## Analysis of

## Exploited Fish Populations

by<br>Robert T. Lackey and Wayne A. Hubert



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## PREFACE

Fisheries science is the study of manipulating the structure, dynamics, and interactions of aquatic habitat, biotic populations, and man in order to achieve specific human goals and objectives. Fisheries science is a broad discipline that encompasses many, superficially unrelated fields.

The purpose of this text is to provide students and practicing fisheries scientists with a basic understanding of the analysis of exploited fish populations. Methods for evaluating the state of a population and techniques which lead to management decisions are presented. Population dynamics is approached from a broad, principle-oriented direction.

The authors hope that this text serves as a bridge between introductory fisheries texts and mathematically oriented population dynamics texts. Basic concepts dealing with populations are discussed from a conceptual approach. Mathematical models and derivations have been kept to a minimum, while attempting to explain the various analysis techniques. Major emphasis is placed on the principles involved, not the fine points of the techniques as used in practice.

Much of this book has been written with the help of fisheries scientists at Virginia Polytechnic Institute and State University. The authors wish to express their appreciation to all those involved, specifically: P. J. Coulston (stock identification), J. R. Wolfe (mortality), L. D. Worthy (growth), W. J. Matter (recruitment), and C. T. Stiff (yield prediction).

## CHAPTER ONE

## INTRODUCTION

The concept of a fishery must be studied at the onset of this book. Just what is a fishery? A fishery can be viewed as being composed of three interacting units: (1) biota; (2) habitat; and (3) man (Figure I-1). Biota includes the plants and animals in the fishery. It involves all the fish, zooplankton, phytoplankton, benthos, etc. in the fishery as well as the animals or plants of interest. The habitat is the physical component and includes all the interactions of such factors as water quality, substrate, morphometry, and geography within the fishery. The third and most poorly understood component of a fishery is man. It includes all the uses and manipulations of the renewable biota resource as a result of human activity. Man's effects on the biotic may be caused by recreational fishing, commercial fishing, industrial activities, agricultural activities, and domestic activities. In short, mearly any human or societal activity may affect a fishery.


Figure I-1. Graphical model of a generalized fishery. Only major system components are included.

If only the first two units of a fishery are considered, biota and habitat, then we are essentially speaking of an aquatic ecosystem. An ecosystem may be viewed as a subset of a fishery. Ecological factors are often very important in the management of a fishery and must be clearly understood. However, most problems in managing a fishery result from man's activity and are indirectly of a social nature.

Now that a fishery has been defined, the role of a fisheries scientist should be explored. What is fisheries science? Fisheries science is a blend of numerous disciplines, including biology, law, economics, management, . . ., all oriented toward manipulation of a specific natural resource -- a fishery. While the subjects of ichthyology, limnology, and aquaculture are deeply rooted, fisheries science as defined in the above sense is a relatively recent innovation. The human elements of fisheries were related quantitatively to fish population response for the first time in the initial decades of the 20th century (Russel1 1931, Cushing 1968).

The theory on fishing was solidified by Russell (1931). Russell expressed the concept that the catch in a fishery was the function of five parameters: abundance; recruitment; growth; natural mortality; and fishing mortality. By manipulation of these parameters it would be possible for man to maximize the harvest from a fishery. The theory assumes that maximization of catch is the objective of fisheries managers.

Expanding Russell's ideas to some degree, a more contemporary theory of fisheries management has been developed (Lackey 1975). In this theory the objectives of a fisheries manager may include several things, social and biological, tangible and intangible. The maximization of societal benefits is the overriding objective of management. The fishery is manipulated within certain constraints to achieve the societal objectives. The theory can be expressed as:

$$
\operatorname{MAX} Q=f\left(X_{1}, X_{2}, \ldots X_{n} \mid Y_{1}, Y_{2}, \ldots Y_{n}\right)
$$

where MAX $Q$ is the maximization of societal benefits. The $X^{\prime \prime}$ s are the "decision variables" and include those things the manager can contro1. The Y's are the "constraints" and are not under the control of the manager (or only partially under his control). This model offers a conceptual framework from which fisheries management may be approached.

Numerous problems confront a fisheries scientist when attempting to manage a fishery. These problems arise out of the three units of a fishery, biota, habitat, and man. The potential problems can best be explained by a hypothetical situation. Suppose that a manager is charged with managing a warmwater stream fishery. Numerous problems are encountered in an effort to do so:

1. Natural variations in fish populations. The variations which occur in unmanaged or unexploited populations are not well understood. Poor or missing year classes often occur for unknown reasons.
2. Dynamic aspects of a fishery. A stream (or any aquatic ecosystem) is a natural system which is in constant flux but maintains a certain degree of dynamic equilibrium. Defining the dynamics is a challenging, if not overwhelming, problem.
3. The environment is uncontrollable. A manager can do very little to affect the environment. Only limited habitat improvement is possible. Perhaps the best thing a manager can do is reduce the influence of negative effects caused by pollution.
4. Conflicting desires of the general public. Use of the stream may be demanded by fishermen, boaters, bird watchers, and other persons seeking recreation. Commercial interests may wish to utilize the stream to support a commercial fishery, to supply water to industry, or to carry away wastes.
5. Conflicting desires of anglers. Fishermen themselves rarely agree as to what a fishery should produce. Should it be managed for trophy fish or panfish, walleyes or smallmouth bass, consumptive or nonconsumptive use, . . . . ?
6. Competition with other special interest. Numerous interests view a stream in various ways. Individuals interested in flood control, pest control, agriculture, and industry all look at a stream with their specific problems in mind.

The major point is that a fisheries scientist is not dealing only with the ecosystem. Man is an integral part. Man is the reason for performing the management and at the same time man causes the greatest problems when trying to achieve management objectives. Because of this, fisheries science is not only ecology and fish biology, but also law, population theory, management science, and economics.

Fisheries is an interdisciplinary, applied science. It draws heavily from many fields. Only a small part of fisheries science is unique to fisheries science. The disciplines of fisheries science are innumerable; however, the major areas are rather easy to define. The following summary identifies the major contributing disciplines.

Biology is a major contributing discipline. Biological information on the life history and physiological requirements of different organisms is needed. Simple questions such as "when do they spawn?" must be answered. Topics of interest within biology are behavior, morphology, and taxonomy.

Mathematics is an integral part of modern fisheries science It $h$ as enabled the transition from descriptive work to quantitative, analytical problem solving. Mathematics is utilized to describe processes (mortality, growth), to predict events based on described relationships (yield, recruitment), and to model complex systems (decision strategies).

Statistical inference is needed in fisheries science. These techniques serve to describe, evaluate, and predict. Statistics are the basis of all experimental studies. Such analyses as stock abundance estimates and yield prediction rely heavily on statistical techniques and theory. Statistics are utilized to develop the mathematical relationships within a fishery.

Chemistry allows an understanding of chemical interaction in water and the subsequent influence on aquatic life. Chemistry is important for several reasons. Fish have basic environmental requirements which must be met at all times.

Engineering is high1y necessary to many areas of fisheries science. Interaction with engineers can serve to enhance, protect, or create fisheries of various types. Engineering supplies information on what and how technological developments can be constructed to influence a fishery, which can be positive (certain stream improvements) or negative (channelization) influences.

Economics is an integral facet of recreational and commercial fisheries. It defines how much a fishery is worth, enables analysis of costs and benefits, and gives tangible value to a fishery.

Sociology is seldom considered as a discipline related to fisheries science, but its importance is overwhelming. Sociology can help explain the desires of people, the behavior of anglers, and the human response to management measures such as seasons, limits, or "fish-fishermen" attracting devices.

Politics is important even if most fisheries scientists would prefer to ignore it. Politics is the basis from which most management agencies are conceived, initiated, budgeted, and governed. Problems with politics include conflicts between government branches, requests for unreasonable objectives, and pressure to produce. A major component of politics is compromise and in order to function in a political system a manager must be willing to do just that. Politics cannot be avoided. A11 fisheries scientists are involved to some degree either at the national, state, and local levels or within the agencies, companies, and universities where they work.

Computer technology is another contributer. Computers can perform computational tasks, but this is mixed with the uncompromising demand for sound models in order for the information generated to be meaningful. As processed data may become readily available to the decision-maker, more demands are placed upon the individual to make rational use of this increased information. Far from replacing man, computers have made certain types of individuals desirable, if not indispensable, to a modern society.

The following chapters discuss the components of a fishery in terms of the target species. The basic population parameters are discussed in relation to their derivation and significance. The final two chapters tie the population parameters into systems analysis and decision analysis concepts. It will be evident as the reader proceeds through the chapters the extent to which the various disciplines have contributed to fisheries science.

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## CHAPTER TWO

## STOCK IDENTIFICATION

## The Unit Stock Concept

Rational fisheries management must include a consideration of the extent to which the animals under exploitation comprise a discrete, uniform, and self-sustaining group. Evaluation of population parameters for understanding the effects of exploitation on populations requires information about a group of organisms or a unit stock. The unit stock concept does not imply that for management to be successful all biological or genetic units in the fishery be delimited and treated separately. It requires that what is being considered a unit stock for management purposes be comprised of organisms which are similar enough in their vital parameters not to obscure the data needed for efficient management.

The unit stock is one of the most fundamental concepts in fisheries management. By unit stock we mean a group of fish or other aquatic animals that can be treated as a single unit for management purposes. It may seem a simple task to identify a unit stock, but it is actually quite difficult. The problem of the definition of the unit stock is common to all studies of animal populations. Some of the apparent inconsistencies of population analysis studies appear to have arisen because the group of fish being studied did not form, to a sufficiently close approximation, a unit stock.

A question that might be addressed is: why do we need to delineate a unit stock? The answer lies in the fisheries theory upon which most modern management strategy is based. Population dynamics models have been developed with the aim of deriving the maximum sustainable yield from a fishery. To realistically apply these models, a unit stock with definable characteristics must be delineated.

The unit stock concept is particularly appropriate to the marine situation, where most management is passive and functions almost entirely by way of regulation. In freshwater, where stocking is practical and alteration of the habitat is common, the unit stock concept takes on an additional dimension. The recognition that different stocks, biological units in this case, have different characteristics as determined by natural selection can allow the manager to choose donor stocks for new or altered bodies of water which are best adapted for a particular situation.

Most of the work on population dynamics models has been done on single target species marine fisheries; e.g., the tuna fishery. Consequently, reference to the unit stock usually has a marine orientation. A unit stock has been defined as "a self-contained and self-perpetuating group, with no mixture from the outside, and within which biological characteristics and impact of fishing are uniform." Careful analysis of this definition reveals that the ideal unit stock would be the exception rather than the rule in nature. The choice of what is to be considered a unit stock must usually be made empirically, depending on requirements set
forth by the manager regarding accuracy and detail in analysis. One basic problem in applying most population dynamics models to freshwater fisheries is defining the appropriate management unit; i.e., the unit stock. In a fishery with several distinct species there are many possible unit stocks.

The idea of recognizing management units as unit stocks can take on several levels of refinement. Three levels are discussed to express the concept: (1) gross management; (2) species management; and (3) strain management. The gross level of stock management involves treating all the target fish in a fishery as an aggregate and in basically the same manner. This is sometimes necessary because of limited knowledge of the fish populations or limited professional staff. For example, a manager may try to manage a small warmwater impoundment with four centrarchid species, but very little information on the populations is available. As a result the four species are lumped together for management purposes and the aggregate is treated as the unit stock. Obviously, any rigid definition of unit stock is violated. If it can be assumed that the statistics of growth, mortality, and recruitment do not vary substantially between the different species, serious errors in analysis would not occur. This would be a very gross assumption to make, but perhaps a necessary one.

Graham applied a population dynamics model to the aggregate of the demersal fishes of the North Sea. He made the assumption that a unit biomass of one species was equal to that of any other species in this area, an assumption which is generally not true. Graham was working with a commercial marine fishery and species of similar habit. The assumption of homogeneity is likely to be more realistic in this case than for freshwater lakes. In some situations (e.g., lack of data on individual species) the only way the total fishery can be evaluated will be to make this assumption and call the aggregate of all species present the unit stock.

Species management would apply to individual animal groups such as rainbow trout, bluegill, blue crabs, or shrimp. This is the most common form of marine fisheries management in use today and usually works well from a population dynamics standpoint. In the hypothetical warmwater impoundment with four centrarchid species, this management level would probably work best. Each species would be designated as a separate stock. Thus, bass would be one stock, bluegill another, and so forth. One problem would be that data would either have to be collected separately for each stock or subdivided over each stock if the data were collected on the fishery as a whole. It is usually most convenient to treat as large a group as possible as a unit stock. This is especially true in freshwater fisheries where data are often scanty.

The corollary is that if data are collected separately on all stocks, statistical analysis will take considerably more time and effort, and probably a separate model would have to be constructed for each stock.

Although individual species unit stocks would conform most closely to the ideal definition of a unit stock, there are still difficulties. There is a possibility that the impact of fishing might not be uniform on a particular stock. An example would be where half of the lake is unavailable for shore fishing due to vegetative growth. The stock would be subject to different fishing pressures on the fishable and unfishable shores. In addition, the interaction between species could act to alter the biological characteristics of the stocks in different parts of the lake. Predation and competition might both play a role here. Hopefully though, the vital statistics of recruitment, growth, and natural mortality would be homogeneous with each stock.

Situations where species management is not applicable are numerous. Sockeye salmon in western North America cannot be effectively managed as a species. The population from each individual spawning stream must be managed as a separate stock. Management of rainbow trout is sometimes a problem because some populations are stream spawners while others are shoreline spawners. In both sockeye salmon and rainbow trout the management by strains is most applicable. The same is true for many other fishes.

Despite the inconsistencies, defining unit stock as a manageable portion of the target fish remains the most practical definition in marine fisheries and especially freshwater recreational fisheries.

## Identifying Unit Stocks

Numerous techniques have been developed for delimiting stocks of fish. Some methods allow a great deal of resolution in determining genetic differences between groups of fish; for instance, electrophoresis of serum proteins. Other methods give only rough estimations of number and range of stocks present. The precision with which the various methods separate stocks is not the sole basis for their selection in a given management situation. Techniques must be chosen on the basis of the precision needed to achieve management objectives given the constraints of budgets and control of fishing.

The following methods of stock identification are presented relative to their ability to delimit stocks:

1. Fish can be separated into stocks based on their comparative life histories. Similarities or differences in habitat preference, food consumed, and general life history are the kinds of criteria used for this type of separation. Trojnar and Behnke (1974) determined that two introduced populations of cutthroat trout (Salmo clarki) of different origins in North Michigan Lake, Colorado, formed two distinct stocks for management purposes based on food and habitat preferences. The population of Snake River cutthroat was the more acceptable from the anglers' point of view because of its proclivity for feeding on terrestrial and surface insects, thereby making it more vulnerable. The Pikes Peak origin cutthroat
trout preferred midwater feeding on copepods. Consequently, the two races of cutthroat effectively formed separate stocks for management purposes. Since populations were maintained solely by stocking, it is logical to stock only the more vulnerable strains provided that improving catch is the objective.
2. Another method which can be used to make separation of population groups is by their distributions. This has been used in marine fisheries management, where the distributions were determined from catch records of commercial fleets. If a fish has a geographically continuous distribution, large or small, this may indicate that the species comprises a single stock. When a species has a patchy distribution, it may indicate the presence of several discrete stocks. Associated with this method is the distribution of spawning areas. The fish may be found over a large continuous area for much of the year and then concentrate for spawning at discrete times or locations. This situation may indicate that there are several populations within the species each with its own spawning ground or time. Carefully designed tagging studies can be used to identify stocks (Cushing 1968). If fish are tagged and released in the fishing area and subsequently recovered on several discrete spawning areas it could probably be concluded that several stocks are being fished simultaneously by that fleet. On the other hand, if all fish marked in a particular area show up on the same spawning ground, then a single stock is probably being exploited by that fleet.

A slightly different approach to analyzing stocks by tagging is to tag fish while concentrated on the spawning grounds. Subsequent recapture of these fish in the fishing area will give the geographical limits of the stocks and indicate where and to what extent different populations mix.
3. A wide range of morphological characteristics have been used to separate stocks of fish. Meristic comparison of such anatomical features as fin rays, vertebrae, or parr marks can be used as indications of populations or stocks. Morphometric analysis, the comparison of the ratios of body measurements, has also been used to separate stocks. Often a sing1e morphological feature will allow fish stocks to be delimited as is the case for herring (Clupea harengus) stocks in the southern Gulf of St. Lawrence (Messieh 1972). In this case the shape of the otoliths is different in different stocks. Evidence for discrete stocks of the winter flounder (Pseudopleuronectes americanus) were found in variations in fin ray counts. Differences in size at maturity provided evidence for two discrete populations of lake white fish (Coregonus clupeaformis) in Maine lakes (Fenderson 1964). Northcote and Tsuyuki (1970) found that young rainbow trout (Salmo gairdneri) showed differences in parr mark numbers above and below a waterfall. This suggests that two discrete populations exist. Lewis (1957) was able to separate the striped bass (Morone saxatilis) of Chesapeake Bay into three discrete populations based on gill raker counts. Meristic counts present two problems in stock identification.

The first of these is that that they can be affected by the environment. It is possible that the members of a single stock which mix freely on the spawning grounds may separate to areas with different environmental conditions the rest of the year. If temperatures are different in the two areas, the fish may show differences in vertebrae or fin ray counts. This may result in the single stock being designated as two stocks in the two areas. The second difficulty with meristic counts for stock identification is that individual fish cannot be recognized as belonging to one stock or another. The reason for this is that within a population the meristic count for a particular structure will show a range of values. Stocks are considered distinct if there is a significant difference in the mean of the counts from samples from each stock. Often the ranges in values overlap.
4. If the fisheries in two adjacent areas have similar catch and effort records this is good evidence that one stock is involved. The idea behind this method is that two different stocks having differences in their vital statistics would respond differently to exploitation and changes in the environment which would be reflected as a divergence in the catch per unit effort in the two areas (Gulland 1974). A second way in which catch data can be used to identify or separate stocks is through the age composition of the catch. A single stock will be fairly uniform from one area to the next in the percentage that a particular year class makes up the total because the population is recruiting from a
single source. Two different stocks will be recruiting from two different sources. In addition, the recruiting classes of two distinct stocks will be subjected to different environmental conditions and survival rates. Also, if growth rates are different for different stocks, then year classes in the different stocks will show up in different proportions due to gear size selectivity. When year class percentages for one area are regressed on the percentages from another area, the line formed should not deviate substantially from $45^{\circ}$ if one stock only is present (Fig. II-2).


Figure II-2. Graph of the percentage of the population in a fishery versus the percentage of the population in another fishery. If the line deviates from $45^{\circ}$, two or more stocks may be involved.
5. Disease and parasites can occasionally be used to differentiate between stocks. If a disease or parasite is endemic to a single population then it can be recognized as a discrete stock. Even if the parasite or disease in question occurs among two stocks a difference in its intensity in two areas would suggest that two stocks are present. Nyman and Pippy (1972) found that two species of parasites were found in significantly different numbers in North American origin Atlantic Salmon than those of European origin in the Greenland fishery. This supported the idea that two genetically distinct stocks were being exploited in that fishery.
6. Since the first demonstration of individual differences in human erythrocyte antigens and subsequent findings of racial differences in the frequency of particular antigens, intensive serological studies have been made on a number of animal groups. Since differences have been shown to be genetically determined, they have been used in identifying groups of marine fishes (Sinderman and Mairs 1959, Vrooman 1964, Wilkins 1968). Groups of golden trout in different watersheds were separated by comparison of the frequencies of blood antigens (Calaprice and Cushing 1967) while two stocks from the same watershed were shown to not be significantly different, as might be expected. Since proteins are but a few steps removed from the gene (Ingram 1960) and do not seem to be as susceptible as meristic characters to environmental modification (Barlow 1961) they have often been chosen in biochemical
studies of differences in stocks. Electrophoresis of tissue proteins is now considered to be the most reliable method of distinghishing stocks of fish. This method has confirmed the conclusions drawn from earlier attempts at delimiting stocks. The theory behind this method is that populations isolated by physical or behavioral barriers will develop genetic based differences in proteins over time. These differences will show up as differences in migration and staining on a specially prepared medium. This technique has been used extensively in the last ten years for identifying populations of fish species (Smith and Clemens 1972; Ridgeway, Sherburne, and Lewis 1970; Nyman and Pippy 1972; Morgan, Koo, and Krantz 1973).

## Application of the Unit Stock Concept

Many of the important stocks of marine fishes are valuable resources upon which depend the livelihoods of thousands of people and economies of numerous countries. Marine stocks are also the source of needed protein for much of the world. Stocks of this importance have been the subject of considerable theoretical and applied management efforts. Commercially important stocks of the North Atlantic have been the impetus for the development of much of the current population dynamics theory in fisheries management. It is in these intensively managed and important fisheries that unit stock identification is often equated with population identification.

Historically, marine fisheries management has had as its major objective the attainment of maximum sustainable yield for all stocks. For this objective to be achieved it is necessary to have a clear knowledge of the vital parameters of the different stocks, which requires precise delineation of these stocks. In important fisheries like the North Atlantic cod fishery, considerable time and effort has been directed at delimiting as carefully as possible the different populations. These efforts have included the employment of several techniques in stock or population identification to insure its precision. Based on the vital parameters of each stock, mesh regulations and other sanctions have been imposed to assure the continued production of each individual stock.

This trend towards careful delineation of stocks will continue as more and more of the world's marine fish stocks become heavily exploited and as protein from these stocks becomes more valuable. As the decisions concerning the stocks become more critical and management more sophisticated, the clarity with which stocks can be delineated will also need to be improved. In marine fisheries management the unit stock will continue to be more and more equated with the population or genetic based unit. This is not possible, however, in all fisheries because of several types of constraints. Often where different stocks mix on the same fishing grounds, they cannot be exploited separately. As long as this situation exists, managers in those fisheries will have to treat as the unit stock a combination of two or more populations and manage given these constraints.

The concept of unit stock in freshwater fisheries management differs substantially from that generally used in marine fisheries management for three reasons. The first is that there exists an enormous number of populations of fish relative to the resources of the manager. Secondly, freshwater fisheries management is generally less oriented toward yield-oriented objectives. Thirdly, fish stocks and habitats can be altered and matched for the purposes of fisheries management.

The first two of these points explain why that, in comparison to marine fisheries management, freshwater managers tend to clump fish stocks when dealing with them. It is obvious that the stocks of largemouth bass, for example, in two reservoirs meet all the criteria for being separate and distinct biological entities. It is, however, highly unlikely that the manager will have the money and manpower to estimate the vital parameters of each population of each species in every reservoir in his jurisdiction and apply the appropriate management measures in each. Few individual freshwater stocks have a value justifying such intensive management.

The result of recreational fisheries managers operating under these kinds of constraints is that populations and even species must be grouped for management. For instance, all largemouth bass in large reservoirs may be treated as a single stock and regulations set based on a generalized model of the needs of a typical bass population in that region. The freshwater fisheries manager is also faced with the problem that fishermen cannot distinguish between different fishes. Thus, it is often necessary to manage all catfish or all sunfish as a single unit stock even though it is known that several species or populations are present.

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## CHAPTER THREE

## ABUNDANCE

Estimation of stock abundance or relative abundance is important in fisheries management as a step to estimating other vital parameters. Some estimate of abundance is needed to evaluate the size of management units and to estimate the exploitation rate due to fishing and other sources. Abundance is used to evaluate the impact of management efforts on a fish population. Abundance estimates are used in turn to estimate mortality rates and recruitment of a fish stock. Probably the most important use of abundance data is in estimating mortality rates, which in turn are reduced to exploitation rates. In all cases the manager should carefully decide exactly why he wants to estimate abundance and then use the simplest method to satisfy his needs.

Many methods and modifications have been developed to estimate abundance. For our purposes, six general approaches are defined and explained. The statistical theory upon which the methods are based is avoided in order to concentrate when and how the methods are applicable without becoming immersed in mathematics. Each technique requires a specific set of assumptions. The validity of the assumptions is important, but it must be recognized that in most cases the assumptions are not met. It is most important to identify the assumptions which are grossly not upheld and the degree or manner in which they are violated.

The methods of estimating abundance to be discussed are: 1) indices of abundance (catch per unit effort); 2) direct enumeration (total counts, partial counts, and correlation methods); 3) mark-recapture methods (single census, multiple census, and multiple recapture); 4) catch composition methods; 5) depletion methods; and 6) virtual population estimates. The population dynamics symbols used in formulas throughout this text are in Table III-1. Formulas for calculation of abundance are presented, but major emphasis is placed upon extracting the principles involved.

Table III-1. Population dynamics symbols used in fisheries management (Internationally Standard).

POPULATION DYNAMICS SYMBOL
(Internationally Standard)

Symbol
A
B
C
D

E
F
G
K
M
N
P
R

S
v
Y
Z

## e

f
$\ell$
$\ell_{c}$
m
n
q
r
t
${ }_{\mathrm{w}}^{\mathrm{w}}{ }^{\mathrm{c}}$
$\mathrm{w}_{\mathrm{c}}$

Term

* Mortality rate (fraction) (often 1-S)

Biomass (general)
Catch of fish (number)

* Natural death rate (fraction)
* Exploitation rate (fraction)
* Fishing mortality rate (instantaneous)
* Growth rate (general)
* Growth rate (von Bertalannfy equation)
* Natural mortality rate (instantaneous)

Number of individuals in a stock (or population)
Biomass of fish in a stock

* Number of recruits (annual recruitment)
* Survival rate (fraction)

Virtual population estimate
Yield (catch of fish in weight)

* Total mortality rate (instantaneous)

Natural base
Fishing effort
Length of individual fish
Length at first capture

Number of fish marked
Sample size
Catchability coefficient (F/f)
Number of fish recaptured
Time
Time at first capture
Weight of individual fish
Weight at first capture

* Rate estimators


## 1. Indices of Abundance

In most situations, the fisheries manager only needs to know the relative abundance of various stocks. Catch from a standard gear unit is one approach that is often used in this situation. A standardized seine haul, a fixed length and mesh size gillnet, or electrofishing over a standard course are examples. Coves can be treated with rotenone or a similar toxicant in a standardized manner and this method is then considered to be a standard gear unit. Advantages of indices are ease of use and simplicity in analysis. Disadvantages include the questionable representativeness of the sample, variability of the index, and weakness of statistical analyses. Replicates are needed to estimate variance, but are usually difficult to obtain with this method.

Catch per unit of fishing effort (C/f) is the most commonly used indice of abundance. The basic assumption is that $\mathrm{C} / \mathrm{f}$ is in some constant or predictable way related to stock size. The difference between this approach and the standard gear unit is that $C / f$ can be calculated on any gear, as long as f is measured in the same units. Creel data can be used in many ways to express $\mathrm{C} / \mathrm{f}$. This method is most commonly used for making year to year comparisons as part of a monitoring program. The same advantages and disadvantages of the standard gear unit also apply to this method. Because of the simplicity and ease of use associated with indices of abundance, they should seriously be evaluated to determine if they supply the needs of the fisheries manager before other, more costly and time consuming methods are utilized.

## 2. Direct Enumeration Methods

Direct enumeration is one of the best techniques for estimating abundance, but it is limited in applicability. It is one of the simplest methods of estimating abundance. This method depends on counting all or a selected portion of the population. Whenever this method can be used, it is preferred because it is usually of limited value because they can only be utilized when the total population may be confined sufficiently to make an actual count of individuals. Three types of direct enumeration have been applied to fisheries management: 1) total counts; 2) partial counts; and 3) correlation methods.

Total Count
Total count of a fish population can be accomplished in various ways. Salmon and trout on their spawning runs can be guided into fishways, weirs, or traps. Fisheries scientists have often erected counting towers along stream banks. Observation is often improved by providing a light colored stream bottom background. Where fishways have been constructed, salmon can be easily counted at the exit, or a T.V. camera and video-tape equipment can be installed in the fishway. Sophisticated equipment such as this can reduce counting error substantially. Small ponds can sometimes be drained adequately to permit recovery of the total population with seines. Because total counts require enumeration of all individuals in the population, there is no statistical analysis involved.

## Partial Count

Partial counts using direct enumeration may also be practical in some fisheries. A portion of the population is counted, then the total population is projected from these data. Towers on the banks of salmon streams are usually not manned continuously, rather, counting periods of 10 minutes per hour can be randomized and then expanded for a complete migration period. A statistically designed sampling scheme allows expansion of the data to an estimate of the total abundance.

In some cases a stream or lake bottom can be stratified, then the results of sampling these stratified areas can be projected to the total population. Cove sampling may be considered a type of partial count. In this method, coves of a reservoir or lake are sampled and these results projected to the population of the entire reservoir.

The estimation of N by this technique and computation of its associated variance are fairly straightforward. Assuming the abundance of the fish remains the same and is uniform throughout the area of concern, arbitrarily divide the area into A equal unit spaces (spatial or temporal) and select a of these to enumerate completely. This yields error-free number $\mathrm{N}_{1}, \mathrm{~N}_{2}, \mathrm{~N}_{3} \ldots \mathrm{~N}_{\mathrm{a}}$ corresponding to subspaces 1,2 , 3 ... a. Then:

$$
\hat{N}=\frac{A}{a} \sum_{i=1}^{a} N_{i}
$$

and

$$
\operatorname{var}(\hat{N})=\frac{A^{2}-a A}{a} \operatorname{var}\left(N_{i}\right)
$$

where

$$
\operatorname{var}\left(\hat{N}_{i}\right)=\frac{a \sum_{i=1}^{a} N_{i}^{2}-\left(\sum_{1=1}^{a} N_{i}\right)^{2}}{a(a-1)}
$$

For example, suppose you mark off a shallow 25 acre lake into 25 one acre grids. Five grids are randomly designated as sampling units and the fish counted by aerial photographs. The results are:

$$
\begin{aligned}
& a_{1}=30 \\
& a_{2}=40 \\
& a_{3}=25 \\
& a_{4}=15 \\
& a_{5}=35
\end{aligned}
$$

then

$$
\begin{aligned}
& \hat{\mathrm{N}}=(25 / 5) \quad(30+40+25+15+35) \\
& \hat{\mathrm{N}}=725
\end{aligned}
$$

The estimated variance of N is calculated as follows:

$$
\begin{aligned}
& \hat{\operatorname{var}}\left(N_{i}\right)=\frac{5\left[30^{2}+40^{2}+25^{2}+15^{2}+35^{2}\right]-[30+40+25+15+35]^{2}}{5(4)} \\
& \hat{\operatorname{var}}\left(N_{i}\right)=92.5
\end{aligned}
$$

then

$$
\begin{aligned}
& \hat{\operatorname{var}}(\hat{N})=\frac{(25)^{2}-5(25)}{5} \\
& \hat{\operatorname{var}}(\hat{N})=9250
\end{aligned}
$$

## Correlated Methods

Often the life history of a fish may be such that some closely related (correlated) sub-adult population may be estimated more readily than the adult population. For example, the number of adults may be related to egg production or the number of nests or redds. In fisheries management, estimation of adult population size from eggs has been attempted for a few marine species which have pelagic eggs. In addition the nests of certain fishes, such as the salmonids and basses, may be used as an estimate of the number of spawning adults.

Fisheries scientists in Alaska often forecast the size of salmon runs using a correlated method or index. Sometimes this method is only able to give an index of population level because sampling of all areas during all time periods is difficult. Forecasts are not only important in determining population size, but are also used for planning and regulatory decision-making. Pink salmon forecasts, for example, are based on the relationship between pre-emergent fry abundance and subsequent adult return. The forecast of the expected number of returning adult pink salmon is obtained by relating past fry indices to corresponding returns of adult pink salmon. Data acquired over past years are analyzed using simple linear regression.

The following is an example of the procedure to forecast pink

```
salmon in runs in Alaska. Let,
    X = pre-emergent fry density (fry per square meter)
    Y = subsequent total return of adult pink salmon (millions
        2 years later)
```

| Brood Year | X |  | (Year) | XY | $\mathrm{x}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1968 | 72.6 | 2.2 | (1970) | 159.72 | 5270.76 |
| 1969 | 111.3 | 20.6 | (1971) | 2292.78 | 12387.69 |
| 1970 | 85.2 | 3.2 | (1972) | 272.64 | 7259.04 |
| 1971 | 124.8 | 9.7 | (1973) | 1210.56 | 15575.04 |
| 1972 | 121.3 | 11.0 | (1974) | 1334.30 | 14713.69 |
| Total | 515.2 | 46.7 |  | 5,270.00 | 55,206.22 |
| $\overline{\mathrm{X}}=103.04$ |  |  |  |  |  |
| $\overline{\mathrm{Y}}=9.34$ |  |  |  |  |  |
| $\beta=\frac{n(\Sigma X Y)-(\Sigma X)(\Sigma Y)}{n\left(\Sigma X^{2}\right)-\left(\Sigma X^{2}\right)}=0.22$ |  |  |  |  |  |
| $\alpha=9.34-0.16(103.04)$ |  |  |  |  |  |
| $\alpha=-12.92$ |  |  |  |  |  |
| Thus |  |  |  |  |  |
| $\hat{Y}=-12.92+0.216 \mathrm{X}$ |  |  |  |  |  |

Current incomplete data include:

| Brood <br> Year | X | [Forecast] <br> Y (year) |
| :---: | :---: | :---: |
| 1973 | 133.9 | $[16.0]$ |
| 1974 | 101.5 | $[9.0](1975)$ |

Pre-emergent fry density (X) in 1973 was found to be 133.9. The estimate of adult pink salmon (Y) returning in 1975 (two year life cyc1e)

$$
\begin{aligned}
& \hat{Y}=\alpha+\beta X \\
& \hat{Y}=-12.9 .2+0.216(133.9) \\
& \hat{Y}=16.00
\end{aligned}
$$

The variance of this estimate is calculated from that point on the regression line:


$$
=1.15
$$

Pre-emergent fry density in 1974 was to be $101.5 / \mathrm{m}^{2}$. The run forecast for 1976 can be made in the same manner (9.0).

Indices of abundance have several advantages: 1) 1ow cost, rather high quality data; 2) the fish often do not need to be captured; 3) there is no marking problem; 4) estimates are obtained over a relatively short period of time. The major drawbacks are their limited application and the rather complicated sampling and analysis that may occur in partial count and correlation techniques.
3. Mark-Recapture Methods

Marked fish may provide information on abundance. These methods are well adapted for use on small, discrete freshwater stocks that support recreational fishing and for which catch statistics are difficult to obtain. The three basic types are the single census, multiple census, and multiple recapture method.

## Single Census

The simplest mark-recapture method is the single census estimator using marked individuals and their recovery. The general method was developed by LaPlace to estimate the human population of France in the 1700's. Peterson (1896) used mark-recapture to estimate exploitation rate (E). Dah1 (1919) applied the method to a lake to estimate abundance (N). Lincoln (1930) applied it to wildlife situations and Jackson (1933) to entomological studies. In fisheries management, the actual estimate of N in mark-recapture is often incidental to estimating exploitation.

For single census estimation, marked fish are released and at a subsequent time, a catch is made which will include marked and unmarked individuals. This method is based on the principle that the ratio of recaptured marked fish (r) to the catch (c) is the same as the total number of marked fish released (m) is to the total population (N).

Basic assumptions to be satisfied are: (1) marked fish have no more mortality than unmarked fish; (2) marked fish are caught at same rate as unmarked fish; (3) marks are not lost: (4) marked fish are randomly distributed or the sampling effort is random; and (5) recruitment is negligible or can be estimated. The simplest estimator is

$$
\hat{M}=\frac{\mathrm{mC}}{\mathrm{r}}
$$

Where: $m=$ number of fish marked

$$
\begin{aligned}
C= & \text { the catch taken for census [total marked ( } \mathrm{m} \text { ) and } \\
& \text { unmarked }(\mathrm{C}-\mathrm{m}) \text { ] }
\end{aligned}
$$

## $r=$ the number of recaptured individuals (marked fish)

in the census.

As an example, suppose 550 fish are captured by fyke net and marked. Over the next two weeks, 8,720 fish are taken by sportsmen of these creeled fish, 157 were marked.

$$
m=550
$$

$$
C=8,720
$$

$$
r=157
$$

$$
\hat{\mathrm{N}}=\frac{(550(8,720)}{157}=30,547
$$

Placing confidence intervals on the estimated abundance (N) is more difficult. The approach to calculation depends on the proportion of the marked fish which are recaptured.

If the number of recaptures (r) is very low (< $10 \%$ ), is treated as a Poisson distribution.

For example, to calculate the confidence interval ( $\alpha=0.05$ )
often depends on adjusting the recapture of marked fish from a Poisson to a normal distribution with the following formula:

$$
r+1.92 \pm 1.96 \sqrt{r+1}
$$

Thus,

$$
157+1.92 \pm 1.96 \sqrt{158}=134 \text { and } 184
$$

then substituting into the estimation formula,

$$
\frac{(8,720)(550)}{134}=35,791 \text { and } \frac{8,720 \times 550}{184}=26,065
$$

The approximate confidence interval at $(\alpha=0.05)$ is $26,100<\mathrm{N}<35,800$.

If the number of recaptures is reasonably large ( $10-20 \%$ ), then $r$ may be considered to have a "binomial" distribution. The variance ( $V$ ) of a binomial population is $n p q$ (where $n=$ population size; $p$ = probability of one alternative; $q$ = probability of the other alternative). In the sing1e census estimator:

$$
\mathrm{V}(\mathrm{E})=\frac{\mathrm{C}}{\mathrm{mN}}\left(1-\frac{\mathrm{m}}{\mathrm{r}}\right) .
$$

Exploitation rate (E) during the sampling period can be estimated by

$$
\hat{\mathrm{E}}=\frac{\mathrm{r}}{\mathrm{~m}}
$$

In the very rare situation where r is very high, normal approximation techniques are utilized to calculate the variance. If such a situation is encountered, an evaluation of the basic assumptions should be performed.

## Multiple Census

The multiple census estimator is a modification of the single census estimator. The method was developed by Thompson (Illinois) and Juday (Wisconsin). Schnabel (1938) and SchumacherEschmeyer (1943) provided much of the mathematical basis. Marked fish are repeatedly added to the population while those removed are recorded by time period to yield an estimate of the population size. As the number of marked fish increases, the variance of the estimate decreases. The assumptions for this estimator are similar to the single census estimator.

As an example, assume we sample fish by fyke net daily. Each sampling time we mark any unmarked fish. Let
$m_{t}=$ total number of marked fish at large at the start of day $t$,
$M_{t}=$ total number marked prior to day $t$,
$C_{t}=$ total sample taken on day $t$,
$r_{t}=$ number of recaptures in the sample $C_{t}$, and
$\Sigma r_{t}=$ total recaptures during the experiment to day $t$.

| $C_{t}$ | $M_{t}$ | $C_{t} M_{t}$ | $r_{t}$ | $\sum r_{t}$ | $\hat{N}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| 80 | 0 | 0 | 0 | 0 | - |
| 100 | 80 | 8,000 | 5 | 5 | 1600 |
| 60 | 175 | 10,500 | 9 | 14 | 1321 |
| 90 | 226 | 20,340 | 15 | 29 | 1340 |

N for each time period is estimated by

$$
N=\frac{\Sigma C_{t} M_{t}}{\sum r_{t}}
$$

With a "low" r, treat $r$ as a Poisson variable to calculate variance. With "high" r, use a normal approximation. DeLury (1958) reviews the mathematical basis for variance estimation in multiple census estimation.

In the previous sample, $N$ has been estimated by

$$
\hat{N}=\frac{\Sigma C_{t} M_{t}}{\Sigma \mathrm{r}_{\mathrm{t}}}
$$

In practice the worker would continue sampling until the confidence interval is narrow enough for the purposes at hand.

## Multip1e Recapture

The multiple recapture method (Jolly-Seber Method) can be used in situations similar to those used in a single or multiple census, but in which a closed population cannot be assumed. However, it is best suited to small lakes where each marked fish can be recognized every time it is recaptured. Remarking and giving double weight to an already captured individual may introduce some bias if the individual is capture-prone or capture-shy. Fortunately, in most cases, fish are not capture-prone or capture-shy and tend to avoid any type of sampling gear.

The multiple recapture procedure is as follows: On the first occasion ( $t=1$ ) the fish are marked, at $t=2$, recaptures are noted and returned, and unmarked fish are given a different mark; at $t=3$, the previous marks of both categories are recorded as well as unmarked individuals.

The data obtained may be set up in tabular form:

| Time Period | Fish Newly <br> Marked | Fish Examined <br> for Marks | Recaptures <br> from 1st <br> Marking | Recaptures <br> from 2nd <br> Marking |
| :---: | :---: | :---: | :---: | :---: |
| t | $\mathrm{m}_{\mathrm{t}}$ | $\mathrm{C}_{\mathrm{t}}$ | $\mathrm{r}_{1 \mathrm{t}}$ | $\mathrm{r}_{2 \mathrm{t}}$ |
| 1 | $\mathrm{~m}_{1}$ | $\mathrm{C}_{1}$ | $\mathrm{r}_{11}$ | $\mathrm{r}_{21}$ |
| 2 | $\mathrm{~m}_{2}$ | $\mathrm{C}_{2}$ | $\mathrm{r}_{12}$ | $\mathrm{r}_{22}$ |
| 3 | $\mathrm{~m}_{3}$ | $\mathrm{C}_{3}$ | $\mathrm{r}_{13}$ | $\mathrm{r}_{23}$ |

A direct estimate of the population at $t=2\left(N_{2}\right)$ can be found by

$$
\hat{\mathrm{N}}_{2}=\frac{\mathrm{m}_{2}\left(\mathrm{C}_{2}+1\right) \mathrm{r}_{13}}{\left(\mathrm{r}_{12}+1\right)\left(\mathrm{r}_{23}+1\right)}
$$

The variance of $\hat{N}_{2}$ is found by approximation techniques described by Seber (1973).

As an example, a small lake containing brook trout was sampled. The data are as follows:

| Time Period | Fish Newly <br> Marked | Fish Examined <br> for Marks | Recaptures <br> from 1st <br> Marking | Recaptures <br> from 2nd <br> Marking |
| :---: | :---: | :---: | :---: | :---: |
| 1 | $500\left(\mathrm{~m}_{1}\right)$ | - | - | - |
| 2 | $400\left(\mathrm{~m}_{2}\right)$ | $480\left(\mathrm{C}_{2}\right)$ | $120\left(\mathrm{r}_{12}\right)$ | - |
| 3 | - | $1000\left(\mathrm{C}_{3}\right)$ | $163\left(\mathrm{r}_{13}\right)$ | $174\left(\mathrm{r}_{23}\right)$ |

$\hat{\mathrm{N}}_{2}=\frac{(400)(481)(163)}{(121)(175)}=1481$

## 4. Catch Composition Methods

Population estimates can sometimes be made by taking the composition of the catch into consideration. The change in ratio (survey-removal) estimate is of this type. In using this estimator, (1) the relative abundance of two kinds of individuals in a population at $t=1$ is determined; (2) changes in the relative abundances are made by removing or adding known numbers of known kinds at some time later than $\mathrm{t}=1$, ; and (3) estimates of the new relative abundances are made at $\mathrm{t}=2$.

The assumptions for this estimator are as follows: (1) the kinds of individuals into which the population is divided must remain constant; i.e., male or female, marked or unmarked; (2) mortality and recruitment between $t=1$, and $t=2$ must be negligible or at least nonselective with respect to the kinds of individuals into which the population is divided; and (3) mortality and recruitment must not occur while additions or removals are in progress.

The basic estimating equation is found by solving a series of simultaneous equations. The symbols used can be defined as follows:

$$
\begin{aligned}
N_{1}= & \text { total number of fish (brook and brown trout, for example) } \\
& \text { in the population at } t=1
\end{aligned}
$$

$\mathrm{X}=$ number (brook trout) added or removed between $\mathrm{t}=1$ and $\mathrm{t}=2$
$\mathrm{Y}=$ number of the other kind of fish added or removed (brown trout)
$p_{1}=$ decimal fraction of population $N_{1}$ which consists of one kind (brook trout) at $t=1$
$p_{2}=$ new decimal fraction (or brook trout) among the $N_{2}$ individuals in the population at $\mathrm{t}=2$
$N_{2}=$ total number of fish (brook and brown trout) in the population at $\mathrm{t}=2$

The two necessary simultaneous equations can be formed as
follows:

$$
\begin{aligned}
& P_{2} N_{2}=p_{1} N_{1}+X \\
& N_{2}=N_{1}+X+Y
\end{aligned}
$$

solving

$$
\hat{\mathrm{N}}_{1}=\frac{\mathrm{X}-\mathrm{p}_{2}(\mathrm{X}+\mathrm{Y})}{\mathrm{p}_{2}-\mathrm{p}_{1}}
$$

There are many possible applications of this method. One possibility likely to occur arises whenever a creel census is conducted on a fishery with more than one species present. For example, a trout population is shown by sampling to consist of $70 \%$ brook trout and $30 \%$ brown trout. If anglers remove 200 brook trout and 30 brown trout, and a second sampling shows that the removal of fish changed the brook to brown trout ratios to $55 \%$ brooks and $45 \%$ browns $\mathrm{N}_{1}$ is found as follows:

$$
\begin{aligned}
& \hat{\mathrm{N}}_{1}=\frac{-200-0.55(-230)}{0.55-0.70}=\frac{-73.5}{-0.15}=490 \\
& \hat{\mathrm{~N}}_{1}(\text { brook trout })=343 \\
& \hat{\mathrm{~N}}_{1}(\text { brown trout })=147
\end{aligned}
$$

Approximation techniques must be used to calculate the variance associated with this estimator.
5. Depletion Methods

The basic conditions required for application of this estimator. (also called the Leslie, Delury, or regression estimator) are that the population must be fished heavily enough to significantly reduce the catch per unit effort ( $C / f$ ) and that a series of $C / f$ and associated catch values (C) are available to be fitted to a regression line.

The depletion method is based on the principle that a decrease in catch per unit of effort (C/f) as the population is depleted bears a direct relationship to the extent of the depletion. This estimator can only be used where at least $50 \%$ of the population can be removed because it depends on the ability to estimate the slope of the regression of $C / f$ on either cumulative catch or effort. Catches from most sport fisheries are unsatisfactory for using this method because of variation in catch. However, this can be overcome by simulating fishing effort and catch by electrofishing. In a valuable sport or commercial fish population, captured fish can be marked and subsequently ignored instead of removing them.

The assumptions are (1) catchability of the fish remains constant; (2) the population is totally available to the fishery; (3) there is no natural mortality or recruitment; and (4) the fishing effort applied is constant.

The number of fish in the population is found by sampling the population a number of times (using a constant fishing pressure), and plotting a regression line of $C / f$ on cumulative catch ( $\Sigma C_{t}$ ) for each time period. The regression line is then projected to the intercept of the X axis, the initial population size. The initial population size can be directly found without plotting by mathematically deriving the intercept using the least squares method.

By definition the $C_{t} / f$ during time $t$ is equal to the catchability (q) multiplied by the population present at the beginning of that time.

$$
\begin{equation*}
C_{t} / f_{t}=q N_{t} \tag{1}
\end{equation*}
$$

The population at the start of time $t$ is equal to the original population less the cumulative catch $\Sigma C$.

$$
\begin{equation*}
N_{t}=N_{o}-\Sigma C \tag{2}
\end{equation*}
$$

substituting into (1)

$$
\begin{equation*}
C_{t} / f=q\left(N_{o}-\Sigma C\right) \tag{3}
\end{equation*}
$$

Equation 3 indicates that $C / f$ plotted against $\Sigma C$ has a slope of $q$. Also, the X axis intercept is an estimate of the original population $N_{0}$, since it represents $\Sigma C$ if $C / f$ and the population were hypothetically reduced to zero by fishing. $N_{o}$ can now be found using the least squares method to obtain the X axis intercept (Figure III-1).


Figure III-1. Regression line calculated to describe the relation between catch per unit effort ( $C / f$ ) and cumulative catch ( $\Sigma C$ ). The X axis intercept gives estimate of abundance.

A hypothetical example follows showing table setup and calculations:

| Time <br> Period | LC (X) | $\mathrm{C}_{\mathrm{t}} / \mathrm{f}_{\mathrm{t}}$ (Y) | (xy) | $\left(x^{2}\right)$ |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 0 | 131 | 0 | 0 |
| 2 | 131 | 69 | 9,039 | 17,161 |
| 3 | 200 | 99 | 19,800 | 40,000 |
| 4 | 299 | 78 | 23,322 | 89,401 |
| 5 | 377 | 56 | 21,112 | 142,129 |
| 6 | 433 | 76 | 32,908 | 187,489 |
| 7 | 509 | 49 | 24,941 | 259,081 |
| 8 | 558 | 42 | 23,436 | 311,364 |
| 9 | 600 | 63 | 37,800 | 360,000 |
| 10 | 663 | 47 | 31,161 | 439,569 |
| Total | 3,770 | 710 | 223,519 | 1,846,194 |
| $\Sigma \mathrm{x}^{2}=1,846,194-3770^{2} / 10=424,904$ |  |  |  |  |
| $\Sigma y^{2}=57,062-710^{2} / 10=6652$ |  |  |  |  |
| $\Sigma \mathrm{xy}=223,519-3770(710 / 10)=-44,151$ |  |  |  |  |
| $\beta=$ slope $=-44151 / 424904=-0.103908$ |  |  |  |  |
| $\alpha=$ Intercept $=710-(-0.103908)(3770)=110.17$ |  |  |  |  |
| $\hat{N}_{0}=\frac{\alpha}{q}=\frac{110.17}{0.103908}=1060$ |  |  |  |  |

## 6. Virtual Population Estimates

An estimate of the actual population can be made from knowing the virtual population, but this method can be applied only when there are extensive creel census data. A yearly age census of the catch and the allocation of the catch among year classes must be carried out. The virtual population can be defined as the minimum estimate of catchable fish present in one year which is the total of the minimum number of fish in existence of each year class. To estimate the actual population from the virtual population, a number of fish must be marked and the number of recaptures of these fish in following years must be recorded.

The assumptions include (1) complete recruitment of the recruiting age class and older; (2) the same rate of exploitation for all age classes; (3) negligible natural mortality at all ages greater than the recruited age; and (4) constant recruitment of the recruiting class from year to year.

To find the virtual population estimate with a variable survival rate, a table of the minimum number of survivors of each brood year is constructed.

| Year <br> Class | III | IV | V | VI | Total <br> Virtual <br> Population | Year |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| 1961 | - | - | - | 1665 | 5553 | 1967 |
| 1962 | - | - | 1371 | 1243 | 4764 | 1968 |
| 1963 | - | 1294 | 1188 | 1165 | 4650 | 1969 |
| 1964 | 1223 | 1193 | 1180 | 1062 | 4774 | 1970 |
| 1965 | 1129 | 1122 | 1059 | 939 | 4711 | 1971 |
| 1966 | 1277 | 1265 | 1229 | 1147 | - | - |
| 1967 | 1388 | 1349 | 1265 | 1121 | - | - |
| 1968 | 1194 | 1174 | 1095 | 1049 | - | - |

The total virtual population is found by summing the entries diagonally from lower left to upper right. Thus, at the start of the 1967 fishing season, there were at least 5553 fish of Age III or older in the lake, 4764 in 1968, 4650 in 1969, etc. Exploitation rate can be calculated by

$$
E_{t}(\max )=\frac{C_{t}}{V_{t}}
$$

The actual population can be found by combining the results of a marking experiment with the virtual population. The total recoveries from $m$ fish marked at the start of year 1 (1967 in this case) in successive years of their appearance in the fishery are $r+r_{2}+r_{3}+\ldots$. then

$$
\hat{\mathrm{N}}=\frac{\mathrm{V}_{\mathrm{m}}}{\mathrm{r}_{1}+\mathrm{r}_{2}+\mathrm{r}_{3}+\cdot \cdot \cdot r_{\mathrm{t}+\mathrm{n}}}
$$

For example, the virtual population in 1967 is 5553.

During that year 500 fish were marked and $r_{1}=53, r_{2}=45$, $r_{3}=75$, then

$$
\hat{N}_{1967}=\frac{(5553)(500)}{53+45+75}=16,049
$$

If we assume a constant age composition in the stock and 1et $X=$ fraction of age $i$, then

$$
V=\sum_{i=1}^{\infty} C_{t}\left(1-X_{1}-X_{2} \ldots X_{i-1}\right)
$$

when

```
V = Virtual estimate of N.
```


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## CHAPTER FOUR

## MORTALITY

The economic importance of fisheries has provided major impetus to the development of methods for estimating fish population mortality rates. Mortality rate is a measure of the probability of a given fish dying in a specified time interval. The actual number of fish dying in a specific situation is not predetermined, but is a chance event. Usually an exact count of the number of deaths cannot be obtained and we must estimate the proportion by some sampling procedure, thus, introducing a source of error into the estimate of the average probability of death (Regier and Robson 1967).

Two basic approaches to calculation of mortality rates can be taken. The simplest to comprehend is annual mortality rate (A) but difficulties arise in partitioning values of annual mortality rates into the fractions due to fishing (E) and to natural causes (D). Another, more useful way is instantaneous mortality rate (Z) which is derived through theories of calculus and can be easily partioned into fishing (F) and natural (M) components.

Annual Mortality Rate
An estimate of mortality rate spans a specific period of time. The simplest and most common is the annual expectation of death of an individual fish (A), expressed as a fraction or percentage. This is the fraction of the fish present at the start of a year which actually die during the year from a given cause (Ricker 1975).

There is an annual mortality rate associated with each cause of death. Both recruitment and survival are assumed to be constant over time. Survival (S) and mortality (1 - S or A), its counterpart, are determined by a comparison of the numbers of a cohort or group of cohorts alive at successive ages:

$$
S=N_{t}+1 / N_{t} \quad \text { and } \quad A=1-S
$$

Where fishing (E) and natural (D) mortality are distributed proportionately within the year:

$$
A=E+D
$$

The expectation of death from fishing (E) is the chance or probability that a fish dies from fishing during the time period being considered. Mathematically, if $C=$ catch:

$$
E=C / N_{0}
$$

The expectation of death from natural causes (D) is the probability that a fish dies of natural causes during some time period.

The major problem with the use of annual mortality is that E and D are not additive. The two terms interact with each other:

$$
A=E+D-D E
$$

For example, if fishing mortality is lower in a given year, the natural mortality may be altered by increasing due to density dependent mechanisms. Because a fish can die only one time, DE subtracts the probability that it dies more than one time. It is impractical to allocate mortality amont the two categories, $E$ and D.

## Instantaneous Mortality Rates

The utility of the definitions of annual mortality rates are distinctly limited because the rates defined in this manner ( $\mathrm{A}=\mathrm{E}+\mathrm{D}$ ) depend upon each other, and the true functional form of this dependence is generally unknown. Where deaths of one kind preclude the possibility of deaths of the other kind, then mortality rates become functionally independent and, hence, operationally useful. By making the time sufficiently short we can be assured that at most one kind of death will occur during the period, thus creating a situation where the two kinds of events are mutually exclusive (Reiger and Robson 1967).

When studying mortalities we are concerned with rates of change and it is most convenient to deal with instantaneous rates of change (Gulland 1973). If the instantaneous rate of mortality (Z) does not vary with time or age of fish, the numbers surviving to successive years of life follow the familiar exponential trend implicit with a constant instantaneous coefficient; their logarithms decrease linearly with time and have a slope equal to $-Z$ (Figure IV-1) (Beverton and Holt 1957) .

For each cause of death, there is an instantaneous mortality rate, equal to the negative natural logarithm of the complement of the annual mortality rate. This represents the number of fish which would die from a given cause during the year if recruitment were to exactly balance total mortality from day to day. Mathematically:

$$
\mathrm{dN}_{\mathrm{dt}}=-\mathrm{ZN}
$$

Thus, the rate of change of cohort or year-class ( $N$ ) with time is proportional (Z) to the number present. The negative sign means numbers are declining (Ricker 1975). Rearranging and integrating:

$$
\begin{aligned}
& \mathrm{dN} / \mathrm{dt}=-\mathrm{ZN} \\
& \mathrm{dN} /{ }_{N}=-Z \mathrm{dt}
\end{aligned}
$$




Figure IV-1. (a) Relationship of number of fish with time.
(b) Age-frequency distribution resulting from $50 \%$ survival and constant recruitment of 1,000 yearlings per year (from Everhart, Eipper, and Youngs 1975).

Integration of the equation yields,

$$
\begin{array}{rlrl}
\ln N_{t / N_{o}} & =-Z t & \text { or } & \ln S=-Z t \\
N_{t / N_{o}} & =e^{-Z} & S=e^{-Z} \\
N_{t} & =N_{o} e^{-Z} & Z=-1 n
\end{array}
$$

The logarithm of the survival during one year gives the simplest arithmetical expression for the mortality (Gulland 1972).

In practice, sources of mortality are usually divided into the two categories, fishing (F) and natural (M) mortality. The separation of the total mortality into these two components becomes a matter of prime concern when predicting the effect of altering the fishing intensity. If we assume that $F$ and $M$ occur simultaneously and constantly over time, then:

$$
Z=F+M
$$

The frequency of encounters between fish and gear will be proportional to the product of the fishing intensity (f) and the abundance of the fish; furthermore, a certain fraction of these encounters will result in capture:

$$
\mathrm{dN} / \mathrm{dt}=-\mathrm{FN}
$$

The instantaneous rate of fishing is proportional to the amount of gear or the effort expended:

$$
F=q f
$$

F might also be calculated by:

$$
{ }^{\mathrm{F}} / \mathrm{Z}_{\mathrm{Z}}=\mathrm{E} /{ }_{1}-\mathrm{S}
$$

For these sample models we assume that the fishing mortality coefficient is constant for $f$ ish between age at first capture ( $\mathrm{t}_{\mathrm{o}}$ ) and the end of the life span, and that fishing effort is distributed uniformly over the population and is maintained at a constant level over a period of years long enough for the population to have reached a steady state.

Fishing mortality is not constant with age. It tends to vary because the large and small fish are distributed differently and also because of mesh selection inherent in gear; i.e., the larger the mesh, the older (larger) the fish at time of fish capture. F then changes suddenly at specific ages. Furthermore, the proportion of the whole population taken by an operation is not constant, but depends on the local density of fish. Therefore, a haul made where the density is high causes a greater mortality than one where the density is low (Beverton and Holt 1957, Gulland 1972)

Natural mortality is the effect of a relatively large number of environmental factors acting independently. The rate of natural mortality at any time depends on the number of fish present at that time, such that:

$$
\mathrm{dN} / \mathrm{dt}=-\mathrm{MN}
$$

(Beverton and Holt 1957).
Natural mortality (M) is equal to total mortality during periods when there is no fishing, but when fishing is occurring the simultaneous natural mortality must be estimated mathematically (Royce 1972).

It is often assumed that natural death is constant. If the natural mortality rate remains constant, the maximum life-span will, hypothetically, be of infinite duration, though in practice there will come a time when the last survivor dies. In addition to a continuous trend in $M$, there is also the possibility of it changing suddenly at one or more stages during the life of the fish. Intrinsic differences in the susceptibility to mortality factors leads to the tendency for more vulnerable individuals to die first, causing a decrease in natural mortality with age as only the more hardy survive (Beverton and Holt 1957).

## Estimating Survival

Recalling the derivation of instantaneous mortality rate ( $\mathrm{Z}=-\ln \mathrm{S}$ ), an estimate of survival can be used to derive Z. Survival can be calculated by two approaches: (1) successive ages; and
(2) catch curves.

## Estimating S by Successive Ages

If we have estimates of the average abundance over some time interval:

$$
\hat{\mathrm{N}}_{\mathrm{t}} \text { and } \hat{\mathrm{N}}_{\mathrm{t}}-1
$$

The ratio of the mean numbers in successive years is then manipulated:

$$
S=\frac{\hat{N}_{t}}{\hat{N}_{t} \neq 1}
$$

An example of the computation of $S$ from fin whale "age composition" data is as follows:

| Age | Frequency (\%) |
| :---: | :---: |
| 0 | 0.3 |
| I | 2.3 |
| II | 12.7 |
| III | 17.2 |
| IV | 24.1 |
| V | 14.1 |
| VI+ | 29.5 |

Survival between Ages IV and V then,

$$
N_{t}=24.1 \quad \text { and } \quad N_{t+1}=14.1
$$

so, $S=\frac{14.1}{24.1}=0.59$

Either stock abundance (N) or relative abundance data can be utilized. The disadvantages of this approach are: (1) some species exhibit highly variable year class strength; (2) fish may not be subject to the same mortality each year; and (3) an unbiased sample is difficult to obtain due to gear selectivity.

## Estimating Z with Catch Curves

The estimation of $Z$ by catch curves is superior to that by successive ages when any kind of variation in survival rate has to be examined (Ricker 1975).

A series of catches per unit effort ( ${ }^{C} / f_{f}$ ) plotted against time form a catch curve. A catch curve is characterized by an ascending arm of incompletely recruited age classes (Figure IV-2). On a logarithmic scale the descending arm of a catch curve is usually a straight line with a slope equal to -Z . Figure IV-3 shows both curve and linear relationships (Royce 1972).

A catch curve generates estimates of $Z$ between successive years. If the mortality rate during instead of between successive years is desired, it can be obtained by taking tangents on the curve at each age (Ricker 1975).


Figure IV-2. Catch curve. Ascending arm represents incompletely recruited age classes; descending arm represents fully recruited age classes.


Figure IV-3. Arithmetic ( - ) and logrithmic ( - ) catch curves from a hypothetical cohort experiencing a constant mortality rate.

Catch curves can also be generated by catch per unit effort and length frequency data. In fact, the original catch curve, derived by Baranov, was determined in this way. In this method, two curves are needed: (1) a curve of mean length against age; and (2) a representative curve of the logarithm of frequency against length. The two curves are combined by taking the slope on each at corresponding points; i.e., at a given age on curve $A$ and at that age's corresponding mean length on curve B. This method of computation suffers from a serious limitation: it is useful only where the increase in the length of the fish is a constant number of units per year (Ricker 1969). Assumptions implicit in catch curves and the estimation of Z are: (1) the survival rate is uniform with age; (2) survival rate is the complement of mortality rate, mortality rate $=$ natural and fishing mortalities and each of these then is uniform; (3) no change in mortality rate; (4) sample is taken randomly from age groups involved; (5) recruitment is equal for each age group (Ricker 1967).

Very rarely do we have estimates of the actual abundance at discrete points in time, nor will Z remain constant. To assume that ${ }^{C} / f$ is an index of stock size (N) is equivalent to assuming that the total amount of effort (f) is an index of F. While in some fisheries the fluctuations in catches per unit effort may follow precisely the fluctuations in abundance, very often the major causes of the fluctuations are availability changes, with the fish being particularly vulnerable to capture at certain seasons. Therefore, short term changes in catch per unit effort should not be used in estimating mortalities; they should be estimated from mean annual values or from periods twelve months apart (Gulland 1972, Royce, 1972).

The ascending left limb and the dome of a catch curve represent age classes which are incompletely captured by the gear used to take the sample; i.e., they are taken less frequently in relation to their abundance than are older fish. Other things being equal, the total mortality rate will be increasing during this period of recruitment. If the curve displays a slowly ascending left leg and a broad flat dome, recruitment is occurring over several age groups, while a steep ascending leg and a narrow sharp dome is the result of recruitment occurring over a few age groups.

Straightness of the right limb indicates a uniform rate of survival of the fish from year to year. The occurrence of such straight limbs is regarded as evidence that recruitment and natural mortality are sufficiently steady to give confidence to the method (Ricker 1975, Royce 1972).

The effort used in a fishery can vary from year to year; similar changes in natural mortality rate may possibly occur at times. The effects of these changes are graphically represented in Figure IV-4. Curve $A$ is the result of a steady survival rate; it has the classic straight right limb. After decreasing the rate of survival (increasing the rate of mortality) by one half, catch data seven years later were used to produce $B$. This curve has a partially concave right limb, which is not representative anywhere of the current (depressed) survival rate. The limb, near its outer end, approximates the original survival rate. Curve C is the result of catch data twelve years after the depression in survival. A one year interval, from seven to eight represents the current survival rate; the outer end still approximates the original slope. $D$ is the curve of the new, balanced population, having existed for 18 years at the lower survival rate. The curve is similar to $A$, but with a steeper slope (Ricker 1975).


Figure IV-4. Catch curves illustrating changes in rate of fishing with time. In every instance recruitment is complete following the first six ages shown, and the instantaneous rate of natural mortality is the same for all ages and years. [ $A=$ constant rate of fishing. $B=$ rate of fishing has increased during the preceding six years. $C=$ five years after $B$, with rate of fishing stabilized. D = balanced curve for a constant rate of fishing. $E=$ rate of fishing has decreased during the preceding six years. $F=$ five years after $E$, with rate of fishing stabilized (from Ricker 1975).]

In A through D, $F$ was increasing, and with a constant $M$; Z increased too. These circumstances might commonly describe the initial exploitation of a fish population. With development catch will begin to decrease so, if $F$ decreases with $M$ remaining constant, then $Z$ will decrease also. This is the situation which produced curves E - F, where the quantitative changes are the same as with $B$ and $C$, but in an opposite direction. The outer limb of E represents the former survival, again a time lag. Curve F, from catch data eleven years after the increase in survival, and five years under constant such survival, estimates with its outer end, again the former survival. This curve has no current estimate of survival for it has no inflection point (Ricker 1948).

In summary, changes in the rate of fishing result in curved right limbs of the catch curve, convex if the fishing rate decreases and concave when the fishing rate increases. The point of maximum slope on the right arm provides an estimate of current survival, though subject to a time lag (Ricker 1948).

Estimating Instantaneous Fishing Mortality (F)
Instantaneous fishing mortality rate (F) and exploitation rate (E) can be related by the following equation:

$$
F=-\ln E \text { and } F=\left[\frac{E}{1-S}\right] Z
$$

Exploitation rate is the probability that a given fish will die during the year due to fishing when all other causes of death are operating. Given an estimate of $E$, then $F$ can be calculated. Exploitation can be derived in three basic ways.

1. Exploitation can be estimated by catch $(\hat{C})$ and abundance $(\hat{N})$ data:

$$
E=\frac{\hat{C}}{\hat{N}}
$$

There are two sources of error common to this method, each acting in opposing directions: (1) since some of the fish in the area covered by the gear may escape, mortality may be overestimated; (2) the abundance of fish in the fished area will be greater than the average density, leading to an underestimate of the fishing mortality (Gulland 1973).
2. Tagging data:

Assuming that tagged fish are subject to constant fishing and natural mortality rates which are the same as in the natural, untagged population, then fishing mortality can be estimated because, unlike the natural population, the initial number in the tagged population is known precisely. If $r=$ the number of recaptures and $m=$ the number of marked fish:

$$
\begin{aligned}
& \text { then } \mathrm{E}=\mathrm{r}_{\mathrm{m}} \\
& \text { and } \mathrm{F}=-\ln \mathrm{E}
\end{aligned}
$$

The above assumes no natural mortality or losses of the marked population of any kind (Beverton and Holt 1957, Gulland 1973).
3. Changes in fishing mortality

A third approach to estimating fishing mortality is to use changes in total mortality. Fisheries with long histories of data are amenable to this approach (Figure IV-5). If the regression line is extended to $f=0$, the only mortality operating on the population would be due to natural causes. Fishing mortality would then be estimated by the mortality rate above the natural mortality rate.

Estimating Natural Mortality (M)
Natural mortality is nearly always estimated by the difference between total and fishing mortality,

$$
M=Z-F .
$$

In a few situations (virgin fisheries or closed fisheries) it may be possible to estimate natural mortality directly, but this is the rare case.

If the amount of fishing changes, thus changing the fishing mortality, it will result in a change in total mortality. The observed changes in $Z$ are related quantitatively to known changes in fishing effort; i.e.:

| if | $\mathrm{Z}=\mathrm{F}+\mathrm{M}$ |
| :--- | :--- |
| and | $\mathrm{F}=\mathrm{qf}$ |
| then | $\mathrm{Z}=\mathrm{q}$ |

If $q$ is a constant, then $M$ changes with changes in $f$ and $Z$. The plot of Z vs. f produces a line whose slope is a q and intercept M (Figure IV-5) (Gulland 1972, Royce 1972). Here again a time lag is possible, allowing for the estimation of some previous natural mortality rate when using values of two successive year-classes at some point in time (Beverton and Holt 1957). In determining $M$ in this way, estimates of $f$ must be accurate and large, so as to produce sufficient variation in Z (Beverton and Holt 1957).


Figure IV-5. If the amount of fishing changes over time, then a plot of total instantaneous mortality (2) versus fishing effort (F) produces a line with a slope q and intercept M (instantaneous natural mortality).

An idea of the value of the natural mortality rate can be gauged from the growth pattern of the species concerned. A fish which approaches its ultimate length quickly is likely to have a high natural mortality, whereas a fish that grows slowly is likely to have a low M. This estimate is not precise, but is often most useful in the early stages of studying a fishery in judging which mortality factor ( $F$ or $M$ ) is likely to be the dominant element in the total mortality (Gulland 1973).

## Functional Value of $\mathrm{Z}, \mathrm{M}$, and F

Manipulating exploitation rate (fishing pressure) is one of the most useful tools in fisheries management. Since

$$
F=\frac{[E]}{1-S} Z
$$

the manager could conceivably adjust E and then predict the effect on F . If E is increased by $25 \%$, the above equation could be solved to determine the effect on F. And since,

$$
F=q f
$$

where

$$
\begin{aligned}
& \mathrm{q}=\text { catchability coefficient } \\
& \mathrm{f}=\text { fishing intensity }
\end{aligned}
$$

then, f could be adjusted to provide the desired level of F .
Although one can measure mortality in the field, it is very
difficult to assess the degree to which various possible causes contribute to it. The direct causes of natural death in fish populations are varied and not well known. By the time most fish become of sufficient size to be important for economic or recreational purposes, most of their contemporaries have died (Pauling 1968, Royce 1972).

Egg and larvae are probably most in danger, young adults are probably subject to the least chance of death, and older adults are subject to a greater chance of death. Larval mortality is extremely high and possibly occurs mainly at certain critical stages in early life. One such may coincide with the exhaustion of the yolk-sac when the larva, for the first time, becomes dependent on its own ability to obtain particular kinds of food and on the abundance of the latter in the immediate environment. Another critical phase may be at metamorphosis (Beverton and Holt 1957, Royce 1972).

Predation undoubtedly covers the manner of death of the vast majority of fishes. It is usually assumed that predators kill most readily those fish which are parasitized or diseased, or are unwe11 from one or a variety of primary causes. If certain predators were reduced, it is likely that at least such unhealthy fish would merely be killed by a different predator. But a predator that consumes some large fraction of a prey population must usually capture healthy fish for the most part (Pauling 1968). This is especially true when man is considered to be a predator. He is a special sort of predator though, for his density which generates the predatory pressure is not necessarily governed by the populations on which he preys (Murphy 1966).

Parasite populations fluctuate from year to year for reasons that are seldom obvious. Thus, while most fish bear parasites, it is usually when the fish become influenced by unfavorable environmental conditions or subjected to physical damage that the activities of the parasites come to harm the fish. Similarly among bacteria and viruses, it is not uncommon for species which are found on unhealthy fish to become pathogenic (Pauling 1968).

There are very many substances and a wide range of conditions which are known to cause pollution. Sources include industry, agriculture, and mining. Fish mortalities due to pollution usually result from sudden discharge of one or more toxic substances into a normally clean water. Any particular population responds to the local conditions that happen to prevail, and when the immediate environment becomes intolerable in some respect there is generally no escape open to the fish, especially in freshwater (Regier and Robson 1967, Pauling 1968).

These are ultimate causes of mortality, but there are many other factors which may adversely affect the health of fishes and thus may be the primary causes of death. These include undernutrition, unfavorable environmental conditions, loss of condition following spawning, social stress, and others (Pauling 1968).

The consequence of all these variable factors is a large variability in number in the population (Royce 1972).

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## GROWTH

Growth is usually defined in fish population dynamics as change in length or weight of an animal over time, but it may also be defined as the increase in biomass of a population produced by assimilation of materials from within its environment. Fish growth is a complex pattern of events involving many different factors, including:
(1) water temperature and quality; (2) size, quality, and availability of food organisms; (3) size, age, and sex of the fish itself; and (4) the number of other fish utilizing the same resource. The pattern of growth can be divided into at least four distinct stages (Weatherley 1972). The first of these stages is larval growth, during which rapid changes in body shape and size occur. The second, the juvenile stage, continues rapid growth in size, but changes in length and weight occur in a more linear relationship. As the fish nears maturity, much of the energy which had been utilized for growth is diverted to gonadal development and growth occurs only after spawning has been completed. This step-wise growth continues until the fish reaches senility, when most energy is utilized for maintenance, with very little incorporated into growth of the individual.

Analysis of growth in fisheries management is usually designed for (1) predicting average fish size at some point in time, and (2) comparing "well-being" of fish in different fisheries or under different management strategies. Managers must know what effect fishing is having on growth and the possible outcome of various management decisions on fish growth.

The importance of growth estimates in population dynamics is evident. Growth affects when fish first breed (maturity), the age composition of the stock (recruitment into the stock), the potential yield of a stock, and mortality.

Growth in fishes is most often described in terms of changes in length or weight over time. Von Bertalanffy (1938) noted that the curves of length and weight over time are different (Fig. V-1). The length curve shows a uniform leveling, with the greatest rate of growth at the beginning, and a continual decrease to the maximum length, $\ell_{\infty}$. The weight curve is more typically sigmoid in shape, showing a slow initial increase in weight and a first point of inflection at about one third of the maximum weight, $w_{\infty}$.

These changes in size of fish have been expressed in three ways (Ricker 1975):

## 1. Absolute Growth

This is the increment in growth over a given year
Absolute Increase $=\ell_{2}-\ell_{1}, w_{2}-w_{1}$
where $w_{1}$ and $w_{2}=$ weight at time $t=1$ and $t=2$
$\ell_{1}$ and $\ell_{2}=$ length at time $t=1$ and $t=2$


TIME $\longrightarrow$


TIME

Figure V-1. (a) Growth in length plotted against time. $\quad \ell_{\infty}=$ maximum length attainable
(b) Growth in weight plotted against time. $\mathrm{w}_{\infty}=$ maximum weight attainable

## 2. Relative Rate of Increase

This is the proportional (usually expressed as a percent)
increase over a given year.
Relative Rate of Increase $=\frac{\ell_{2}-\ell_{1}}{\ell}$, or $\frac{w_{2}-w_{1}}{w}$

## 3. Instantaneous Rate of Increase

Absolute Rate of Increase $=\frac{\ell}{1 n_{\ell_{2}}}-\frac{\ell}{\ln _{\ell_{1}},}$ or $\ln w_{2}-\ln w_{1}$.
Weight varies as a power of length:
$\mathrm{w}=\alpha \ell^{\beta}$, where $\alpha$ and $\beta$ are constants.
If the value of $\beta$ is equal to three, the growth is said to be isometric; otherwise it is allometric.

## Age-Growth Determinations

To determine growth rates an acceptable means for estimating past growth must be found. Of several approaches, three are most often used: (1) length-frequency curves to trace year class modes through a population; (2) marking and releasing individuals of predetermined age and size for later recapture; and (3) calculating past growth by analyzing the growth rate of annuli of scales or other bony structure.

The first of these is appropriate when good catch data are available, as in large-scale commercial fisheries. One difficulty with this method is that not all age-classes have the same growth rate and, therefore, the same sizes at the same age. This means that there could be considerable overlap, especially in older age-classes.

The second method is perhaps the best in terms of providing accurate information about age-class changes. In some species this is the only method of tracing age and growth. Problems with this method are that very large numbers of individuals must be marked to insure adequate recapture and the effects of marking are often deleterious to the health of the fish.

The last method, scale-length analysis, is the most often used and gives an immediate indication of growth of the organism. This method assumes that the growth of scales (or other structures) is directly proportional to the growth of the fish (Weatherley 1972):

$$
\ell_{x}=\ell_{y} \frac{T_{x}}{T_{y}}
$$

where $\ell_{x}=$ length of fish at age $x$

$$
\begin{aligned}
& \ell_{y}=\text { length of fish at present age } \\
& T_{x}=\text { length of scale to annulus } x \\
& T_{y}=\text { length of scale to present edge (present age) }
\end{aligned}
$$

The relationship of fish length to scale length over time is often curvilinear and a correction factor must be applied. Once determined, a nomograph may be constructed which will allow a quick and simple method of computating growth from scale measurements (Hile 1970). In addition, use of computers makes the computation simpler. One problem encountered with use of scale-body length calibrations is that they must be used for the sampled population only, and recalculated for each new sample-population because of the high variability in growth rates among different populations of even the same species.

Length and weight have been shown to be highly correlated. If the proportional increase in length is linear to the increase in weight and assuming isometric growth (weight increases as a factor of the cube of length), then the relative "health" of the organism or population may be compared to others by use of the condition factor, or coefficient of condition, CF , where $\mathrm{CF}=\mathrm{w} / \ell^{3}$.

## Growth Models

Growth models are designed to explain and to predict changes which occur in a fish population over time. The simplest of these models are broad descriptions of growth parameters and they have little predictive value. The more sophisticated models require large amounts of data but are called upon to forecast possible changes in a fish population under alternative management decisions. These complex models are of particular concern to commercial fisheries managers, who must know as accurately as possible the condition of the stocks under exploitation or potentially under exploitation.

A model describing fish growth should possess a number of characteristics to be useful in fisheries management work. The model should be relatively easily fitted to data. Second, growth characteristics should be reasonably well described over the desired range of time. Third, the number of assumptions should be as few as possible and reasonable. A final characteristic of a useful growth model is the ease with which it can be intergrated with other population dynamics models.

The von Bertalanffy (1938) growth equation is one of the most widely used models for estimating of length or weight of fish at a future point in time. This model expresses change in length, ${ }_{t}$, over time as a function of the maximum length, $\ell_{\infty}$, and a growth coefficient, K. The equation is most commonly stated as:

$$
\ell_{t}=\ell_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right],
$$

Assuming isometric growth, the equation stated in terms of weight ( $\mathrm{w}_{\mathrm{t}}$ ) is:

$$
w_{t}=w_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right]^{3}
$$

Values for $K, l_{\infty}$ (or $w_{\infty}$ ), and $t_{o}$ may be obtained by plotting length at age $t+1$ ( $y$ axis) against length at age $n$ ( x axis) for each successive age (Fig. V-2) (Walford 1946).


Figure V-2. Walford plot of annual increment in length. Length at time $t$ plotted against length at time $t+1 . \quad \ell_{\infty}=$ maximum length attainable. The $45^{\circ}$ line indicates the line of equality between $\ell_{t}$ and $\ell_{t+1} . K=$ von Bertalanffy growth coefficient ${ }_{-k}$ Equation for the $e_{K} 1$ ine is: $\ell_{t+1}=l_{\infty}\left(\ell-e^{-K}+\ell_{t} e^{-k}\right)$ where slope $=e^{-K} \quad(K=-\ln$ siope $)$.

A least squares regression of the points (Stevens 1951)
provides a relationship for the Walford line:

$$
\ell_{t+1}=\alpha+\beta \ell
$$

where $\alpha=$ intercept and $\beta=$ slope.
The maximum length $\ell_{\infty}$ is equal to the point at which the length ${ }^{\ell}{ }_{t+1}$ intercepts the $45^{\circ}$ line. This point is:

$$
\ell_{\infty}=\frac{\alpha}{1-\beta}
$$

The growth coefficient of the von Bertalanffy equation is equal to natural 10 g of the slope of the Walford plot:

$$
K=\ln \beta
$$

Taking the natural log of the von Bertalanffy equation and rearranging we have:

$$
\ln \left(\ell_{\infty}-\ell_{t}\right)=\ln \ell_{\infty}+K_{o}-K_{t},
$$

which may be plotted as a straight line. Plotting the natural log of $\ell_{\infty}^{-\ell} t$ against age $t$ (Fig. V-3), provides a slope ( $\beta$ ) of $-K$ and an intercept ( $\alpha$ ) equal to $1 n \ell_{\infty}+K t_{0}$. A value of $\ell_{\infty}$ giving the best linear fit may be chosen and a better estimate for K determined as well. The intercept value of this regression may then be used to solve for $t_{0}$ :

$$
t_{0}=\frac{\alpha-\ln \ell_{\infty} .}{K}
$$

Other mathematical descriptions of growth have been developed. For a review of these techniques we refer the reader to Ricker (1975).


Figure V-3. Plot of $\ln \left(\ell_{\infty}-\ell_{t}\right)$ against age in years. Line shows fit of $\ell_{\infty}$ and $K$ for the von Bertalanffy growth equation.

The question of which kind of data are important or necessary and which model to use will depend entirely on the situation at hand. If it is deemed desirable to be able to predict the size of the average catch at some time in order to tailor gear to exploitation at a certain size or to advertise for commercial angling, then it may be necessary to estimate the size and rate of growth of the stock in question. It may be desirable to have some estimation of the "health" of certain populations of fish in order to take some action to improve a poor resource or increase pressure on a possibly under-exploited resource. A fish farmer may want to know how soon his fish will be ready for market. The accuracy and extent of the predictive power of the model chosen will rest on its appropriateness and on the extent and accuracy of data used to calculate the results.

The digital computer has been employed more and more often for compiling, sorting, and calculating the various analysis traditionally used in fisheries management. Gerking (1965) introduced a program to describe the scale radius-body length/weight relationship. A program for the von Bertalanffy equation which automatically plots the Walford data to give $\ell_{\infty}$, as well as $K$ and $t_{0}$, their standard errors, fitted lengths for ages from zero to the maximum in the sample, sample mean length by age, as well as all standard errors and variance-covariance matrix has been developed (Abramson 1971).

In addition to these programs, computer programs have been written of extremely sophisticated input models which weigh effects of a multitude of environmental, physiological, and test parameters (Paloheimo and Dickie 1965, Menshutkin and Kislyakov 1967). In addition to monitoring actual population growth, computer useage has allowed simulation of natural and theoretical events to extend the predictive potential of fisheries science. However, even though the analytical capability is very sophisticated, the fisheries manager should always carefully select the conceptual model most appropriate to the problem at hand.

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## CHAPTER SIX

## RECRUITMENT

Recruitment is often defined as the addition of new members to the aggregate under consideration. Although such a definition is sufficiently encompassing, it does not immediately make clear two important considerations in fisheries management, exploitation and sexual maturation.

To the exploitor, recruitment is the entry of young fish into the area of exploitation. To the fisheries manager, charged with the responsibility of maintaining high catches, recruitment indirectly hinges on passage into the spawning stock. Therefore three types of "recruitment" may be distinguished:
(1) recruitment to the stock;
(2) recruitment to the fishable stock (i.e. that part subject to exploitation);
(3) recruitment to the mature stock of egg producers (Hancock 1973).

The first two types of recruitment may result from changes in a fishes' physical location, habit, or size; while maturation recruitment (the third type) is more strictly a function of growth. This multidimensional view of recruitment is often requisite to effective management, especially to avoid the overexploitation of immature fish and yield declines from unnecessary protection of mature stocks.

Recruitment and its relationship to stock size and environmental conditions is a difficult but important subject. As the annual increment to a stock, recruitment is a vehicle of population continuity and the base of future yield. The failure of many important fisheries has been caused by recruitment failure (Cushing 1968, 1973; Bennett 1970; Hancock 1973). Cushing (1973) suggests that the problem of overfishing expressed in terms of growth has been replaced by the more serious, recruitment overfishing (in which the degree of stock reductions has resulted in recruitment declines). The desire and need to know structure and function of the recruitment complex, especially in acquisition of predictive capabilities, has led to development of stock-recruitment models.

A number of factors can affect recruitment, including size of the spawning stock, environmental factors, predation, and competition. These factors can be categorized as either density-independent or densitydependent.

Density-independent factors act in a manner unrelated to population leve1. Pollution, floods, and water temperature act independent of population level. A fisheries manager must of ten handle these as probabilistic or stochastic events.

Density-dependent factors are related to population level or ecological interrelationships. Competition, predation, and disease may be, in part or in total, related to population level and can be considered density dependent factors.

## The Ricker Model

Ricker (1954) has pointed out that a fish population, even when not exploited, is limited in size. This is merely an extension of the general concept that a biotic population at the long-term equilibrium point is under the approximate condition of births equaling deaths. Ricker recognized that for this condition to exist, the population must be under some natural controls. This regulator was hypothesized to be some density-dependent mortality which had its major impact during the early life stages of the individual fish. Changing mortality was not pronounced in the adult stages, although growth rate probably does change somewhat as a density-dependent function. The regulatory mortality acts as a compensatory mechanism, with the greatest effect at high population levels and little effect at low stock levels. Such compensatory mechanisms might include the prevention of breeding due to a limited number of breeding sites; the maintenance of territories by spawners; limited living space or food for larvae and/or fry; cannibalism of eggs, larvae, and/or fry; increased disease and parasitism; "conditioning" of the water due to accumulation of waste materials causing a depressing effect (Ricker 1954); decreased fecundity with reduced food supply (B1axter 1969); or predation on immatures (Everhart et al. 1975).

There are also non-compensatory or density-independent mechanisms acting to produce changes in mortality; for example, temperature, salinity, pH , wind action, or pollution. These factors are usually random effects which result in changes unrelated to stock size.

The average size of the maturing group (i.e. recruitment) represents the average result of the action of density-dependent and densityindependent mortality acting on the sexual products produced by a given stock level. Under the assumption that the density-dependent factors dominated the stock-recruitment relationship, Ricker developed a family of "reproductive curves," plotting existing stock against the future stock produced (Fig. VI-1). The axes can conveniently be labeled as numbers of eggs produced. The asymetrical dome-shaped curve is generated from the expression:

$$
\mathrm{R}_{R_{r}}=\left(\mathrm{P}_{\mathrm{P}_{\mathrm{r}}}\right) \mathrm{e}^{\left(\mathrm{P}_{\left.\mathrm{r} / \mathrm{P}_{\mathrm{m}}\right)}\left(1-\mathrm{P} / \mathrm{P}_{\mathrm{r}}\right)\right.}
$$

where:
$\mathrm{R}=$ recruitment
$R_{r}=$ recruitment at the replacement point of stock, $P_{r}$
$\mathrm{P}=\mathrm{stock}$
$P_{m}=$ the stock at which maximum recruitment is found
$P_{r}=R_{r}$
If $\alpha=\left({ }^{P} / \operatorname{Pr}\right)$ and $\beta=\left({ }^{\mathrm{Pr}} / \mathrm{P}_{\mathrm{m}}\right)$, then the expression may be rewritten,

$$
R_{R_{r}}=\alpha e^{\beta(1-w)}
$$



Fig. VI-1. The two classical stock-recruitment curves; A, the Ricker curve, and B, the Beverton-Holt curve.

The $45^{\circ}$ bisector is significant in that it represents exact replacement of the parent stock by subsequent recruits. The curvilinear expression thus represents recruitment as a fraction of maximum and replacement reproduction. With density-dependent mortality operating, the curve rises above the replacement line, peaks, and then falls through the bisector. From simple manipulation of the model, the compensatory action can be demonstrated, with reductions in recruitment at high stock levels and "surplus recruitment" above that required for replacement at low and moderate stock levels. It can also be seen (Fig. VI-1) that at some stock abundance an absolute maximum in recruitment is achieved, indicative of some carrying capacity, while at some lower stock density, a maximum surplus recruitment occurs. The attainment of this later point has been proposed as a desirable management objective. An infinite number of such curves can be generated, each differing in the location and acuity of the maximum.

The Ricker model is usually applicable in situations where there is only one target fish, as is often the case in Pacific salmonid fisheries. The model is not ideal for many lake and stream situations where similar species occur. The Ricker model assumes that maximum fish production is the management objective and is concerned with the total weight of fish in the stock and thereby does not incorporate individual growth differences. It assumes generally that the spawning population will spawn only one time.

Beverton-Holt Model
Cushing $(1968,1973)$ presents a detailed development of the Beverton-Holt stock-recruitment curves. Recognizing that densitydependent and density-independent mortality factors are acting on young fish, Beverton and Ho1t used the expression:

$$
\mathrm{dN} / \mathrm{dt}=\left(\mathrm{u}_{1}+\mathrm{u}_{2} \mathrm{~N}\right) \mathrm{N}
$$

where:
$\mathrm{N}=$ the number of larval fish
$u_{1}=$ the instantaneous coefficient of density-independent mortality $u_{2}=$ the instantaneous coefficient of density-dependent mortality. The curves produced are asymptotic (Fig. VI-1) rather than domed, as in the Ricker curves. The former imply that recruitment is in equilibrium within a wide range of stock abundance.

Gulland (1974) points out that if the density-dependent mortality acting on pre-recruit fish is proportional to the density of adults or the initial density of eggs or young, then a Ricker type curve will apply. If the mortality at any instant of time is governed by the current density of young fish, a Beverton-Holt curve is derived. The applicability of the models may also bear some relationship to the level of fecundity associated with the species.

## Recruitment Regression Models

A number of workers have combined density-dependent and densityindependent factors into multiple regression models. The general case is

$$
R=f(N, \text { Environmental Factors })
$$

Recruitment is predicted as a function of population level and any number of environmental factors, such as water temperature and weather conditions. An example of data to which this approach is applicable has been derived for a hypothetical warmwater impoundment.

| Year | Bass <br> Recruitment | Stock <br> Size | Day Water Reached $65^{\circ} \mathrm{F}$ | Crappie Stock |
| :---: | :---: | :---: | :---: | :---: |
| 1960 | 2,000 | 2,600 | 110 | 4,500 |
| 1961 | 2,900 | 2,100 | 102 | 2,800 |
| 1962 | 3,400 | 2,000 | 122 | 3,200 |
| 1963 | 1,900 | 3,400 | 108 | 4,500 |
| 1964 | 2,200 | 3,100 | 118 | 6,800 |
| 1965 | 2,600 | 2,900 | 122 | 8,200 |
| 1966 | 3,300 | 3,900 | 106 | 1,200 |
| 1967 | 3,900 | 1,800 | 136 | 1,500 |

Using the multiple regression model

$$
\mathrm{R}=\mathrm{f} \text { (Stock, Day Water Reached } 65^{\circ} \mathrm{F} \text {, Crappie Stock) }
$$

a prediction of $R$ and a measure of the variance accounted for by the three independent variables can be computed. Extensive date is required in order to apply regression techniques to most fish populations.

## Limitations to the Classical Models and Possible Alternatives

The stock-recruitment models discussed deal specifically with the quantity of the parent stock, assuming that its quality is even throughout. In contrast, Slobodkin (1973) summarizes the importance of the "reproductive value" of the individual, where reproductive value is a function of age, life expectancy, and fecundity. It is clear that certain individuals have considerably higher reproductive value than others. Fisheries science, and the study of population dynamics in particular, may now be at a point where the mean and variance of characters such as fecundity, growth rate, dispersal tendency, and survival under specific conditions must be quantified for the parent stock (Wolda 1970). Ponomarenko (1973) provides an apt example with cod in the Barents Sea. The probability of a strong year-class of cod is greater when the proportion of repeat spawners is high then when new recruit spawners predominate the egg producers. In this light, high stock numbers is no reproductive safeguard, realizing that a large stock having little reproductive value is in a much more "dangerous" situation than a considerably smaller stock with individuals possessing a high reproductive value (Slobodkin 1973).

Another criticism of the standard models is that they do not adequately reflect the true dynamics of many important fishes. In support of such a contention is the inability of many workers to positively correlate stock level to subsequent recruitment (Backiel and LeCren 1967; Cushing 1968, 1973; Gulland 1970, 1974; Dragesund and Nakken 1973; Hyelen and Dragesund 1973; Lett et. al. 1975; Ricker 1975).

The apparent lack of correlation may truly be due to the inability of the models to adequately explain natural population phenomena; however, it is clear that the influence of environmental factors is also a dominant source of variation. Recruitment may vary by a factor of two (e.g. Pacific salmon) to a factor of two orders of mganitude (e.g. some herring) (Cushing 1973). Year to year differences in environmental characteristics may result in reproductive fluctuations much greater than any associated with variations in stock density (Ricker 1975).

Cushing (1973) has critized the Ricker model for its lack of ease of application to multi-aged stocks. Many, if not most, of the important species are made up of several exploitable ageclasses, each adding their sexual products to the "pool" from which the recruits come forth. In this way the number of age-groups in a population provides a buffering capacity against environmental variation. The number of age-classes may even be a function of a population's natural variability in recruitment. The inability to fit the Ricker or Beverton-Holt curves to herring and cod stocks, the inability to explain the sudden and dramatic changes in recruitment in some stocks, and the inability to predict changes mediated by environmental influences led Cushing (1968, 1973) to attack the problem of identifying the compensatory mechanism and its mode of operation.

Cushing (1973) has developed a model in which density-dependent mortality is evaluated relative to environmental changes. In the model he distinguishes between stock-dependent functions, density-dependent functions, and density-independent functions. Stock-dependent functions are those which are a direct result of the parent stock abundance; density-dependent functions are related strictly to the current number of larvae; and density independent functions bear no relation to stock or larval densities.

Many of these points can be observed in freshwater systems. A lack of correlation between spawning stock and subsequent year-class strength has been reported for largemouth and sma11mouth bass (Coble 1975; Eipper 1975; Pflieger 1975; Summerfelt 1975) and for walleye and for northern pike (Priegel 1970; Hassler 1970). Wide ranging variability in recruitment has most often been attributed to environmental influences such as air and water temperature, wind action, water level, siltation, pH, light, and dissolved oxygen. Upon closer examination, most of these physical parameters could exert their influence on recruitment through alteration in the amplitude and timing of freshwater production cycles.

The larvae of smallmouth and largemouth bass, walleye, yellow perch, and northern pike all utilize a variety of zoo- and phytoplankton in their diets initially and then move through a progression of larger sized prey, from insects to fish and crayfish. High larval mortalities linked to reduced growth as a result of reduced food availability have been reported by Hassler (1970), Aggus and E1liott (1975), and Allen and Romero (1975). It is also widely reported that recruitment is already determined in the young-of-year fish, usually in the first few weeks after hatching but certainly before the onset of their first winter (Maloney and Johnson 1955; Priegel 1970; Coble 1975; Summerfelt 1975). For this reason estimates of larval or fry abundance by seining or trawling yield a high correlation with year-class strength. Coble (1975) also reports that variations in year-class strength for smallmouth bass may extend to all of the lakes or streams in a given area and Eipper (1975) notes that such variations may also extend over several fish families within any one water body. These studies suggest that some general meterological phenomenon might be the controlling factor, possibly by influencing the production cycle.

From a purely scientific standpoint it is important to know the exact mechanism of mortality and compensatory phenomena leading to the strength of recruitment, but from a more practical view, it is usually essential only to know which parameters significantly govern year-class strength and supply predictive capabilities.

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## CHAPTER SEVEN

## PREDICTING YIELD


#### Abstract

Fisheries managers require predictions on the possible consequences of alternative management strategies in order to reduce uncertainties in decision making. Formal predictions concerning the future status of fish populations result from analysis of empirical yield models when applied to the appropriate data.

Simple yield models demand less information and have inherent generality, but they often have poor predictive power and account less for the dynamics of the stocks. More complex models have higher predictive power and provide greater insight into the dynamics of a population, but require more data. Model selection is of primary importance because it determines the data requirements.


A useful and reliable yield prediction model should be appropriate to the objectives of the fisheries management program. The chief requirement of the yield model is to enable the right choice to be made between alternative management decisions, within tolerable limits of uncertainity. Model formulation should be a dynamic process capable of evolving from simple monitoring models employed in early stages of population exploitation to more demanding and complex models used to describe better known fisheries. Certain management situations demand that only the approximate magnitude of change in abundance of yield be monitored until reaching a critical level of exploitation. Over-exploited economically valuable stocks require more accurate indicators of change and, therefore, models of higher predictive reliability.

Model formulation also provides a check against collection of insufficient or superfluous data. It is important that the model fulfills the stated objectives, and that the model chosen is the simplest alternative. Unnecessary predictive reliability (and unnecessary data acquisition) is a waste of management resources.

This chapter discusses single and multiple stock yield models and includes examples of their applications in commercial and recreational fisheries management. Models will be discussed according to the information needed, the assumptions on which the mathematical development is based, the relative predictive reliability, and the advantages and disadvantages in practice. The models can be grouped into five categories: (1) the macro-production models, which use certain gross physical, physiochemical, and biological characteristics of the fishery to determine the potential yield from various types of waters; (2) the surplus yield models, which need only a long series of catch and effort data, and combine effects of recruitment, growth, and natural mortality into a single valued function of population biomass; (3) the dynamic pool models, which consider the population as the sum of its individuals, and thus predict yield based on catch data and growth and mortality rates; (4) the trophic dynamic models, that elucidate trophic level interactions by use of functional notation and the simultaneous solution of sets of resulting differential equations; and (5) the multidisciplinary multi-stage decision models, which extend the yield predicting capabilities of management to the allocation of catch and the maximization of value.

## Macro Production Models

An accurate prediction of the potential yield available from a fish population presumes availability of large quantities of data pertaining to vital statistics on growth, mortality, population strucuure, movements, behavior, and biomass for the stock. In addition, information on the physical characteristics of the habitat, climatic effects, composition of the biotic community, various abiotic factors stressing the fish population, temporal and spatial nutrient relations, social and cultural traditions, and the state of the local economy contribute to understanding of a complex system. When only a minimum amount of data is available, rough approximations of potential yield can be developed to guide planning and decision making. For reliable predictions, a long term series of replicated observations on yield, species composition, and catch per unit effort are important. However, when these data are absent (which is typical), certain gross characteristics of the stock can determine with statistical reliability the potential yield from various types of fisheries. Fish production (or yield) is affected by three environmental influences: morphometric; edaphic; and climatic. Thus, physical characteristics, such as lake area, mean depth, maximum depth, flushing tiem, and shoreline development; physiocochemical characteristics, such as the total dissolved oxygen and mean temperature; and biological characteristics, such as the number of trophic levels and their compositions, can be used to roughly assess the production attainable from a fish population complex.

Ryder (1965) conducted a regression analysis of fish production on morphometric and edaphic factors. This morphoedaphic index estimated potential productivity of north temperate lakes as a function of mean depth and total dissolved solids, and accounted for $75 \%$ of the variation.

Multiple regression techniques, while less subjective, must be used carefully. Many independent variables are partially correlated which decreases efficiency of the regressions. Problems with use of regression methods for determining fish production include: (1) varying fishing pressure between lakes or fishing grounds; (2) inadequacies of catch records from certain recreational and commercial fisheries; (3) relative accessibility of lakes to markets; and (4) noncomparable production rates between stocks which occupy different trophic levels (Ryder 1965).

Specific criteria for regression treatment of yield and the morthoedaphic index are: (1) relatively homogeneous climatic conditions;
(2) fairly constant ionic ratios; (3) approximately proportional flushing rates per unit of lake volume; (4) intensive fishing effort on a number of species over a period of years; and (5) inorganic turbidity of the same order of magnitude (Ryder et al 1974). The morphoedaphic index serves as a potentially powerful monitoring device to indicate environmental pollution, degradation, or general biological stress.

The regression treatment of homogenous groups of lakes has been applied to commercial and recreational fisheries. Ryder and Henderson (1975) have used the morphoedaphic index to approximate potential fish yields from Lake Nasser. Not enough catch and effort data (or other population dynamics information) were available for this recently created reservior to make realistic estimates of potential fish yield. Instead, morphometric and edaphic data were utilized to establish yield predictions in relation to other tropical lakes. This approach provides a valuable function of monitoring the expansion of the Lake Nasser fishing effort in order to guide current management planning. In commercial fisheries, such as Lake Nasser, a more gradual and deliberate succession of exploitation can be accomplished by using the morpho-edaphic model as a first approximate technique.

The morphoedaphic index constitutes an ecosystem model of great generality. The major problems with the model are (1) that it does not account for density dependent factors in fish and community dynamics, and (2) it gives estimates of production which are not species specific. However, when used with an appreciation of their limitations, macro production models offer an important diagnostic tool to guide development, predict yield when land use practices change, and evaluate decisions in many fisheries. These models will become more useful and gain greater acceptance when the functional relationship can incorporate climatic changes (treating the climate as another independent variable), and when their use can be extended from closed systems, such as lakes, to consideration of oceanic systems.

## Surplus Yield Models

Surplus yield models are single stock models characterized by requiring no data on the age structure of either the catch or the stock. The basic approach for single stock models is summarized by the following equation:

$$
P_{2}=P_{1}+R+g-m-c
$$

where $P_{2}=$ Total biomass of stock at $t_{o}$
$P_{1}=$ Total biomass of stock at $t_{1}$
$R=$ Addition of biomass from recruitment
$\mathrm{g}=$ Addition of biomass from growth
$m=$ Loss of biomass from natural mortality
$\mathrm{C}=$ Biomass of the annual catch
Factors which affect the level of a population involve considerable interdependence and form complex interactions. The surplus yield model provides an adequate formulation of past events, but is of less value in predicting future yields because factors are represented by their effects. A predictive model, however, can be developed relating stock size to fishing mortality rate (Schaefer 1954). Catch per unit effort data can be used to estimate stock size; instantaneous fishing mortality rate can be measured by total fishing effort. The surplus yield model requires a long series of catch and effort data and combines effects of recruitment, growth, and natural mortality into a simple function of population biomass which is a description of population dynamics under equilibrium conditions.

The conceptual basis of the surplus yield model is the tendency for a population to increase along a sigmoid or logistic curve, and in a given stable situation, to have a long term average abundance (Fig. VII-1). Thus, when a population experiences increased mortality, it attempts to increase abundance by means of increased growth, reproduction, or survival. The greatest rate of natural increase occurs at the inflection point (Fig. VII-1). The natural rate of increase decreases as the population increases in abundance (with increasing mortality and decreasing reproduction and growth) until reaching zero at the maximum or limiting population size $\left(P_{\infty}\right.$ and often defined as carrying capacity).

Yield from a fish population is a function of the population abundance and total fishing effort; therefore, the population size is a function of effort. The rate of change in yield relative to abundance can be expressed as in Figure VII-2. The highest yield occurs where the slope equals zero on the logistic curve, which corresponds to a population size one-half that of the original unexploited stock. Further increases in fishing effort produce a decrease in equilibrium yield, and a condition of overfishing (Fig. VII-2).


Figure VII-1. Sigmoid growth curve of abundance (N) versus time with the asymptotic level's relation to carrying capacity.


FISHING EFFORT (f)

Figure VII-2. Equilibrium yield versus effort. Broken line represents the exponential model and solid line the logistic mode1.

The assumptions inherent in the logistic model are: (1) population abundance is the only factor causing variation in the annual natural rate of increase; (2) all fundamental rate parameters of the population can be combined to produce a simple functional relationship between the rate of increase and stock size; (3) catch per unit effort is proportional to the stock size; (4) instantaneous fishing mortality rate is proportional to fishing effort; (5) time lag between spawning and recruitment has no effect on the population; and (6) a symmetrical relationship exists between yield and effort (i.e., q is constant). The first four assumptions form the basic framework under which the model was developed and provide the logic for the simplicity of the model and are often reasonable first approximations of a complex ecosystem.

The commercial yellowfin tuna in the eastern tropical Pacific is a population whose population fluctuations are well predicted by the logistic surplus yield model (Gulland 1972). App1ication of the exponential model predicts nearly the same maximum equilibrium yield, even though the fishing effort required by the logistic model is considerably less. Thus both models give good estimates of yield, but require different levels of fishing effort to take the equivalent maximum yie1ds. The exponential model appears to describe the data better for yellowfin tuna of the western Atlantic Ocean. In this area the catch and effort data exhibit a curvilinear relationship typical of an exponential model (Fox 1970). Therefore, symmetrical growth is typical of some stocks for some time intervals, but does not apply to others.

Surplus yield models are particularly valuable in the early stages of an investigaion to make preliminary appraisals before more biological data are available. They are also important when biological data do not exist or only catch and effort data can be easily obtained. Their greatest advantage is that they require only a long series of catch and effort data, which is available for many commercial fisheries.

Dynamic Pool Models
Dynamic pool models are single stock yield prediction models of greater mathematical complexity which require extensive catch and effort data and data on the size and age composition of the catch. These "analytical" models consider the population as the sum of the individual fish. The models are more flexible in predicting yield for different amounts of fishing effort and different ages of recruitment to the stock. Assuming that recruitment is independent of stock size and that stock level is in equilibrium, then the average potential yield from the stock during any period is proportional to the average recruitment. Therefore, yield from an average cohort during its life is equal to the average yield from all cohorts during any year. In addition, the yield from a cohort is proportional to the number recruited to it. Yield per recruit is thus an expression of yield, which is proportional to the total potential yield from the stock, and no attempt is made to estimate the actual number of fish recruited to the population.

Total yield is predicted by the basic dynamic pool model with the following general expression:

$$
Y=f(F, N, W)
$$

where:
$Y=$ total yield
$F=$ the instantaneous fishing mortality rate
$\mathrm{N}=$ the number of fish in the population
$\mathrm{W}=$ the average weight of an individual fish
Application of the model involves a number of assumptions, and the usefulness and reliability of conclusions from application of the model depend on the extent to which these assumptions are reasonable. The basic assumptions are: (1) that fish die once and only once; (2) that fish grow as they get older. Specific applications, in addition, incorporate the convenient assumptions that (1) behavior of the population can be described by the sum of average individuals (there is no need to account for differences between individuals), and (2) actual relationship of growth, mortality, and recruitment to abundance can be described by numerous functional expressions.

Ricker (1958) and Beverton and Holt (1957) have developed mathematical solutions for the model. In comparison, the Ricker method provides a more flexible solution than the Beverton-Holt model in that it permits realistic simulation of growth and mortality when these cannot be expressed as simple functions of age. For example, this method is superior for short-lived species such as plaice, where seasonal variations in growth and mortality can be averaged over the fishable life span, and where age of recruitment to the stock is short relative to life span.

The Ricker model, however, also adequately describes this population. The major disadvantage to the Ricker model is the massive amount of calculation involved to process the frequent measurements of size by age as well as the need for extensive data on natural mortality. The advantage of the Ricker model over the Beverton-Holt method is its flexibility in investigating effects of different management strategies. The latter model permits investigation of only adjustments in total fishing effort and age at entry into the stock. The Ricker mode1, however, can also evaluate effects of closed seasons by assuming a zero mortality rate during closed intervals, instead of reducing the overall value of fishing mortality to adjust for closure. Therefore, in recreational fisheries, the effect of opening the season at a later time can be predicted (Ricker 1975). The major advantage of the Beverton-Holt model lies in its mathematical compactness, which expresses rate parameters as simple functions of age.

The fundamental difference between the two models is that the Ricker model is based on an intensive study of instantaneous mortality rate summed over variable length periods. The Beverton-Holt model, on the other hand, is a comprehensive study of all population rate parameters expresses as mathematical functions, which are integrated over all age classes.

Trophic dynamic models do not assume a steady state population structure in a nondynamic single stock situation. They are broadly biologically and theoretically encompassing and offer an appealing approach to yield prediction. The surplus yield and dynamic pool models approach the fish population as a nondynamic, single stock system, but many fisheries resources are exploited as multi-species resources. The logical step is to analyze component interrelationships and model the system with dynamic interactions. This modeling approach has the greatest data requirements. The information needed for trophic dynamic models to have maximum predictive reliability is age distribution of the stock, growth rate for each year class, and data on hydrographic factors, interspecific competition, pathogen and predator population levels, and any other factors which can govern productivity of the population.

The degree of complexity required to establish and express basic interrelationships of any ecosystem requires that simpler models should first be explored and evaluated before proceeding to more elaborate models such as a trophic dynamic approach. Many empirical values of coefficients for complex models cannot be approximated with our current knowledge and many mathematical equations are at best only crude approximations of the behavior of complex ecosystems. Saila and Parrish (1972) assumed interacting components had linearity and steady state conditions and used graph theory to construct a simplified system. Basic ecological trophic components were combined to form a more complex model.

This first approximation technique provides basic insight into ecosystem behavior, and in some instances could provide a reliable empirical model.

Ecosystem components thus need to be diagrammed to illustrate possible interrelationships. Block and arrow models can then be stated in mathematical terms as functional relationships between interacting components. Sets of differential equations representing the system can be solved simultaneously with use of computer facilities. Lackey and Zuboy (1975) constructed a simple three species model which accounted for interspecific competition and predation based on the spawning sequence. This model thus used species interrelationships to create a set of differential equations. Walter and Hoagman (1971) developed a general multi-species model that could be used on the Great Lakes and could account for as many variables as the user wanted to use. Plant et. al. (1973) modeled the biological, physical, and management components of the Cayuga Lake ecosystem. Effects of various fishing rates were then examined by varying instantaneous fishing mortality. Parrish (1975) constructed a mathematical model for performing dynamic simulations of groups of interacting marine fishes. Trophic webs of any size or form could be constructed using the basic model. Formulation of any of the above models points out the nature of the data required. The primary advantage of trophic dynamic models is to show data needs and guide future studies and to provide insights into the processes of the ecosystem.

## Multidisciplinary Multi-Stage Decision Models

This final group of models extends the yield prediction capabilities of management to allocation of catch, maximization of value, and in general the accomplishment of any specific management objective. These models merge the economic realities with the biological factors limiting yield. Rothschild and Balsiger (1971) used linear-programming to allocate catch of salmon among the days of the salmon run, and then maximized the value of the catch under certain economic constraints. These types of models will become increasingly important as more stocks are exploited.

Effectively managing multi-stock fisheries is a perpetual enigma in fisheries management. Successfully managing a single species is difficult at best, but managing a fishery with two, three, or more competing species is a formidable, if not impossible, task. To enhance understanding of fisheries and thereby increase management capabilities, mathematical models, such as those covered in this chapter, have been formulated which attempt to describe how fish populations and complexes function. Some of these models have become classical tools in fisheries management. Unfortunately, none of the models are easily applicable in multispecies situations which are characteristic of many fisheries. The classical models best apply to single species fisheries as found in the marine commercial situation and sometimes in freshwater.

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## CHAPTER EIGHT

## SYSTEMS ANALYSIS

Systems analysis is a process of translating concepts about a complex system into a generalized abstraction of the system and manipulating the abstraction to evaluate various decision alternatives. This definition is quite comprehensive and its full impact may not be easily recognized. A system is classically defined as "regularly interacting and interdependent components forming a unified whole." An ecosystem involves simultaneous functioning of a group of populations and the non-living environment which surrounds them. The functioning of an ecosystem can be analyzed in terms of energy circuits, food chains, diversity patterns in time and space, nutrient cycles, evolution, and cybernetics. All of these are vital considerations to determining interactions taking place within an ecosystem. An ecosystem forms the basic structure of a fishery and acts as the constraint in management.

The interactions taking place within an ecosystem present a complicated puzzle to fisheries scientists. No organism can exist by itself. It is dependent on other organisms as well as its environment. Such interdependence produces a multitude of relationships within an ecosystem. For example, game fish depend on forage fish for their energy requirements. These forage fish in turn rely on insect larvae which feed on algae. Algae utitlize the sun's energy to initiate the food chain. The number of interactions taking place within any ecosystem is overwhelming.

Several characteristics of an ecosystem are especially important to ecosystem analysis. The two most important of these are spatial and temporal relationships. No ecosystem analysis can be fully understood without a knowledge of the relationships of the activities of the organisms in an ecosystem in terms of both time and location. Thresholds, limits, and discontinuities are other important features. Thresholds, refer to behavior differences among the organisms in an ecosystem. For example, game fish will strike at a forage fish only after a certain hunger threshold has been reached.

Limits involve non-linear aspects of an ecosystem. The gut of a game fish can hold only so many forage fish at one time. Discontinuities deal with non-linearity in ecosystems. Homeostasis is the property of an ecosystem to resist change and maintain itself in a state of equilibrium. Natural controls involve feedback mechanisms. For example, if a population begins to grow too large for its food supply adult fish may consume increasingly larger volumes of their own young, thus tending to decrease the size of the population. All of the interactions taking place within an ecosystem tend to maintain system stability which results in a state of continuous but dynamic equilibrium. The ecosystem (systems) analysis approach is oriented toward the whole system by study of the workings of system components. Ecosystem analysis procedure is best explained by a series of steps:

1. Define the objectives of the analysis. An objective of an analysis of a warmwater fishery might be to maximize equilibrium yield of largemouth bass.
2. Determine which components of the ecosystem are relevant to meeting the objectives of the analysis.
3. Conceptualize, identify, and quantify interrelationships between system components.

The third step requires a thorough knowledge of the population dynamics of the organisms contained in the system. When dealing with fish populations this means estimating population size (N), growth rates (K), recruitment (R), and mortality rates (Z,F, and M) for each fish population included in the analysis. This may require many stages of refinement for each component of the system. For example, the interactions between population levels of adult and young game fish can be conceptualized and refined through several stages of development (Fig. VII-1). As soon as the degree to which interactions take place has been initially estimated, quantification must be accomplished. Statistical tools used in quantification procedures include:
a. FIRST PASS:

*MATHEMATICAL EXPRESSIONS NEEDED (DIFFICULT TO OBTAIN)
b. SECOND PASS:

c. THIRD PASS:

I. CONTINUE TO REFINE THE SYSTEM; 2. KEEP OBJECTIVES IN MIND;
3. DO NOT FALL IN LOVE WITH THE MODEL.

Figure VIII-1. Example of the steps in conceptualizing a model of the interaction between population levels of adult and young game fish.

## 1. Multiple Regression Analysis

Multiple regression analysis related simultaneous changes in several independent variables (ecosystem components) to changes in a dependent variable (defined objectives). For example, the catch $\left(C_{t}\right)$ of rainbow trout from a lake could be represented by the regression model:

$$
C_{t}=\alpha+\beta C_{t-1}+\lambda F_{t-1}+\delta f_{t}+\varepsilon
$$

where:

$$
\begin{aligned}
& \mathrm{C}_{\mathrm{t}-1}=\text { Catch of year class } \mathrm{i} \text { in year } \mathrm{t}-1 \\
& \mathrm{f}_{\mathrm{t}}=\text { Fishing effort expended to catch all year classes in year } \mathrm{t} \\
& \mathrm{f}_{\mathrm{t}-1}=\text { Fishing effort expended to catch all year classes in year } \mathrm{t}-1 \\
& \text { and } \alpha, \beta, \lambda \text {, and } \delta \text { are regression coefficients }
\end{aligned}
$$

## 2. Correlation Analysis

Correlation analysis differs from regression analysis in that the functional relationship of one variable to another is not considered. There is no distinction between dependent and independent variables in correlation analysis. Multiple correlation analysis measures the amount to which variables co-vary. Covariance is negative when one variable increases and the other decreases and positive when both increase or decrease at the same time. If the variables are not linearly related to each other, then covariance is zero.

After the interrelationships of the system components have been quantified, the next step is constructing a mathematical model. There are many kinds of models (Fig. VII-2). Verbal and graphic models are informal. Systems analysis involves formal models which are deve1oped using statistical and mathematical tools. In formal ecosystem modeling, system components and their quantified interrelationships are defined in terms of mathematical equations to create an abstraction of the real ecosystem.
a. VERBAL MODEL - WORD DESCRIPTION "NUMBER OF YOUNG BASS PRODUCED IS RELATED TO HOW MANY SPAWN."
b. DIAGRAMS - BOXES AND ARROWS
ADULT

BASS $\quad$ SPAWNING $\longrightarrow$| YOUNG |
| ---: |
| BASS |

c. GRAPHIC MODEL

d. MATHEMATICAL MODEL

$$
R=f(N)
$$

Figure VIII-2. General types of models applicable to fisheries science.

For example, suppose the objective is to explain the change in catch in a lake over time as the lake ages. The catch in biomass (C) could be described by the equation:

$$
\frac{\mathrm{dC}}{\mathrm{dt}}=\mathrm{F} \mathrm{~N}_{\mathrm{t}} \mathrm{~W}_{\mathrm{t}}
$$

where:

```
\(W_{t}=\) Average weight in fish of age \(t\)
F = Instantaneous fishing mortality
\(N_{t}=\) Number of fish (age \(t\) ) alive in a typical year class
```

Continue with mathematical development

$$
C_{t}=N_{t} W_{t}(A)^{t} \frac{F}{Z}
$$

where,
A = Annual total mortality
$\mathrm{Z}=$ Instantaneous total mortality
This is an example of a rather simple model, but the mathematical interrelatıonsnips are defined and produce a formal abstraction of a real ecosystem.

Differences in formal models are often due to the mathematical description of parameters and forcing functions. Models which include the effects of chance variation in the description of these elements are known as stochastic models. A model which allows (by some probability) for massive dieoffs due to winterkill in a fishery would be a stochastic model. Deterministic models do not include chance variation in their mathematical equations, and consequently, the possibility of a random catastrophic event is not considered. Ecosystems described by deterministic models are perceived as remaining fairly constant. Stochastic models are mathematically more difficult to develop and, consequently, deterministic models are more popular.

After an initial working model has been developed, it must be refined until it satisfactorily mimics the real situation and fulfills the objectives of the analysis. This phase of model development is popularly known as exercising and optimizing the model and often involves extensive analysis. Model analysis provides an insight into the workings of the real ecosystem. The previously discussed homeostatic properties of feedback and stability are important in model sensitivity analysis. Models help to determine the relative effectiveness of different feedback mechanisms in maintaining system stability. The equations which represent these mechanisms can be changed and the resulting responses of the model studied. Using an ecosystem model, the effects of increased primary production due to fertilization could be determined by changing the value of a function so as to represent fertilization. Weaknesses of a model, which are often due to a lack of information about a certain aspect of the ecosystem, can be traced to areas of data acquisition and handing where improvements are needed.

There are three basic goals of model building: (1) realism; (2) precision; and (3) generality. Realism describes the amount of correlation between the mathematical equations of the model and the system. Precision is a measure of the model's ability to mimic new data from the ecosystem on which it is based. Generality refers to the number of different situations to which the model is applicable. If the model successfully accomplished the objectives for which it was developed, then the model is a success. The major benefit of systems analysis is in eliminating effort by directing management and research endeavors. Management is really an application of systems analysis to solving specific problems.

Systems analysis in fisheries science offers potential to solve many problems confronting modern society, but individuals with an educational range covering many disciplines are needed. These kinds of fisheries scientists should have extensive training in the fields of resource management, statistics, mathematics, and computer programming.

Coupled with the wide acceptance of systems analysis, resource managers, either directly or indirectly, have been influenced by the ready availability of high-speed computers. The issue is not whether computer use is inherently good or bad, but when and how can we use these tools effectively. To what degree computers will improve resource management effectiveness cannot be ascertained at this point, but use of computers in many situations is very promising.

The most common application of computers in natural resource management is data tabulation, processing, and analysis. The potential advantages in terms of quantity and speed of data handling are obvious, but less apparent is the problem of determining when to implement a computer approach. There is no simple solution. Thorough familiarization with computer capability allows a potential user to make "good" decisions on a case by case basis, but there are presently few generalizations to assist professionals without such specialized backgrounds.

A second common application of computers deals with automated and semi-automated monitoring systems which could range from a completely automated system, such as environmental sensing connected directly to a computer facility, to using creel clerks to record data on forms than can be processed directly by computer support equipment. In the correct circumstances, use of computer support in this manner can be highly efficient in fisheries management.

A third category of computer useage is applications to enhance natural resource education, especially at the university level. Since resource management problems are very complex and dynamic, it is difficult to transmit to students a realistic appreciation of management problems. Computer simulations of particular resources can be used as case studies for students to practice management.

Evaluation of management strategies with the aid of computerimplemented simulators may be considered a fourth category and is a very promising application of computers. Simulation allows the user to cope with the large number of variables inherent in a complex system and manipulate decision variables to ascertain likely results of a particular set of decisions. Management of reservoir fisheries, one of the most formidable problems facing our profession, has been approached with the aid of computer simulations.

The fifth category of computer application involves improving understanding of ecological interrelationships by employing computer simulation. The continual interactive refinement between modeling and data acquisition, and modelers and field personnel, is in itself a vehicle to improve understanding of ecological systems. The biggest problem with this approach, as with many new tools and techniques, is knowing when to use it and in what format.

A sixth and final class of computer applications involves facilitating numerical analysis. One of the perpetual difficulties in fisheries management is developing best strategies. The problem of maximizing (or minimizing) the objective function by manipulating control (decision) variables, subject to system constraints, is the core of resource management. Computers can be useful in handling these types of problems.

Fisheries management modeling in the future will probably include the major components of an ecosystem as well as feedbacks. In order to characterize these feedback loops, models of ecological phenomena such as abundance-reproduction relationships and predator-prey relationships will probably be employed.

Most importantly, a fisheries management model must use concepts of optimization. If a fishery is to be managed effectively, the best decisions must be made from the available alternatives. Optimizing a fishery implies that effective measures of the fishery's performance have been developed; i.e., the management objectives have been formally defined, but in most systems this is far from true.

## CHAPTER NINE

## DECISION ANALYSIS

Objectives are the key in management decision making. The quality of management decisions is based upon the degree to which the decision leads to reaching management objectives. Objectives serve numerous purposes or functions in fisheries mangement. They are basic organizers which direct activities toward a desired end. Objectives serve as a scale or level against which all management activities are evaluated. They enable managers to determine how well the agency is doing. Objectives help agencies to set priorities and allocate funds, personnel, and equipment for the best possible or optimum return. Objectives aid in research by identifying needs and guiding data acquisition. Above all other functions, objectives discipline thinking and organize the desires of people, both agency personnel and the general public.

Management objectives are unique in their character. They have specific characteristics that set them apart from agency goals or missions. The four characteristics of a management objective are:

1. It must be formal. The objective must aim at a specific, well-stated, endpoint such as maximum yield or maximum recreational use.
2. It must be measurable. The accomplishment of an objective must be able to be measured. In order to be so, the objective must be stated in terms of measurable units such as kilograms per hectare yield or angler-use days.
3. It must be acceptable to the public and to professionals.

If an objective is not agreed upon by the major human facets that it affects, then it is likely not to be realized. The agreement of public and professional sectors is often very difficult to achieve.
4. In most cases management objectives are conceptually simple, but technically difficult to handle. For example, it may be very easy to maintain the quality of panfish fishing in a lake by limiting the harvest of top carnivores, but the problems of instituting and enforcing harvest restrictions on the carnivores may be very difficult to accomplish.

Selection of management objectives incorporates input from two sources, the public and the agency itself. Public involvement is very important in order to receive needed social or political support. An agency must find a way of incorporating public input into selection of objectives. This phase of objective selection has been historically ignored on the basis that the public does not understand the resource system or the decision alternatives. A major problem in obtaining public input is obtaining a balance between the vocal, special interest groups and the "silent majority." The problem is further complicated because societal objectives are constantly changing. Relative to agency involvement in selection of objectives, questions arise as to the level at which actual objectives should be aimed. Should objectives be defined in terms of national, regional, state, district, county, or local concerns? The "scope" of a management objective must be well defined by those who select it.

The quantitative aspect of management objectives must be emphasized. Only through quantification can accomplishments be measured or can the systems approach be applied. Quantified management objectives can be quite varied. For example, the management objectives of a warmwater stream fishery could possibly be any of the following:

1. Maximize yield to anglers
2. Maximize the quality of angler experiences
3. Maximize species diversity
4. Maximize aesthetics
5. Preserve certain or all species

Any one of these objectives could interfere with the objectives of other fisheries managers, or forestry, wildife, agriculture, or recreation interests. Developing an interface between all competing uses of a resource is quite difficult.

The basic strategy associated with most management objectives is the optimization of some aspects of the resource. The management analysis involved in achieving optimization is conceptually simple, but can become complex in practice. An overview of the basis for optimization can be expressed by the general model:

$$
Q=f\left(X_{1}, X_{2}, \ldots X_{n} \mid Y_{1}, Y_{2}, \ldots Y_{n}\right)
$$

where:
Q is the social benefit (s) to be optimized;
X's are possible decision variables, and
Y's are constraints (social, budgetary, etc.) (The vertical
line reads "given that.")
The model can be solved given an understanding of the system involved, as well as the array of decision variables and constraints encountered. Numerous tools are at the managers disposal. The tools can include the more subjective means of logic and experience. More formal and objective approaches involving mathematical models, linear programming, and computer simulation are applicable in many situations. The methods used depend on the nature of the objective as well as the information and resources available to the manager.

Examples of strategies used in deriving management decisions are numerous. Given that an objective is defined and accepted, the job of the manager is to meet that objective within specified constraints. Strategies are the various routes to meet the management objective.

There are few generalizations available in reviewing various management strategies. Any management problem should, however, be systematically attacked from a systems analysis standpoint. Six examples of population analysis strategy used to achieve defined objectives are presented with their advantages and disadvantages.

1. Stock-Recruitment Strategy

Assume that our management objective is MAX Y (maximum sustained yield) of a stock and stock level is closely related to the number of spawning adults. Such conditions are most closely met by Pacific salmon and, to a lesser extent, by other anadromous or adfluvial species. If we can reasonably accept that the number of spawners determines the number of progeny that recruit, a stock-recruitment model may form the basis of a management strategy (Fig. IX-1). By maximizing the difference between the recruitment population level and the equilibrium population level, the maximum equilibrium yield can be maintained.

The stock-recruitment strategy has several advantages in practice: (1) only data on adult fish are necessary; (2) the model is well studied and there is much published literature on its use; (3) the model may be a good approximation of a complex ecological system; and (4) the effectiveness of management efforts is relatively easily measured since the unit of system output is the captured fish.

Disadvantages of the stock-recruitment strategy include:
(1) the assumption that the relationship is solely due to densitydependent factors; (2) the assumption that the adult stock is homogeneous (no fluctuation in age structure); and (3) the assumption that MAX Y is the desired management objective.


Figure IX-1. Stock-recruitment model expressing the relation between density of spawners and density of recruits.

## 2. Regression Prediction Strategy

Most management situations do not warrant use of the stockrecruitment model, but rather some other approach. Regression prediction is an approach in which key factors are used to predict maximum equilibrium yield.

For example, we may wish to predict the catch of lake trout in a particular fishery. Catch in a particular year is hypothesized to be a function of last year's catch, the fishing effort last year, and the fishing effort in the particular year. Therefore,

$$
C_{t}=\alpha+\beta C_{t-1}+\nu f_{t-1}+\delta f_{t}+\varepsilon
$$

where,
$C_{t}=$ Catch in year $t$
$C_{t-1}=$ Catch in year $t-1$
$\mathrm{f}_{\mathrm{t}}=$ Fishing effort in year t
$\mathrm{F}_{\mathrm{t}-1}=$ Fishing effort in year $\mathrm{t}-1$
$\varepsilon=$ Unaccounted for variation
$\alpha, \beta, \nu$, and $\delta$ are regression coefficients calculated from data

In practice, data for a number of years are used to solve models of the above type. Then, by manipulating decision variables (such as angling pressure through season regulations), the manager can determine maximum yield or the yield under a potential management decision. Selection of the independent factors ( $C_{t}, C_{t-1}, f$, and $f_{t-1}$ ) is often difficult in practice. Such parameters as total dissolved solids, water temperature, barometric pressure, and average lake depth have been used.

Advantages to using a regression prediction strategy include: (1) relative ease of mathematical analysis; (2) data are often available; (3) extreme flexibility in model structure; and (4) densitydependent and density-independent factors can be mixed, although analytical difficulty increases rapidly.

Disadvantages of the regression prediction strategy are: (1) a stable environment must generally be assumed; (2) a stable age class structure must usually be assumed; (3) selecting initial independent variables may be difficult; and (4) the error term ( $\varepsilon$ ) may always, even with a highly complex model, account for most of the variation.
3. Constant Environment Strategy

Usually the general principle underlying strategies that assume a constant environment is an effort at manipulating population statistics to achieve maximum yield. This type of strategy is often considered to be classical population dynamics. Most of the variation in fish abundance, growth, and mortality is assumed to be predictable based on certain population statistics and their interrelationships. Such an approach usually requires a rather complicated mathematical and conceptual development. Derivation of an equation to predict yield based upon abundance ( $N$ ), recruitment (R), growth (K), total mortality (Z), and fishing mortality (F) has been outlined in Chapter VII. An example of the manner in which the various populations parameters are incorporated into a yield model is as follows:

First consider total mortality (Z):

Since,

$$
\frac{\mathrm{dN}}{\mathrm{dt}}=-\mathrm{ZN} \mathrm{t}
$$

And,

$$
\begin{aligned}
& t_{c}^{t_{\infty}} d N=\int-Z N_{t} d t \\
& N_{t}=N_{o} e^{-Z \Delta t}
\end{aligned}
$$

But, since we are primarily interested in fish after they recruit

$$
N_{t}=R e^{-Z \Delta t}
$$

Following the same reasoning relative to fishing mortality ( $F$ ), it is known that the more fish harvested from a stock, the lower stock leve1 (Fig. IX-2).


Figure IX-2. Relation between fish harvest (C) from a stock and the stock abundance ( N ) over time.

Then,

$$
\frac{\mathrm{dC}}{\mathrm{dt}}=\mathrm{FN}_{\mathrm{t}}
$$

And,

$$
\begin{aligned}
& \mathrm{t}_{\mathrm{f}_{\mathrm{c}}^{\infty}} \mathrm{dC}=\int \mathrm{FN} \mathrm{t}_{\mathrm{t}} \mathrm{dt} \\
& \mathrm{C}_{\mathrm{t}}=\int_{\mathrm{t}}^{\mathrm{t}_{\infty} \mathrm{FN}} \mathrm{t} \text { dt }
\end{aligned}
$$

But,

$$
\left.N_{t}=N_{o} e^{-Z t} \quad \text { (if } \Delta t=1\right)
$$

Then,

$$
C=\int_{t_{C}}^{t_{\infty}} F\left[\operatorname{Re}^{-Z t}\right] d t
$$

Finally, by intergrating over the time an age class will be vulnerable to fishing.

$$
C=R\left[1-e^{-Z t}\right] \frac{F}{Z}
$$

(3) When growth (K), it was shown that

$$
\frac{\mathrm{d} \ell}{\mathrm{dt}}=\mathrm{K}\left(\ell_{\infty}-\ell\right)
$$

can be reduced to

$$
w_{t}=w_{\infty}\left[1-e^{-K\left(t-t_{0}\right)}\right]^{\beta}
$$

By adding the expression for $w_{t}$, $C$ becomes $Y$ and

$$
Y=R\left[1-e^{-Z t}\right] \frac{F}{Z}{\underset{t}{c}}_{t_{c}^{\infty}}^{\int_{c}}\left(w_{\infty}-w_{t}\right)^{d t}
$$

This equation for estimating $Y$ is called a "yield equation" and is a mathematical statement of the "theory of fishing." (See Chapter I)

The advantages of classical population dynamics as a strategy are: (1) the relatively simple conceptual basis; (2) there are of ten large quantities of available data, especially in commercial fisheries; (3) the vital statistics can be controlled (at least somewhat) by practical decisions; and (4) the models can easily be computer-implemented.

Disadvantages include: (1) rate statistics are assumed to be constant (this may be adjusted for, but it is difficult); (2) constants are difficult to accurately estimate; (3) extrinsic factors may be very important to the system; and (4) the model may not adequately ref1ect the fishery.

## 4. Variable Environment Strategy

If environmental factors act in a variable manner to such a degree that relatively simple strategies are inappropriate, the manager may be found to use a "big mode1" approach.

For example, assume we can control largemouth bass survival at various stages in the life cycle (selective chemical treatment, stocking, regulations, predator control, etc.). We then wish to manipulate these various controls (survivals) to maximize catch.

Then

$$
N_{i j}=N_{i o} S_{i 1} S_{i 2} S_{i 3} \cdot \cdots \cdot S_{i j}
$$

where

$$
N_{i j}=\text { Number of bass in the ith year class surviving }
$$ to the jth birthday

$S_{i n}=$ Probability of survival of individual bass in the ith year class from the $n-1$ to the nth age $N_{\text {io }}=$ Number of bass in the ith year class that hatched

Since

$$
\begin{gathered}
\mathrm{E}=\mathrm{f} \text { (angling pressure) } \\
\text { where }
\end{gathered}
$$

$$
E=\text { Exploitation rate }
$$

then

$$
C_{i j}=E N_{i j}
$$

The advantages of this approach are: (1) any system can be described, at least conceptually; and (2) the model structure bears a close relationship to biological and realistic mechanisms.

Disadvantages include: (1) bookkeeping and analytical problems may be tremendous - one needs computer support; (2) model quantification results in a relatively large data requirement; (3) modeling detail may obscure management objectives; and (4) cost of this strategy may exceed benefits.

## 5. Strategy to Maximize Profit

In commercial fisheries the participants wish to maximize their personal profit or net income. Yield is important only as it affects profit (Fig. IX-3). The "total cost" line may be linear or bend up with time, but in any case it must rise with additional fishing effort. Total revenue from the catch will increase rapidly with additional fishing effort at lower levels. With heavier fishing pressure, total revenue will stabilize and then decrease.


## NUMBER OF FISHERMEN (EFFORT)

Figure IX-3. Relation between economic yield (\$) and the amount of fishing effort on a particular stock.

To maximize total profit, fishing effort should be held at a point that results in maximum deflection between total cost and total revenue. In practice, fishing effort tends to stabilize around the intersection of total cost and total revenue. This point is, of course, zero profit for the total fishery, although some fishermen will show a profit while others lose money.

This strategy is intuitively acceptable from a societal standpoint, but are fisheries managed for the benefit of the participants or society as a whole? In practice it is difficult to control fishing effort without reducing the fishermen collectively to a zero profit level.

## 6. Management Benefit Unit Strategy

In all the previously discussed strategies, we measured fishery output in pounds, numbers, or dollars. In recreational fisheries these measures of output have often been criticized as being poor measures of true benefits. Aesthetic and other intangible factors are important in recreational fisheries, but they are difficult to measure.

Assume that we develop a scale of benefit measure produced from a fishery (management benefit unit or mbu). The output from a fishery as measured in mbu's may be composed of factors such as yield, water quality, crowding, user conveniences, and others (Fig. IX-4). The shape of output line may be highly irregular, but should rise rapidly, level off, and then decline. The cost line may be equally irregular, but should at least continuously rise.

A strategy to maximize the net mbu's (maximum deflection between cost and output) seems reasonable. However, people will still participate or enter the fishery as long as they show a net profit. The total profit will thus, without management, tend toward zero.


Figure IX-4. Relation between management benefit units, fishing effort, cost, and output from a fishery.

The variety of approaches by which management decisions may be reached is exemplified by these six examples. The entire scope of analysis of exploited fish populations is to lead to rational, justifiable management decisions that produce results conducive to stated objectives. All information on abundance, mortality, growth, and so forth is gathered for the purpose of improving management decisions. Understanding and utilizating the various population parameters is an intergral part of management strategies, whether they are highly mathematically oriented or based on logic and experience.

