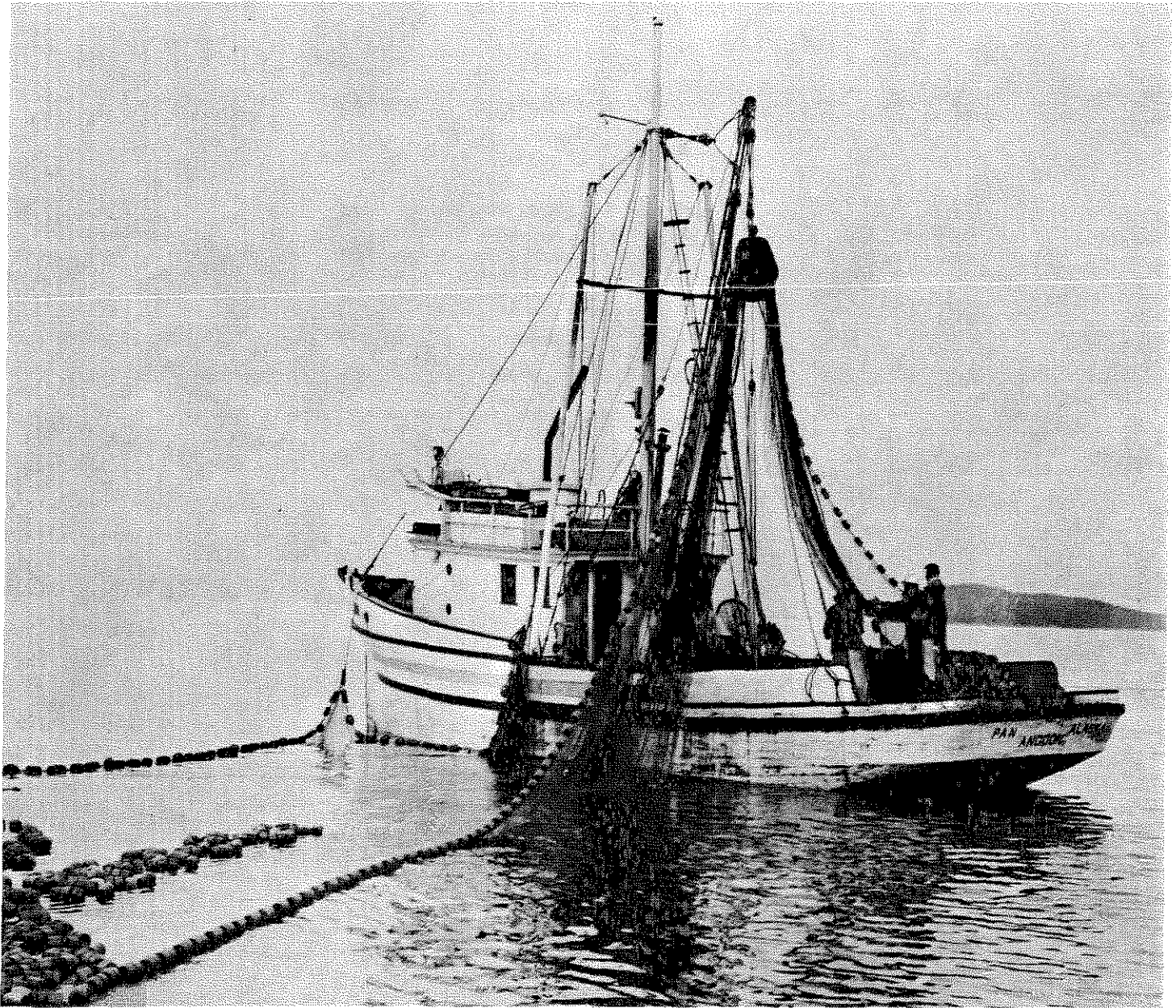# A GENERAL POPULATION DYNAMICS THEORY
FOR LARGEMOUTH BASS

U. S. Forest Service

A General Population Dynamics Theory for Largemouth Bass[1]

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ABSTRACT

In this report, we develop a general theory of the relationship between life history and population structure for largemouth bass. 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.

Three general conclusions are presented. First, 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 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 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 we are familiar. The third conclusion to be drawn is that population structure, at least averaged over time, should be fairly stable in large populations. Effects of variation in small populations, on the other hand, have not been analyzed and might be important.

Applications to largemouth bass populations are not conclusive for any realistic fisheries management problems, but are intended to illustrate some possible uses of the model. Some conclusions may be drawn from these, however. The application to 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.

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 amenable 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.

As usually occurs, the research contained in this report has led to more questions than it has answered. Further research is needed to:
1) develop all alternative forms of this theory, preferably in the context of specific fisheries 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 size structure and abundance of prey to food consumption, growth, and mortality of bass, especially as they lead to density-dependence; and
5) determine effects of year-class fluctuations on production and yield of bass populations.

I. INTRODUCTION

Managers of largemouth bass *(Micropterus salmoides)* populations are usually confronted with highly variable habitats containing a diverse fish community and several species may be concurrently harvested. The literature on bass management is disjointed and often contradictory. Rarely is there a coherent generalized understanding of the structure, dynamics, and production capability of the populations to be managed.

In an effort to enhance understanding of fish population dynamics and thereby increase management capabilities, mathematical models or theories have been formulated which attempt to describe how fish populations behave. Some of these models have become classical tools in fisheries management. Unfortunately, none of the models is particularly useful for the bass manager because each assumes dynamic independence of fish populations and other ecosystem components.

The largemouth bass occupies a variety of habitats from the saline coastal marshes of Louisiana to the boreal lakes of the Canadian Pre-Cambrian shield. In the southern part of the United States, it is most successful in warm, shallow reservoirs, and in the everglades, lakes, and clear sluggish canals of Florida. In the Midwest and along the Atlantic coast bass are most abundant in larger reservoirs and smaller lakes fringed with shallow weedy bays. Near the northern limits of its range, in Ontario and Quebec, the largemouth bass has a scattered distribution determined largely by temperature. Throughout its range, the largemouth bass thrives in agricultural ponds and clear sluggish rivers (Robbins and MacCrimmon 1974).

Although fish communities containing only bass (Buck and Thoits 1970) or bass and one other species (Swingle 1950, Regier 1963a, and Regier 1963b) have been extensively studied, under natural conditions there are usually many fish populations to consider. Jenkins (1968) reported positive correlations of standing crops of largemouth bass with the standing crops of spotted gar, spotted bass, white bass, black and white crappie, chain pickerel, gizzard shad, top minnows, bluegill, warmouth, longear and green sunfish, channel and blue catfish, bullhead, carp, and largemouth buffalo in 140 reservoirs. Jenkins' analysis illustrates the potential complexity of fish communities containing largemouth bass.

Angler diversity, i.e., the variety of sport fishermen, is also high. Some anglers exclusively pursue a single fish species, while others exhibit little species preference. Management strategies for a trophy bass fishery may be very different from those for a family-oriented fishery. Recent work (Anderson and Funk 1974, Anderson 1975 a,c) has shown the need for greater understanding of the influence of fishing on bass populations and of factors influencing the quality of bass fishing.

One possible approach to improving the management of largemouth bass fisheries is by use of models (Lackey, Powers, and Zuboy 1975). Simulation models provide a framework for describing complex systems, allow rapid and inexpensive evaluation of alternative management strategies, help identify gaps in available data, and provide a means of constructing and evaluating theories explaining the behavior of a fishery.

In a model, representing each relationship between components of a bass population may be relatively simple. For example, the population density of one age group of some species may influence survival of fry of another species. When many such relationships are integrated, however, the behavior of the model may be extremely complex. Further, a manager is frequently faced with the question: "What will happen *if* I follow a particular management strategy?" Often the tool best suited for addressing this question and the complexity of the interrelationships is computer simulation. For example, a manager could easily examine the probable impact of changing bass size limits if he had a suitable simulator of a bass population.

A very difficult decision in fisheries management or research is which and how much data to collect. Data are expensive to collect, analyze, and interpret and the benefits of data collection may be unclear. Simulation can serve to identify the type of data to be collected and its frequency and location of collection, and to appraise the costs and likely benefits of having it analyzed and used.

Modeling and simulation are heuristic tools. Often, a modeler must hypothesize the existence and form of relationships that have never been considered. His ideas may then be tested empirically for relevance and validity.

Deutsch (1966) has suggested that models are devices for putting items of information into the context of other items. As theories, models help us find contexts for our data; as information retrieval schemes, they help us find data for our contexts. Thus, a model of dynamics of largemouth bass populations should incorporate as much of the existing information on largemouth bass populations as possible and should provide information on the behavior of such systems for use in management theory.

The objective of this bulletin is to present a conceptual population dynamics theory with applications to largemouth bass populations.

II. MODELS

There is nothing inherently exotic about modeling or models. A model is simply a verbal, graphical, physical, or mathematical abstraction of a real system (Lackey 1975). Verbal models may be as simple as, "A fishery, either recreational or commercial, is a system composed of three major interlocking components: habitat, aquatic biota, and man." A fishery can also be described by graphical models. A physical representation of a system, such as an artificial stream aquarium, is another type of model. Physical models allow laboratory control over certain variables of a system while maintaining certain useful physical characteristics of that system. Mathematical models quantitatively simulate real systems through arithmetical calculations. Currently, fisheries modeling usually connotes modeling of a mathematical nature.

Uses of Models

Most models, even those seemingly unrelated, are really quite similar in philosophy and approach, but there is substantial variation between models when they are viewed according to their intended use or function. The evolution of fisheries models has not followed a discrete path, but rather a disjointed and often circuitous route. Major trends apply equally to recreational or commercial fisheries and marine or freshwater fisheries, but with different evolutionary trends being of greater importance when evaluated by scientific effort expended.

Modeling in fisheries management can be justified in many ways, some of which result in benefit/cost ratios greater than unity and others which do not. As a group, fisheries modelers have tended to oversell the potential management benefits derivable from modeling, a characteristic all too frequent in emerging scientific disciplines. The potential benefits of modeling in fisheries management are many, and it is clearly preferable to err on the conservative side as an advocate.

The first and perhaps most obvious potential benefit of modeling in fisheries management is organization. Fisheries are highly complex systems and modeling (graphical or mathematical) does provide a medium for clarification and organization. Used in this context, a model is a theory about the structure, dynamics, and function of a fishery or a component of a fishery.

A second potential benefit of modeling in fisheries management is as a self-teaching device to the builder or user. There may not be a better way to develop an understanding of a fishery than to formally model it. Some fisheries models, particularly computer-implemented models, serve as useful management exercises in universities (Titlow and Lackey 1974).

Identifying gaps in our understanding of resource systems is a third potential benefit from modeling in fisheries management. In modeling, the modeler may become painfully aware of areas of missing data. Acquisition of these data may well be top priority for improving management. Sensitivity analysis in modeling will identify the parameters of most importance in determining model output, and data acquisition and/or research efforts may be allocated accordingly.

Models used as research tools may be considered as a category of potential benefits. Manipulation of the model itself may generate "data" which are unattainable from the real system. For example, the impact of rainfall and water temperature may each have an impact on certain biotic components, and certain combinations of rainfall and temperature levels have been observed in the field to quantify the impact. Exercising the model may permit a reasonable assessment of the *general* relationship by interpolation (based on existing data combinations).

The fifth and most discussed potential benefit of modeling in fisheries management is predicting impact of alternative management decisions or external influences. Historically, managers of commercial fisheries have been interested in predicting impact of a proposed fishing or exploitation rate expressed in the form of a season, mesh size, or quota. Recreational fisheries managers wish to estimate the impact of decisions on the number of realized angler-days, catch, or some other measure (Lackey 1975).

Criteria for Evaluating Models

Theories, taxonomies, models, and schemes for information classification and retrieval are all alike in one important respect: they are devices for putting items of information into the context of other items. When we speak of the "need for a theory," we usually mean that we have at hand some items of information and that we are seeking a context of other data in which they will be meaningful, or more meaningful than before. When we speak of the "need for information," on the other hand, we mean that we have at hand some more or less organized information which gives rise to our "questions" or requests for data and that we are seeking to locate some items of information or data which will be relevant in that context, and thus will function as "answers" to our questions. A model used as a theory helps us to find contexts for our data; it tells us where to put them, or what to make of them. A model used as an information retrieval and organizational scheme helps us find data for our contexts of management analysis. A model of largemouth bass population dynamics, for example, serves multiple purposes. It should explain population behavior by placing information about the biology and ecology of the largemouth bass into a population context, while placing population phenomena in a form useful in the context of fisheries management.

There are several characteristics which an adequate model must possess, at least to some extent. These include generality, realism, comprehensiveness, and completeness. Any increase in one or more of these characteristics necessitates an increase in the complexity of the model. Deutsch (1966) has identified several criteria for evaluating models which can be interpreted in the context of the characteristics just mentioned. Each of these can be related to complexity.

There are two aspects of complexity which must be considered: structural complexity and functional complexity. Structural complexity is roughly the number of quantities and relationships considered in a model. Functional complexity is the number and difficulty of the rules for using the model. Functional complexity generally will increase with an increase in structural complexity in a series of rapid increases and temporary plateaus (Fig. 1).
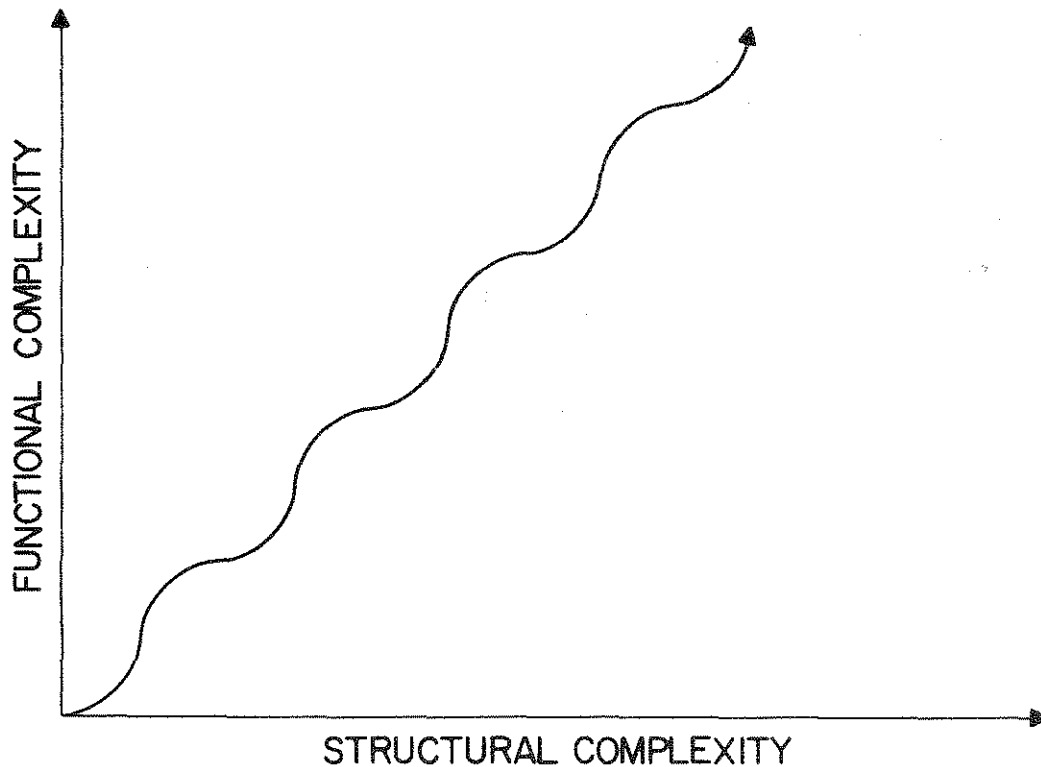

Figure 1. Relationship between functional and structural complexity in models.

The organizing power, or the number and extent of integration of independently established phenomena, of a model can be expected to increase at rapid rates with increases in complexity in simple models and at much slower rates in more complicated models (Fig. 2).
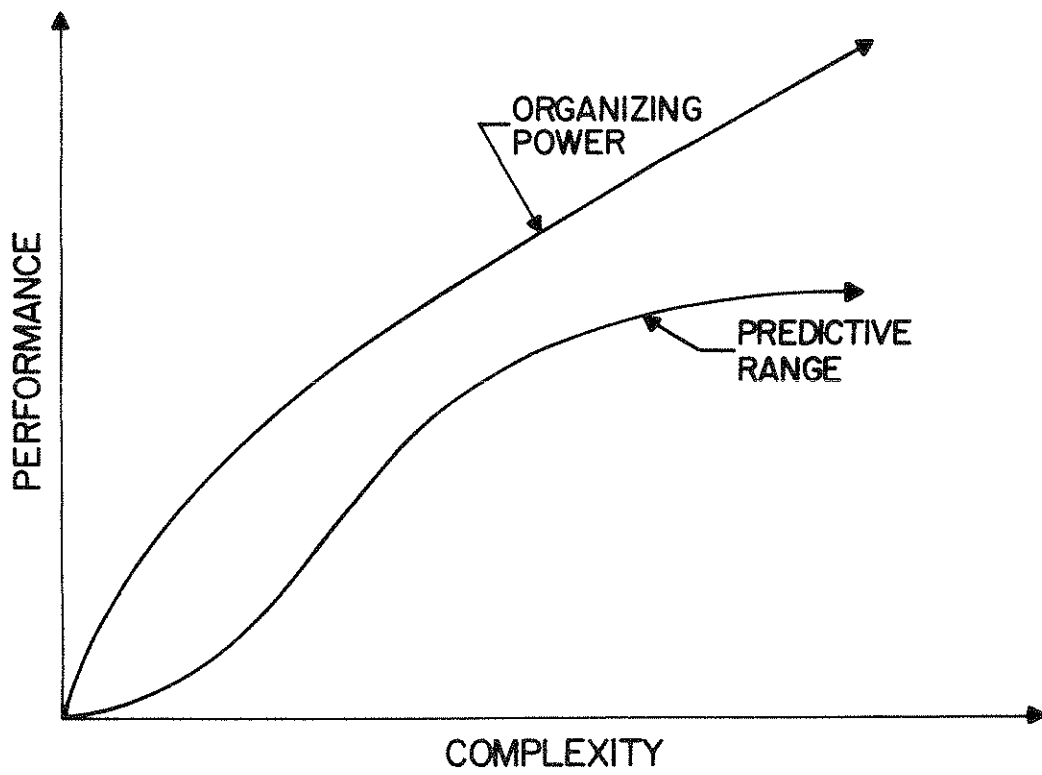

Figure 2.   Relationship between model complexity and its organizing power and predictive range.

The predictive range, or number of verifiable predictions, of a model will be very sensitive to the quality of a model but appear to increase toward an asymptote as complexity is increased (Fig. 2). The asymptotic limit is expected because the number of possible predictions from a given information base is finite, at least in a practical sense.

One of the often mentioned advantages of models is the low average margin of predictive error they provide. Quantitative predictions not based on models are rare. Nonetheless, models should be looked at more closely than they generally are in this respect. The two components of predictive error, precision and accuracy, are difficult to measure but it appears that as the complexity of a model increases, its accuracy or closeness to reality becomes asymptotic. Uncertainty, which is approximately the inverse of precision, will increase exponentially (Fig. 3) beyond some level of complexity.
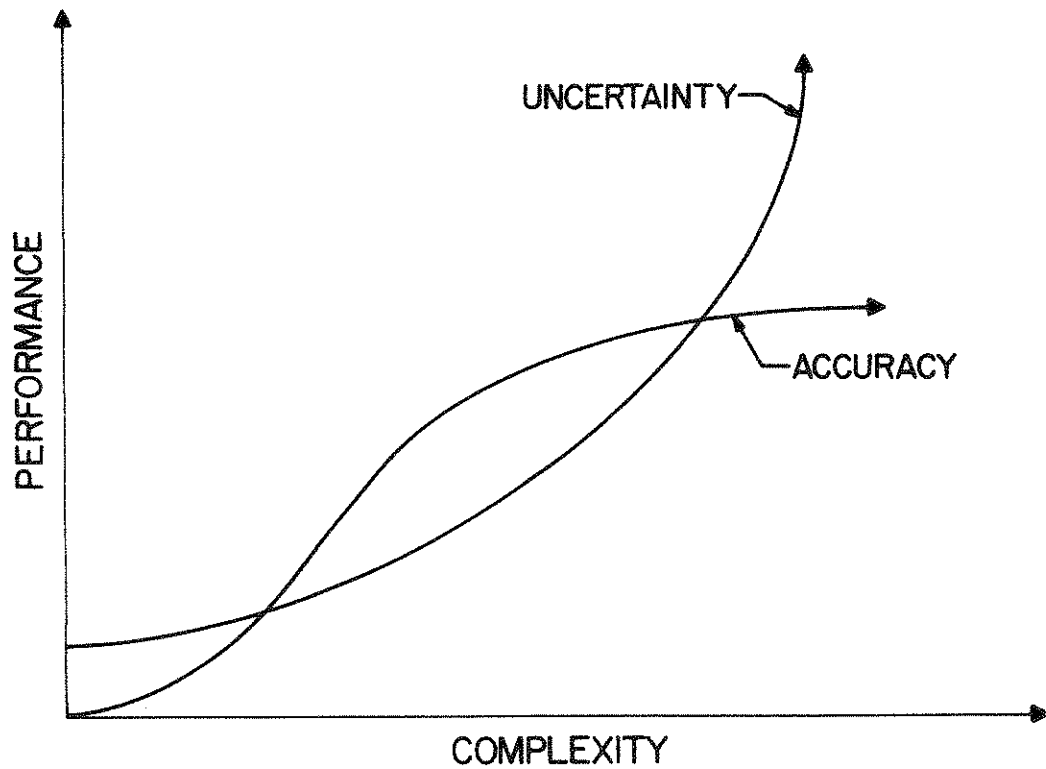
Figure 3. Relationship between model complexity and accuracy and uncertainty.

We must consider cost as well as performance of a model. Establishment cost increases as complexity increases. Beyond a certain point this is probably linear. Operating cost usually follows functional complexity (Fig. 4).
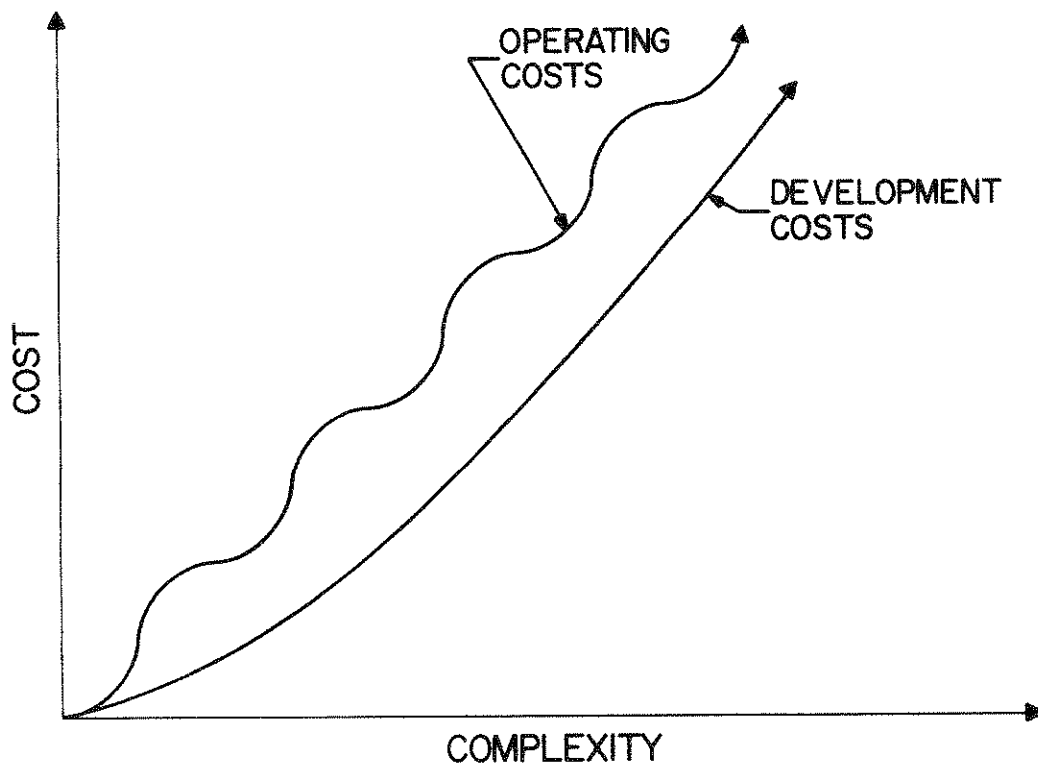
Figure 4. Relationship between model complexity and operating and establishment costs.

There are two other characteristics which need mention: fruitfulness and self-transcendence. Fruitfulness, the probability of a model leading to new observations and experiments, is most likely increasing at low complexity and decreasing at high complexity. Self-transcendence, the probability of leading to a new and better model, will decrease as models become more complex and less room is left for improvement, but may increase somewhat for highly complex models which are likely to be replaced by simpler but equally powerful models (Fig. 5).

Figure 5.   Relationship between model complexity and self-transcendence and fruitfulness.

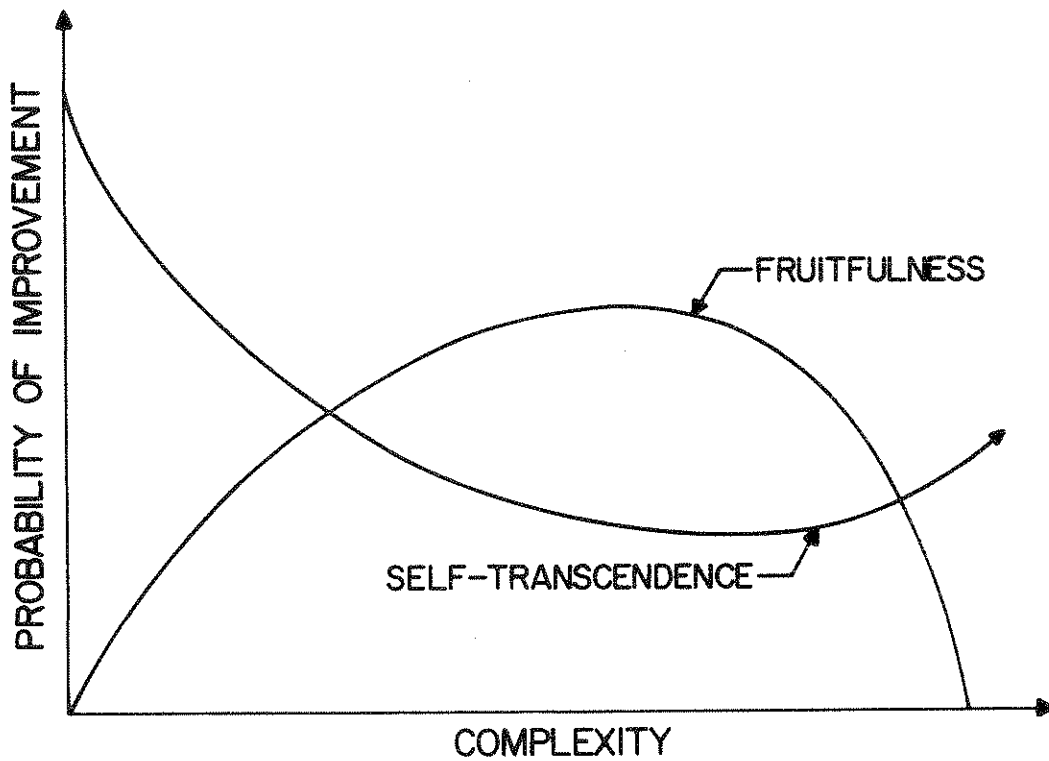Each of these criteria is largely independent of the purposes for which a model is constructed. Benefits of modeling previously mentioned include heuristic value, evaluation of alternative theories, development and analysis of alternative management strategies, and tactical planning. These uses of models are valid, but there are few models in existence which have been used for each of these purposes. The heuristic value, however, is the only benefit on which we can always depend.

Suppose, for example, that we want to test two alternative growth functions for largemouth bass by comparing model predictions with measured growth of fish within a population. If a model were already available, it would certainly be less expensive than an experiment following the growth of individual fish. A comparison of length-frequency predictions based on the two growth functions might reveal that one is more realistic than the other. There are real restrictions on the utility of models used for this purpose, however. Any such comparison is statistical. Because model predictions are uncertain, we are faced with two distributions of possible outputs. The usefulness of the model in this situation corresponds to the power of a statistical test. The sensitivity of the model to the alternatives and the precision, or variance, of predictions will determine the power of the test (Fig. 6). If the model is highly sensitive and very precise, we will have a powerful test. Populations, however, are stochastic and realistic population models will usually have low precision. If the tested alternatives are very different, and if the function is very important in determining output, we will have high sensitivity and a powerful test. If either of these conditions fail, however, the test will not be very powerful and whatever confidence level we choose is likely to lead to accepting a false alternative.
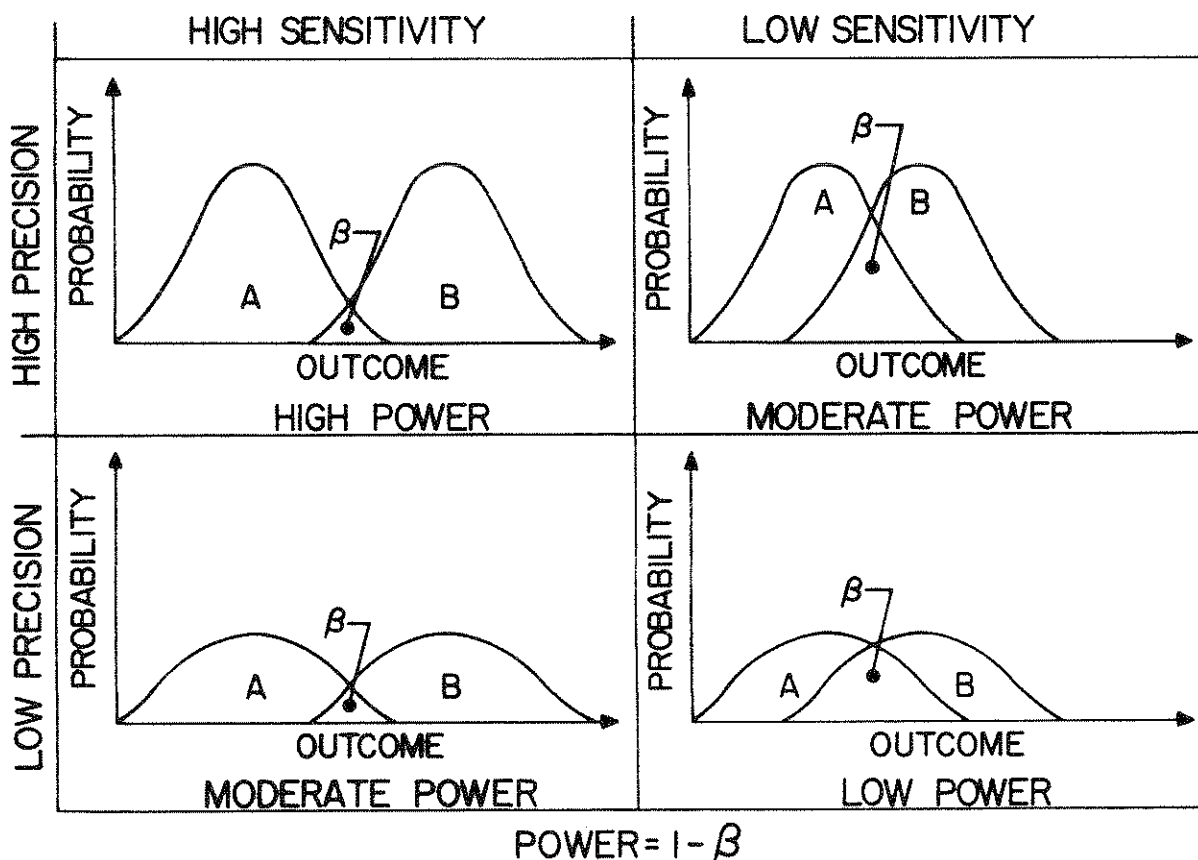
Figure 6. Experimentation with models and the relationship to precision, sensitivity, and power.

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A similar argument applies to alternative fisheries management strategies. Thus, to evaluate alternative strategies effectively, the strategies must be very different in their effects and must have a powerful influence on the managed system. Given a particular strategy, or set of activities, we may want to optimize our efforts. This is called tactical planning. The sensitivity of the model once again influences the value of the model. If we have restricted our alternatives to a set of very similar tactics and if sensitivity is low, the alternatives will not produce very different yields (Fig. 7). In this case a broad range of tactical combinations will be near optimal and planning should take the form of minimizing costs within that range.

Figure 7.   Relationship between management (tactical planning) and predicted yield.

III. ISSUES IN LARGEMOUTH BASS MANAGEMENT

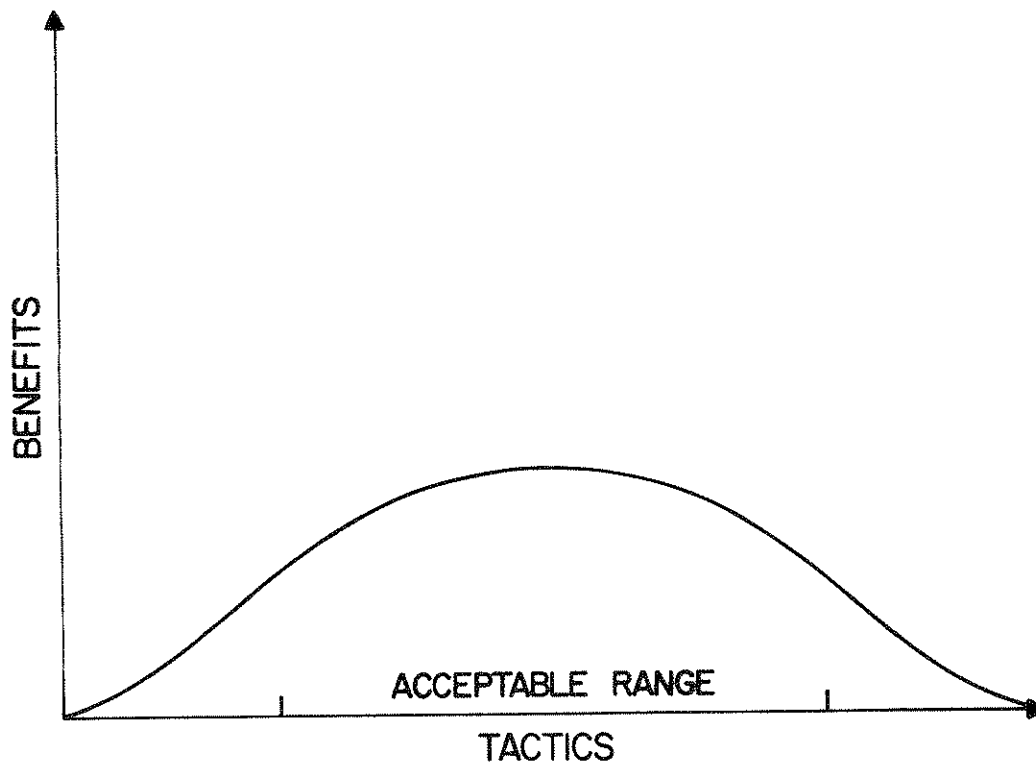1.   Sport and prestige seem to be major factors making largemouth bass popular among anglers. Anderson (1975a) has argued that the quality of bass fishing is best measured by an index incorporating catch rate, size of fish caught, species combination creeled, and positive value from fish caught and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

Bass become catchable between 250 mm and 300 mm (10-12 inches) in length, but angling techniques and preferences are highly size selective so that catchability declines (Bennett, et al. 1968). Observations by Bennett (1949), Lagler and DeRoth (1953), and Anderson and Heman (1969) suggest that this decline in catchability may be due to learning by bass; however the possibility that declining catchability is due to removal of inherently more catchable individuals from the population has not been rigorously studied.

Data presented by Redmond (1974) indicates that catchability varies seasonally with very low rates in winter and peaks of catchability in spring and fall. Holbrook (1975) presented evidence that relative catchability of females compared to that of males is high in early spring, declines before spawning season, then again increases. Overall, female bass constitute a significantly larger percentage of the total bass harvest in fishing tournaments.

2.   A common consequence of harvesting biological populations is a decline in average age of individuals in the exploited population (Usher 1973). Harvesting organisms, including most fishes, before they reach maximum size 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, the 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. Anderson (1977) presents alternatives to traditional bass harvest regulations.

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, 1975 a,b) has emphasized use of size limits in maintaining a desirable size structure and balance between bass and bluegill, *Lepomis macrochirus*. His concern with management of predator-prey relations led to consideration of protecting certain size ranges of bass while allowing fishing for bass both smaller and larger than the protected ones.

Bennett (1974) and Rasmussen and Michaelson (1974), on the other hand, found that bass smaller than the minimum size limit exhibited slower growth and caused 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 actually kept by anglers.

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 objectives for managing fish communities in ponds and small lakes. 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 well 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 is 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 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.

IV. CONCEPTUAL MODEL OF LARGEMOUTH BASS POPULATIONS

The management issues described in the preceding section suggest the need for a fairly general theory of the dynamics of largemouth bass populations, especially the dynamics of their size structure and production. The traditional models used to describe 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 analysis of populations in which many animal characteristics are size-specific. They also 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-structures, variation in life history, and permits calculation of production, yield, and the size structure of harvest.

In the remainder of this bulletin a model will be developed based on the relationship between life history and population dynamics, its relationship to various other models will be shown, and its application to largemouth bass in a special case for which sufficient data are available will be illustrated.

Life History
Life history has been defined as the history of the changes which an organism passes through in its development from the egg, spore, or other primary stage until its natural death (Webster 1959). 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 process by which an organism's phenotype changes in time from the organism's origin until its death.

Definition: The specific sequence of development 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 T $(T_1, \ldots, T_n)'$. The set of all possible trait vectors will be denoted by 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. Because 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 specific 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 function generated by the life history, which is a stochastic process. Thus, particular lives 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 corresponds to 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 $\{\underline{T}(a; t_b)\}$.
Traits of organisms generally change in two ways: continuous processes and event processes. In a continuous process, a trait will change in a smooth, regular 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, we will 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 Ito (Ito 1950, 1951, Ito and McKean 1965) could be used in place of the following arguments.

Event processes are specified by a rate function which describes temporal occurrence of events and a jump function which describes magnitudes of changes in traits which occur at each event. We will assume that rate functions of both continuous and event processes and jump functions of event processes will depend only on the present state of the organism and its environment, and not its past life. This assumption, known as 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.

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

Under the above assumptions, the following notation will be used:

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 vector magnitude of the jump occurring at any discrete event by $\underline{j}$. Assume $\underline{j}$ is taken from a distribution function $H(\underline{j}; \underline{T}, a, t_b)$. If the distribution has density populations, 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 be given by $\lambda(a; t_b)$ $E_\emptyset[exp(-\int_0^a \mu(\underline{T}(t, \omega), t; t_b, \omega))]$.

5) Summarize the probability that an organism survives to age a and has phenotype $\underline{P}$ with $P_i \leq T_i$, $i = 1, ..., n$, for arbitrary $\underline{T}$ by the function $F(\underline{T}; a, t_b)$. Clearly, $F(\underline{0}; a, t_b) = 0$ and $F(\infty, a, t_b) = \lambda(a; t_b) \leq 1.0$. The function F is similar to a distribution function except that its upper bound, $\lambda(a; t_b)$, is less than 1.0. If there is a function analogous to a density, 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 $\mathbf{T}$ 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: Given the assumptions and notation stated above, the density function f must satisfy the differential form:

$$\frac{\partial f(\underline{T}; a, t_b)}{\partial a} = \int \cdots \int_{\mathbf{T}} f(\underline{X}; a, t_b)\, r(\underline{X}, a; t_b)\, h(\underline{T}; \underline{X}, a, t_b)\, dX_1 \cdots dX_n$$

$$- f(\underline{T}; a, t_b)\, r(\underline{T}, a; t_b) + \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\partial^2 [\sigma_{ij}(\underline{T}, a; t_b)\, f(\underline{T}; a, t_b)]}{\partial T_i \partial T_j}$$

$$- \sum_{i=1}^{n} \frac{\partial [m_i(\underline{T}, a; t_b)\, f(\underline{T}; a, t_b)]}{\partial T_i} - \mu(\underline{T}, a; t_b)\, f(\underline{T}; a, t_b) \qquad (1)$$

where m_i and σ_{ij} are the instantaneous means and covariances of the **continuous 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 $\underline{T}$ 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 $\underline{T}$, while the second RHS term is the likelihood of a jump from phenotype $\underline{T}$ to some other phenotype. The next two terms describe flux in the density due to the continuous process $\underline{g}$. The final term is the likelihood of death occurring at age a with phenotype $\underline{T}$.

Derivation: see Appendix A

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

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

In the above analysis, dependence on time has been denoted by 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 characteristics 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.

Definition: A group of organisms is self-renewing if it is reproductively 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 include age. To simplify later notation, use $\underline{P}$ 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 $\underline{X} < \underline{P}$. 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 $\eta(P, t) = \Sigma f_i (P, t)$ where the summation is over all members of the population. The function η is then subject to a functional equation similar to the life history operator equation (1), namely,

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

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

$$\eta(0, \underline{T}; t) = \beta(\underline{T}, t) \quad (3)$$

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 alteration, and continuous stochastic 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 absence of temporal variation in life history parameters, and thereby excluding density dependence and environmental variation, the equations can be solved analytically for η. In principle, the equations can be solved numerically under more general assumptions, but the standard centered-difference and grid techniques require an extremely large number 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 effects of statistical fluctuations in finite populations.

A more fruitful approach is to use stochastic integral equations corresponding to (2) and (3). When applied to the density η 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

$$B(\underline{P}_n, t) = \frac{1}{p} \int \ldots \int_T b(\underline{P}_n, t; \underline{P}_p) n (\underline{P}_p; t) d\underline{T}$$

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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

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

where $f(\underline{P}, t; \underline{P}_n, \tau)$ is the likelihood an organism born at time τ 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

$$n(\underline{P}, t) \doteq \int \cdots \int_T [K(\underline{P}, t; \underline{P}_n, 0) + \int_o^t B(\underline{P}_n, \tau) \; f(\underline{P}, t; \underline{P}_n, \tau) d\tau] \; d\underline{T}. \qquad (6)$$

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

$$\phi(t, \tau) = \int \cdots \int_T \int \cdots \int_T \int \cdots \int_T b(\underline{P}_n, t; \underline{P}_p) \; f(\underline{P}_p, t; \underline{P}, \tau) \; d\underline{T}_n \; d\underline{T}_p d\underline{T}.$$

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

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

where q(t), the contribution of the initial population is $q(t) = \frac{1}{p} \int_t^A \phi(t, a-t) \; n(a-t, o) \; da.$

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 analagous argument leads to a stochastic version of this equation, namely

$$B(t, w) = q(t, w) + \frac{1}{p} \int_o^t \phi(t, \tau; w) \; B(\tau; w) \; d\tau \quad w \epsilon \Omega \qquad (8)$$

where w indexes the particular outcome of the process. It is shown in Appendix B 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 $\phi(t; w)$. In the remainder of this work, it will be assumed that $\phi(t; w)$ 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 $\triangle$ t approaches O. 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 (1938), and Pearl and Reed (1920). 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 conditions also appear to be necessary. Secondly, under the linearity assumption, the model implies an asymptotically stable density function over the entire set of traits.

Theorem: If the processes B(t; w) and $\phi(t; \tau; w)$ 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 $\lambda(t; \tau; w)$ and $b(t, \tau; w)$ are also uncorrelated, then

$$E_\Omega[B(t; w)] = E_\Omega[q(t; w)] + \int_o^t E_\Omega[\lambda(t, \tau; w)] \; E_\Omega[b(t, \tau; w)] E_\Omega[B(\tau; w)] \; d\tau.$$

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

$$E_{\Omega}[B(t; w)] = E_{\Omega}[q(t; w)] + E_{\Omega}[\int_{0}^{t} \phi(t, \tau; w) B(\tau; w) d\tau]$$

$$= E_{\Omega}[q(t; w)] + \int_{0}^{t} E_{\Omega}[\phi(t, \tau; w) B(\tau; w)] d\tau$$

$$= E_{\Omega}[q(t; w)] + \int_{0}^{t} E_{\Omega}[\phi(t, \tau; w)] E[B(\tau; w)] d\tau$$

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

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 stable for any nonzero initial population (Lopez 1967). Because 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 apparent that

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

under the assumption of independence of λ, 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.

Theorem: 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 $n(a, t)$. But the expected distribution of phenotypes at a given age is $f(\underline{T}; a, t)$ so we have expected structure function $n(a, \underline{T}; t) = n(a, t) f(\underline{T}; a, t)$.

Lopez (1967) has shown rigorously that the age structure predicted by the classical model is of the form $n(a, t) = N e^{r(t-a)} \lambda(a)$, where r is the asymptotic growth rate of the population and N is the initial abundance. If we assume that the population has approximately constant abundance, then $r = 0$ and $n(a, t)$ is proportional to $\lambda(a)$. Therefore $n(a, \underline{T}, t) = N \lambda(a) f(\underline{T}; a, t)$ 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 $n_i(T_i)$ is obtained by a standard change of variables and we have $n_i(T_i, t) = \sum_j n_a(m_{ij}^{-1}(T_i), t) \cdot \cdot m_{ij}^{-1'}(T_i, t)$ 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 this case where $m_i(a)$ is monotone, this trait distribution and corresponding differential equation reduce to the model of "physiological age distributions" studied by Van Sickle (1976).

V. APPLICATION OF THE MODEL

The four issues in largemouth bass management discussed in a previous section were the principal motivation for developing the model. None of these issues can be resolved here because of an absence of empirical information on which to base specific models. The purposes of this section are (1) to illustrate use of the model and outline possible directions to their solution, and illustrate some of the effects of exploitation; (2) to present a possible approach to selection of size limits; (3) to outline the information necessary for a theoretical investigation of the predator-prey balance concept of Jenkins and Morais (1977); and (4) to derive, through the differential equation form of the model, 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 typical 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 μ 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 $f(c; o) = g(c)$. 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

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

The expected catch rate at time t will then be

$$C(t) = \int_0^\infty cf(c; t) dc = \int_0^\infty ce^{-(cE + \mu)t} f(c; o) dc.$$

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

$$C(t) = \int_0^\infty ce^{-(cE + \mu)t} \frac{1}{\Gamma(n)} \alpha^n e^{-\alpha c} c^{n-1} dc$$

$$= \frac{e^{-t}}{\Gamma(n)} \frac{\alpha n}{(\alpha + Et)^n} \int_0^\infty c(\alpha + Et)^n e^{-(\alpha + Et)c} c^{n-1} dc$$

$$= \frac{n\alpha^n e^{-\mu t}}{(\alpha + Et)^{n+1}}.$$

Since the abundance of the population is declining with time, mean catchability will be $c(t)/f(\infty; t)$, or $n/(\alpha + ET)$ The variance of catchability will be $\frac{n}{(\alpha + Et)^2}$ A graph of catchability under these assumptions is shown in Figure 8.

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 to the von Bertalanffy equation:

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

or

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

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

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

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

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

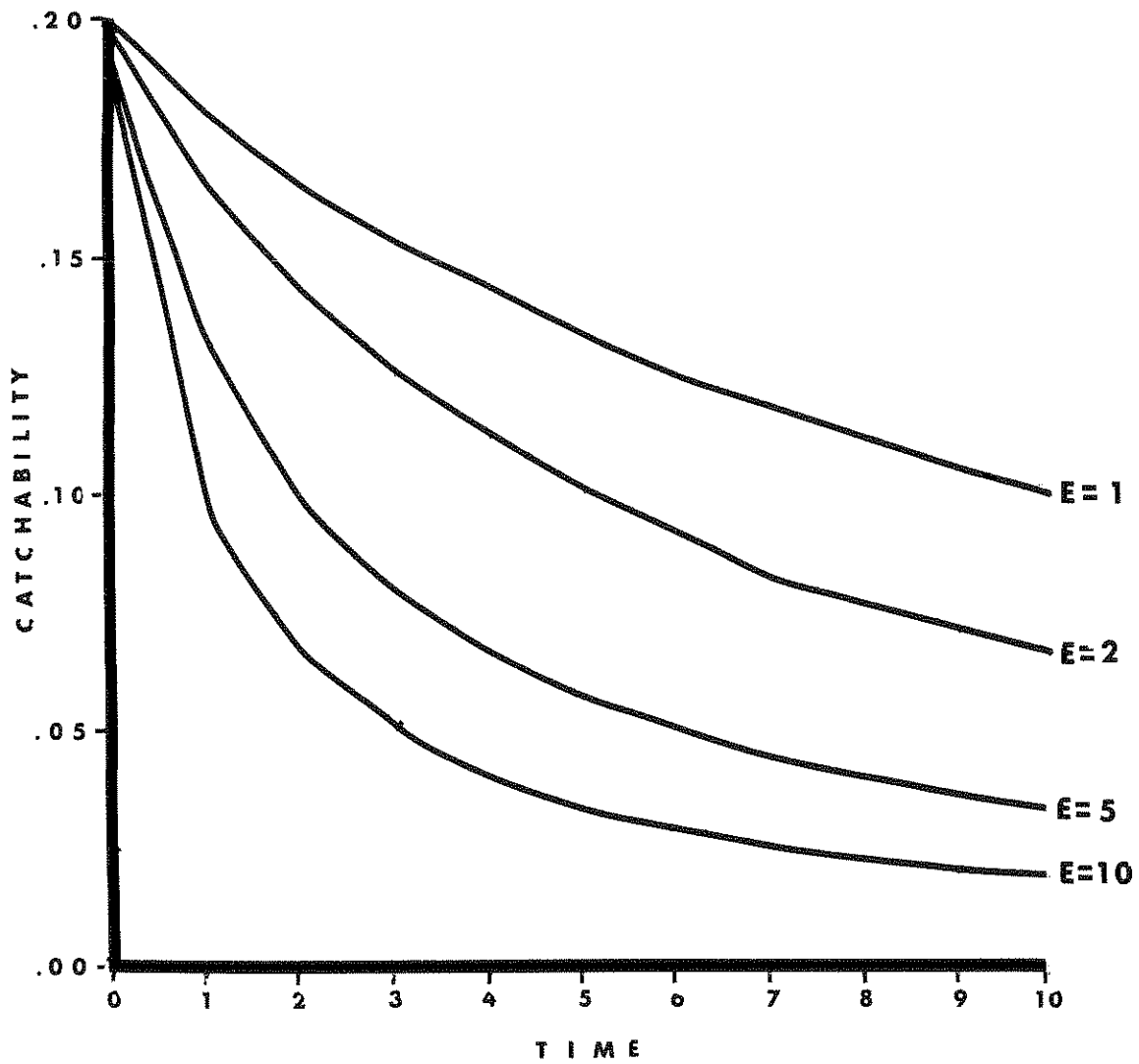These size structures are illustrated in Figure 9 for the case $z_\infty = 500$, K = 0.3, μ = 0.4, f = 0.4

Figure 8. Change in average population catchability resulting from removal of more catchable individuals. Graph based on an initial gamma distribution of catchability with parameters α = 10, n = 2. E is effort per unit time.
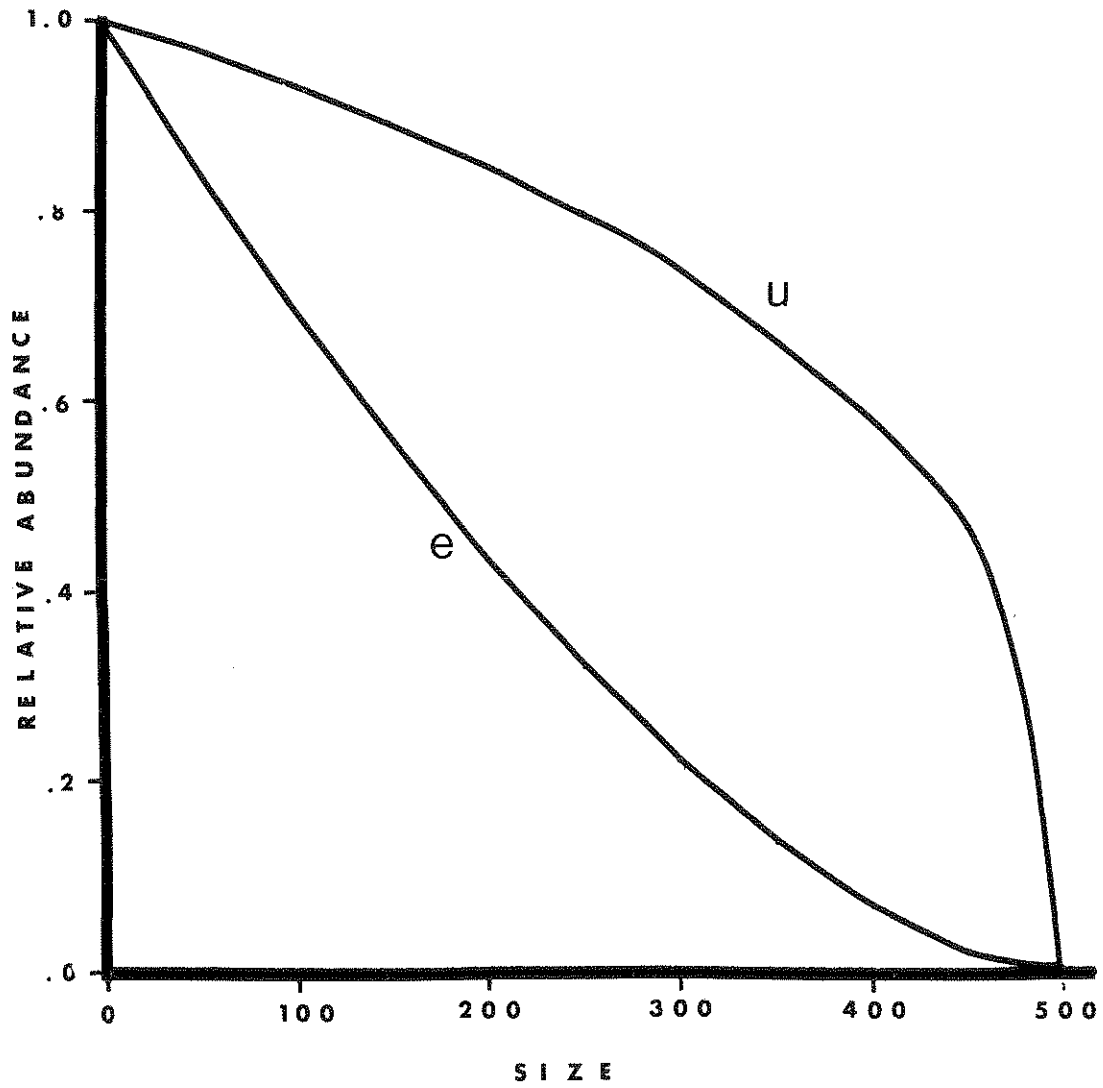
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Figure 9.   Size structure of an artificial population with asymptotic individual size $z_\infty = 500$, instantaneous growth rate K = 0.3, and natural mortality rate $\mu = 0.4$ without exploitation (u) and with a fishing mortality rate of f =   0.4 (e).

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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 when released exceeds its present value.

A number of measures of value may be appropriate in various situations. 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 $\dfrac{f}{f+\mu}$.

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

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

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

$$= \frac{f}{3K}\,e^{(f+\mu)\,a(z_0)}\int_{z_0}^{z_\infty}z\,[z_\infty^{1/3}z^{2/3}-z]^{-1}\,[1-(\tfrac{z}{z_\infty})^{1/3}]^{(f+\mu)/K}$$

$$= \frac{f}{3K}\,e^{(f+\mu)\,a(z_0)}\int_{z_0}^{z_\infty}(\tfrac{z}{z_\infty})^{1/3}\,[1-(\tfrac{z}{z_\infty})^{1/3}]^{(f+\mu)/k-1}\,dz$$

$$= z_\infty\,[1+\frac{3K}{\mu+f+K}\,e^{-Ka(z_0)}-\frac{6K}{\mu+f+K}\,e^{-2Ka(z_0)}+\frac{3K}{\mu+f+K}\,e^{-3Ka(z_0)}$$

$$+\frac{2K}{\mu+f+3K}\,e^{-(\mu+f+3K)\,a(z_0)}-\frac{2K}{\mu+f+2K}\,e^{-(\mu+f+K)a(z_0)}].$$

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

$$z_0 = z_\infty\,(1-\exp[-K\ln\{(\frac{\mu+f+K}{3})^{1/(\mu+f+K)}\}])^3..$$

Thus any zone of protection should center about 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 to net energy availability in terms of growth lability and mortality rates.

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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 (Chapman 1967). 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.

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

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

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

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

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_∞ and no reproduction occurs. Because production is typically computed over times not including spawning, this will often be appropriate. Now, because production is change in biomass plus biomass lost through death, instantaneous production is given by

$$P'(t) = \frac{\partial W(t)}{\partial t} + \int_0^{z_\infty} z\mu(z;t)\eta(z;\, t)\, dz = \int_0^{z_\infty} g(z;\, t)\eta(z;\, t)\, dz.$$

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

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

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

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

and yield over a period of time will be given by

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

Van Sickle (1976) has shown these yield and production equations to be equivalent to traditional equations 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.

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VI. APPENDICES

APPENDIX A:

Derivation of Life History Operator Equation

Let $F(\underline{T}; a, t_b)$ be the probability that 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 $\underline{0} \leq \underline{P} \leq \underline{T}$ due to the growth and event processes or a result of the death process. Hence,

$$\frac{\partial F(\underline{T}; a, t_b)}{\partial a} = -\int_0^{T_n} \cdots \int_0^{T_1} \mu(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$-\int_0^{T_n} \cdots \int_0^{T_1} \overline{H}(\underline{T}; \underline{P}, a, t_b) f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$+\int_{T_n}^{\infty} \cdots \int_{T_1}^{\infty} H(\underline{T}; \underline{P}', a, t_b) f(\underline{P}'; a, t_b) r(\underline{P}'; a, t_b) dP_1' \cdots dP_n'$$

$$+\int_S f(\underline{P}; a, t_b) (\underline{g}(\underline{P}; a, t_b) \cdot \underline{n}) ds$$

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

$$\int_0^{T_n} \cdots \int_0^{T_1} H(\underline{T}; \underline{P}, a, t_b) f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$- \int_0^{T_n} \cdots \int_0^{T_1} f(\underline{P}; a, t_b) r(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

whence (1a) becomes

$$\frac{\partial F(\underline{T}; a, t_b)}{\partial a} = -\int_0^{T_n} \cdots \int_0^{T_1} \mu(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$-\int_0^{T_n} \cdots \int_0^{T_1} r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$+\int_0^{\infty} \cdots \int_0^{\infty} H(\underline{T}; \underline{P}, a, t_b) r(\underline{P}; a, t_b) f(\underline{P}; a, t_b) dP_1 \cdots dP_n$$

$$+\int_S f(\underline{P}; a, t_b) (\underline{g}(\underline{P}; a, t_b) \cdot \underline{n}) ds \ .$$

But $H(\underline{T}; \underline{P}; a, t_b) = \int_0^{T_n} \cdots \int_0^{T_1} h\underline{P}'; \underline{P}, a, t_b) dP_1' \cdots dP_n$ and h is non-negative,

so by the general Fubini-Stone Theorem, we may interchange the order of integration, obtaining

$$
\frac{\partial F(\underline{T};a,t_b)}{\partial a} = \int_0^{T_n} \ldots \int_0^{T_1} [(-(\mu(\underline{P};a,t_b)+r(\underline{P};a,t_b))f(\underline{P};a,t_b)
$$

$$
+ \int_0^\infty \ldots \int_0^\infty h(\underline{P}';\underline{P},a,t_b)r(\underline{P};a,t_b)f(\underline{P};a,t_b)dP_1' \ldots dP_n']dP_1 \ldots dP_n
$$

$$
+ \int_s f(\underline{P};a,t_b)(\underline{g}(\underline{P};a,t_b)\cdot\underline{n})ds. \tag{2a}
$$

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

$$
\int_0^{T_n} \ldots \int_0^{T_1} [\sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 [\sigma_{ij}(\underline{P};a,t_b)f(\underline{P};a,t_b)]}{\partial P_i \partial P_j}
$$

$$
- \sum_{i=1}^n \frac{\partial [m_i(\underline{P};a,t_b)f(\underline{P};a,t_b)]}{\partial P_i}] dP_1 \ldots dP_n .
$$

Now, since $F(\underline{T};a,t_b) = \int_o^{T_n} \ldots \int_o^{T_1} f(\underline{P};a,t_b) dP_1 \cdots dP_n$, interchanging differentiation and integration on the left hand side and collecting terms gives

$$
0 = \int_o^{T_n} \ldots \int_o^{T_1} [\frac{\partial f(\underline{P};a,t_b)}{\partial a} + \mu(\underline{P};a,t_b)f(\underline{P};a,t_b) + r(\underline{P};a,t_b)f(\underline{P};a,t_b)
$$

$$
- \int_o^{T_n} \ldots \int_o^\infty h(\underline{P}';\underline{P},a,t_b)r(\underline{P};a,t_b)f(\underline{P};a,t_b)dP_1' \cdots dP_n'
$$

$$
- \sum_{i=1}^n \sum_{j=1}^n \frac{\partial^2 [\sigma_{ij}(\underline{P};a,t_b)f(\underline{P};a,t_b)]}{\partial P_i \partial P_j} - \sum_{i=1}^n \frac{\partial [m_i(\underline{P};a,t)f(\underline{P};a,t_b)]}{\partial P_i}
$$

$$
dP_1 \cdots dP_n.
$$

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

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APPENDIX B:

Proof of the Existence and Uniqueness of a
Solution to the Integral Equation of the Birth Process

Theorem: The stochastic integral equation

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

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

i) $||| \phi(t, \tau; w) ||| \leq Me^{-\nu(t - \tau)}$ for $0 \leq \tau \leq t < \infty$,

where v and M are positive constants;

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

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

where M* is the infimum of the set of all constants M satisfying (i) and v^* is the supremum of all v satisfying $\lambda(a; w) \leq e^{-va}$ 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 solution of the form (1b) if the Banach spaces involved are admissible with respect to the integral operator

$$(T\chi)(t; w) = \int_0^t \phi(t, \tau; w) \chi(\tau; w) \, ds. \qquad (2b)$$

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; w) 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

$$\| (T\chi)(t; w) \| \leq \int_0^t \| \phi(t, T; w) \chi(T; w) \| \, dT$$

$$\leq \int_0^t ||| \phi(t, T; w) ||| \; \| \chi(T; w) ||| \, dT$$

$$\leq \sup_{t \leq 0} \| \chi(t; w) \| \int_0^t ||| \phi(t, T; w) ||| \, dT$$

$$\leq \| \chi(t; w) \|_c M \int_0^t e^{-\nu(t-T)} \, dT.$$

Thus, since

$$\int_0^t e^{-\nu(t - T)} \, dz = \frac{1}{\nu} (1 - 3^{-\nu t}),$$

$$\| (T\chi)(t; w) \| \leq \| \chi(t; w) \|_c \frac{M}{\nu} (1 - e^{-\nu t}) \qquad t \geq 0.$$

Therefore (TX) (t;w) is bounded in means-square and is in C by definition. Hence the pair (C,C) is admissible with respect to the operator T. Since

$$\sup_{t \geq 0} \left| \left| \chi(t; w) \right| \right|_C = \left| \left| (T\chi)(t; w) \right| \right|_C$$

$$\leq \left| \left| \chi(t; w) \right| \right|_C (M/v) \sup (1 - e^{-vt})$$

$$= \frac{M}{v} \left| \left| \chi(t; w) \right| \right|_C$$

the norm of T is M^*/v^* where M^* is the least upper bound of b(t; w) for almost all w and $e^{-v^* + a}$ is the greatest lower bound of $\lambda(a; w)$ for all a and almost all w.

Now, we must verify that q(t; w) is in C. We will assume that the size of the population at time 0 is finite and bounded by $N > 0$; i.e.,

$$\int_0^\infty n(a, o; w) \, da \leq N \text{ for almost all } w \varepsilon \Omega$$

Then

$$q(t; w) = \int_t^\infty K(0, a, t) \, b(a, t; w) \, n(a - t; 0; w) \, da$$

$$\leq e^{-v^* t} M^* N_0 < \infty \text{ for almost all } w \text{ by the assumption that}$$

b(a, t; w) is bounded by M^* and $K(o, a, t) \leq e^{-v^* t}$. Therefore

$$\int_\Omega \left| q(t; w) \right|^2 \, dR(w) \leq \int_\Omega \left| e^{-v^* t} M^* N_0 \right|^2 \, dR(w)$$

$$= (e^{-v^* t} M^* N_0)^2 < \infty \qquad t \varepsilon R_+$$

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

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

which means that q(t; w) is bounded in $L_2(\Omega, A, R)$. Therefore there exists a unique random solution of the stochastic integral equation (1b) provided that $M^* < v^*$ and $\left| \left| q(t; w) \right| \right|_C = M^* N^* \leq_p [1 \cdot M^* / v^*]$ since we have

$$\left| \left| q(t; w) \right| \right|_C = \sup_{t \geq 0} \left| \left| q(t; w) \right| \right|_{L_2} = M^* N^* \text{ where } N^* \text{ is the infimum of N, completing the proof.}$$

APPENDIX C

List of Symbols

$\underline{T} \equiv (T_1, \ldots, T_n)'$ — trait vector or phenotype description where each vector element represents one trait

T — space of possible trait vectors

t — time

t_b, t_d — times of birth, death

a — age

w, Ω — w specifies a particular outcome from the set of lives indexed by Ω

$\underline{g}(\underline{T}, a; t_b)$ — derivative of the continuous part of the life history

$r(\underline{T}, a; t_b)$ — rate function of the life history event process

$H(\underline{j}; \underline{T}, a, t_b)$ and $h(\underline{j}; T, a, t_b)$ — distribution of phenotypes resulting from the event process; 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 $P \leq T$. $f(T; a, t_b)$ is the corresponding density over T.

$\underline{P} \equiv (a, \underline{T}')'$ — 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 (P, t) is the corresponding 'density.'

$n(\underline{P}, t)$ — expected value of n (P, t)

$\beta(\underline{T}, t)$ — expected number of births at time t of organisms with phenotype 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 $\underline{P}_n$.

τ — substitute time parameter

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$K \ (\underline{P}_2, \ t_2; \ \underline{P}_1, \ t_1)$ — 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 t

c — catchability

E — effort per unit time

μ — natural mortality rate

$C(t)$ — average catchability at time t

z — body weight

k — von Bertalanffy growth rate

z_∞ — 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

$W(t)$ — population biomass at time t

$P \ (t_1, \ t_2)$ — population 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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