1966. A continuity equation for cell populations. *Bull. Math. Biophys.* 28: 545-554.
- Pearl, L. and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. Nat. Acad. Sci.* 6: 275-288.
- Rasmussen, J. L. and S. M. Michaelson. 1974. Attempts to prevent largemouth bass overharvest in three Northwest Missouri lakes. Pages 69-83 in J. L. Funk, ed. *Symposium on overharvest and management of largemouth bass in small impoundments*. North Central Div., Amer. Fish. Soc. Spec. Publ. No. 3. 116 pp.
- Redmond, L. C. 1974. Prevention of overharvest of largemouth bass in Missouri impoundments. Pages 54-68 in J. L. Funk, ed. *Symposium on overharvest and management of largemouth bass in small impoundments*. North Central Div., Amer. Fish. Soc. Spec. Publ. No. 3. 116 pp.
- Ricker, W. E. 1945. A method of estimating minimum size limits for obtaining maximum yield. *Copeia* 1945 (2): 89-94.
- Sanderson, A. E., Jr. 1958. Smallmouth bass management in the Potomac River Basin. *Trans. North Amer. Wild. Conf.* 23: 248-262.
- Shaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Bull. Inter-Amer. Trop. Tuna Comm.* 1: 26-56.
- Sinko, J. W. and W. Streifer. 1967. A new model for age-size structure of a population. *Ecology* 48 (6): 910-918.
- Swingle, H. S. 1950. Relationships and dynamics of balanced and unbalanced fish populations. *Alabama Polytech. Inst., Agr. Expt. Sta. Bull.* 274. 73 pp.



- Trucco, E. 1965. Mathematical models for cellular systems: The Von Foerster equation. Part I. Bull. Math. Biophys. 27: 449-472.
- Usher, M. B. 1963. Biological conservation. Allen and Unwin, Inc., London.
- Van Sickle, J. 1976. The theory of physiological age distributions in biological populations. Ph. D. Thesis, Michigan State University. 113 pp.
- Verhulst, P. F. 1838. Notice sur la loi que la population suit dans son accroissement. Corr. Math. et Phys. 10: 113-121.
- Von Foerster, H. 1959. Some remarks on changing populations. Pages 382-407 in F. Stohlman, Jr., ed., The kinetics of cellular proliferation. Grune and Stratton, New York.
- Webster's New International Dictionary, 2nd ed. 1959. G. & C. Merriam Company, Springfield, Mass.
- Wright, S. 1931. Evolution in Mendelian populations. Genetics 16: 97-159.

APPENDIX I: Derivation of life history operator equation.

Let  $F(\underline{T}; a, t_b)$  be the probability than an organism described by the given life history has phenotype  $\underline{P} \leq \underline{T}$  at age  $a$ . Any change in  $F(\underline{T}; a, t_b)$  must be the result of flux across the boundary of the solid given by  $0 \leq \underline{P} \leq \underline{T}$  due to the growth and event processes or a result of the death process. Hence,

$$\begin{aligned} \frac{\partial F(\underline{T}; a, t_b)}{\partial a} = & -\int_0^{\underline{T}} \dots \int_0^{\underline{T}} \mu(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \dots dP_n \\ & -\int_0^{\underline{T}} \dots \int_0^{\underline{T}} \bar{H}(\underline{T}; \underline{P}, a, t_b) f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \dots dP_n \\ & +\int_{\underline{T}_n}^{\infty} \dots \int_{t_1}^{\infty} H(\underline{T}; \underline{P}', a, t_b) f(\underline{P}'; a, t_b) r(\underline{P}'; a, t_b) dP'_1 \dots dP'_n \\ & +\int_S f(\underline{P}; a, t_b) (\underline{g}(\underline{P}; a, t_b) \cdot \underline{n}) ds \end{aligned}$$

where  $\bar{H} = 1 - H$ ,  $s$  is the surface of the solid  $0 \leq \underline{P} \leq \underline{T}$ ,  $ds$  is a surface element, and  $\underline{n}$  is the inward normal of  $s$ . Now since  $\bar{H} = 1 - H$ , the second RHS term may be written as

$$\begin{aligned} \int_0^{\underline{T}} \dots \int_0^{\underline{T}} H(\underline{T}; \underline{P}, a, t_b) f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \dots dP_n \\ - \int_0^{\underline{T}} \dots \int_0^{\underline{T}} f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \dots dP_n \end{aligned}$$

whence (1a) becomes

$$\begin{aligned} \frac{\partial F(\underline{T}; a, t_b)}{\partial a} = & -\int_0^{\underline{T}} \dots \int_0^{\underline{T}} \mu(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \dots dP_n \\ & -\int_0^{\underline{T}} \dots \int_0^{\underline{T}} r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \dots dP_n \\ & +\int_0^{\infty} \dots \int_0^{\infty} H(\underline{T}; \underline{P}, a, t_b) r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \dots dP_n \\ & +\int_S f(\underline{P}; a, t_b) (\underline{g}(\underline{P}; a, t_b) \cdot \underline{n}) ds . \end{aligned}$$

But  $H(\underline{T}; \underline{P}; a, t_b) = \int_0^{\underline{T}_n} \dots \int_0^{\underline{T}_1} h(\underline{P}'; \underline{P}, a, t_b) dP'_1 \dots dP'_n$  and  $h$  is non-negative, so by the general Fubini-Stone Theorem, we may interchange the order of integration, obtaining

$$\begin{aligned} \frac{\partial F(\underline{T}; a, t_b)}{\partial a} &= \int_0^{\underline{T}_n} \dots \int_0^{\underline{T}_1} [(-\mu(\underline{P}; a, t_b) + r(\underline{P}; a, t_b)) f(\underline{P}; a, t_b) \\ &+ \int_0^\infty \dots \int_0^\infty h(\underline{P}'; \underline{P}, a, t_b) r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP'_1 \dots dP'_n] dP_1 \dots dP_n \\ &+ \int_S f(\underline{P}; a, t_b) (\underline{g}(\underline{P}; a, t_b) \cdot \underline{n}) ds. \end{aligned} \quad (2a)$$

Bharucha-Reid (1972), in proving the  $N$ -dimensional forward Kolmogorov equation, has shown that terms of the form of the last RHS term are equivalent to

$$\begin{aligned} &\int_0^{\underline{T}_n} \dots \int_0^{\underline{T}_1} \left[ \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 [\sigma_{ij}(\underline{P}; a, t_b) f(\underline{P}; a, t_b)]}{\partial P_i \partial P_j} \right. \\ &\left. - \sum_{i=1}^n \frac{\partial [m_i(\underline{P}; a, t_b) f(\underline{P}; a, t_b)]}{\partial P_i} \right] dP_1 \dots dP_n. \end{aligned}$$

Now, since  $F(\underline{T}; a, t_b) = \int_0^{\underline{T}_n} \dots \int_0^{\underline{T}_1} f(\underline{P}; a, t_b) dP_1 \dots dP_n$ , interchanging differentiation and integration on the left hand side and collecting terms gives

$$\begin{aligned} 0 &= \int_0^{\underline{T}_n} \dots \int_0^{\underline{T}_1} \left[ \frac{\partial f(\underline{P}; a, t_b)}{\partial a} + \mu(\underline{P}; a, t_b) f(\underline{P}; a, t_b) + r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) \right. \\ &- \int_0^\infty \dots \int_0^\infty h(\underline{P}'; \underline{P}, a, t_b) r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP'_1 \dots dP'_n \\ &\left. - \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 [\sigma_{ij}(\underline{P}; a, t_b) f(\underline{P}; a, t_b)]}{\partial P_i \partial P_j} - \sum_{i=1}^n \frac{\partial [m_i(\underline{P}; a, t_b) f(\underline{P}; a, t_b)]}{\partial P_i} \right] dP_1 \dots dP_n. \end{aligned}$$

But  $\underline{T}$  is arbitrary, so the integrand must be zero. Q E D

APPENDIX II: Proof of the existence and uniqueness of a solution to the integral equation of the birth process.

Theorem: The stochastic integral equation

$$B(t;\omega) = q(t;\omega) + \frac{1}{p} \int_0^t \phi(t,\tau;\omega)B(\tau;\omega)d\tau \quad \omega \in \Omega \quad (1b)$$

has a unique random solution  $B(t;\omega)$  in the space  $C$  of all second-order stochastic processes defined on  $R_+$  which are bounded and continuous in mean-square, such that  $\|B(t;\omega)\|_C \leq \rho$  for some  $\rho > 0$ , if

i)  $\|\phi(t,\tau;\omega)\| \leq M e^{-\nu(t-\tau)}$  for  $0 \leq \tau \leq t < \infty$ , where  $\nu$  and  $M$  are positive constants;

ii)  $q(t;\omega) \in C$ ; and

iii)  $\|q(t;\omega)\|_C \leq \rho[1 - M^*/\nu^*]$  and  $M^* < \nu^*$

where  $M^*$  is the infimum of the set of all constants  $M$  satisfying (i) and  $\nu^*$  is the supremum of all  $\nu$  satisfying  $\lambda(a;\omega) \leq e^{-\nu a}$  for all  $a$ .

Proof: It has been shown by Bharucha-Reid (1972) that under conditions equivalent to (i) and (ii) there exists a unique random solutions of the form (1b) if the Banach spaces involved are admissible with respect to the integral operator

$$(Tx)(t;\omega) = \int_0^t \phi(t,\tau;\omega)x(\tau;\omega) ds. \quad (2b)$$

Therefore, it is sufficient to establish that the pair of spaces  $(C,C)$  is admissible with respect to the operator  $T$  given by (2b) and verify that  $q(t;\omega)$  is in the space  $C$ .

Taking the norm in  $L_2(\Omega, A, P)$ , the space of all measurable functions defined on  $R_+$  such that the function is bounded in mean-square for all  $t \in R_+$ , we have

$$\begin{aligned} \|(Tx)(t; \omega)\| &\leq \int_0^t \|\phi(t, \tau; \omega)x(\tau; \omega)\| d\tau \\ &\leq \int_0^t \|\phi(t, \tau; \omega)\| \cdot \|x(\tau; \omega)\| d\tau \\ &\leq \sup_{t \geq 0} \{\|x(t; \omega)\|\} \int_0^t \|\phi(t, \tau; \omega)\| d\tau \\ &\leq \|x(t; \omega)\|_c M \int_0^t e^{-\nu(t-\tau)} d\tau . \end{aligned}$$

Thus, since

$$\int_0^t e^{-\nu(t-\tau)} dz = \frac{1}{\nu} (1 - e^{-\nu t}) ,$$

$$\|(Tx)(t; \omega)\| \leq \|x(t; \omega)\|_c \left(\frac{M}{\nu}\right) (1 - e^{-\nu t}) \quad t \geq 0$$

Therefore,  $(Tx)(t; \omega)$  is bounded in mean-square and is in  $C$  by definition. Hence the pair  $(C, C)$  is admissible with respect to the operator  $T$ . Since

$$\begin{aligned} \sup_{t \geq 0} \|(Tx)(t; \omega)\| &= \|(Tx)(t; \omega)\|_c \\ &\leq \|x(t; \omega)\|_c \left(\frac{M}{\nu}\right) \sup_{t \geq 0} (1 - e^{-\nu t}) \\ &= \frac{M}{\nu} \|x(t; \omega)\|_c \end{aligned}$$

the norm of  $T$  is  $M^*/\nu^*$  where  $M^*$  is the least upper bound of  $b(t; \omega)$

for almost all  $\omega$  and  $e^{-v^*a}$  is the greatest lower bound of  $\lambda(a;\omega)$  for all  $a$  and almost all  $\omega$ .

Now, we must verify that  $q(t;\omega)$  is in  $C$ . We will assume that the size of the population at time 0 is finite and bounded by  $N > 0$ , i.e.,  $\int_0^\infty n(a,0;\omega)da \leq N$  for almost all  $\omega \in \Omega$ . Then

$$\begin{aligned} q(t;\omega) &= \int_t^\infty k(0,a,t)b(a,t;\omega)n(a-t;0;\omega)da \\ &\leq e^{-v^*t} M^*N_0 < \infty \text{ for almost all } \omega \end{aligned}$$

by the assumption that  $b(a,t;\omega)$  is bounded by  $M^*$  and  $k(0,a,t) \leq e^{-v^*t}$ . Therefore

$$\begin{aligned} \int_\Omega |q(t;\omega)|^2 dP(\omega) &\leq \int_\Omega |e^{-v^*t} M^*N_0|^2 dP(\omega) \\ &= (e^{-v^*t} M^*N_0)^2 < \infty \quad t \in R_+ \end{aligned}$$

and so by definition  $q(t;\omega)$  is in the space  $L_2(\Omega, A, P)$ . Also

$$||q(t;\omega)|| = \{\int_\Omega |q(t;\omega)|^2 dP(\omega)\}^{1/2} \leq e^{-v^*t} M^* N_0,$$

which means that  $q(t;\omega)$  is bounded in  $L_2(\Omega, A, P)$ . Therefore there exists a unique random solution of the stochastic integral equation (1b) provided that  $M^* < v^*$  and  $||q(t;\omega)||_c = M^*N^* \leq \rho[1-M^*/v^*]$  since we have  $||q(t;\omega)||_c = \sup_{t \geq 0} ||q(t;\omega)||_{L_2} = M^*N^*$  where  $N^*$  is the infimum of  $\{N\}$ , completing the proof.

### APPENDIX III

#### List of Symbols Used.

- $\underline{T} \equiv (T_1, \dots, T_n)'$  - trait vector or phenotype description where each vector element represents one trait
- $\tau$  - space of possible trait vectors
- $t$  - time
- $t_b, t_d$  - times of birth, death
- $a$  - age
- $\omega, \Omega$  -  $\omega$  specificies a particular outcome from the set of lives indexed by  $\Omega$
- $\underline{g}(\underline{T}, a; t_b)$  - derivative of the continuous part of the life history
- $r(\underline{T}, a; t_b)$  - rate function of the life history event process
- $H(j; \underline{T}, a, t_b)$  - distribution of phenotypes resulting from the event process;  
and
- $h(j; \underline{T}, a, t_b)$  -  $h$  is the corresponding density
- $\mu(\underline{T}, a; t_b)$  - instantaneous death rate function
- $\lambda(a; t_b)$  - probability of survival to age  $a$ , given birth at  $t_b$
- $F(\underline{T}; a, t_b)$  - probability an organism survives to age  $a$  and has phenotype  $\underline{P} \leq I$ .  $f(I; a, t_b)$  is the corresponding density over  $\tau$ .
- $\underline{P} \equiv (a, \underline{T}')$  - vector containing age and trait vector
- $N(\underline{P}, t)$  - number of individuals in a population at time  $t$  with phenotype  $\underline{x} \leq \underline{P}$ .  $n(\underline{P}, t)$  is the corresponding 'density'.

- $\eta(\underline{P}, t)$  - expected value of  $n(\underline{P}, t)$
- $\beta(\underline{T}, t)$  - expected number of births at time  $t$  of organisms with phenotype  $\underline{T}$ .
- $b(\underline{P}_n, t; \underline{P}_p)$  - actual rate of production of neonates with phenotype  $\underline{P}_n$  by parents with phenotype  $\underline{P}_p$  at time  $t$
- $B(\underline{P}_n, t)$  - actual number of births at time  $t$  of organisms with phenotype  $\underline{P}_n$ .
- $\tau$  - substitute time parameter
- $k(\underline{P}_2, t_2; \underline{P}_1, t_1)$  - likelihood that an organism with phenotype  $\underline{P}_1$  at time  $t_1$  will survive to time  $t_2$  and have phenotype  $\underline{P}_2$
- $\phi(t, \tau)$  - expected number of offspring produced at time  $t$  by an individual born at time  $\tau$
- $c$  - catchability
- $E$  - effort per unit time
- $\mu$  - natural mortality rate
- $c(t)$  - average catchability at time  $t$
- $z$  - body weight
- $k$  - von Bertalanffy growth rate
- $z_\infty$  - asymptotic size
- $f$  - fishing mortality rate
- $Ev(z)$  - expected value of a fish of size  $z$  if released rather than kept when captured at that size



- $\omega(t)$  - population biomass at time  $t$
- $P(t_1, t_2)$  - production between times  $t_1, t_2$
- $Y(t_1, t_2)$  - yield in the interval from  $t_1$  to  $t_2$

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A GENERALIZED POPULATION DYNAMICS THEORY FOR  
LARGEMOUTH BASS FISHERIES

by

Douglas Brewer Jester, Jr.

ABSTRACT

Resolution of the main issues in largemouth bass management will require the ability to predict the effects of exploitation on population structure, optimally select size limits, relate bass population structure to prey population structure, and predict the effects of fluctuations in recruitment on production and yield. A general model of population structure was developed for use in studying these problems.

The model was derived by examining the relationship between life history and population structure. Life history processes are described as mixed continuous and jump stochastic processes. The model was derived in two forms, an integro-differential equation and a stochastic integral equation, which include all of the classical continuous-time population models as special cases.

Two general results concerning the model were proven. First, the stochastic integral equation was shown to predict the same expected population structure as a deterministic model using average birth and death rates whenever the processes are uncorrelated. However, it is very unlikely that birth rate, death rate, and density will be independent, so the stochastic and deterministic models will

generally diverge. Second, it was shown that with density-independence the expected population structure in the stochastic model is asymptotically stable.

Special cases of the model were used to illustrate the possible effects of exploitation on average catchability and population structure. Methods for calculation of optimal length limits and production and yield were illustrated for simple cases. Use of the full power of the model, however, must await more detailed description of factors influencing mortality and growth, especially the effect of the density and size structure of available prey.