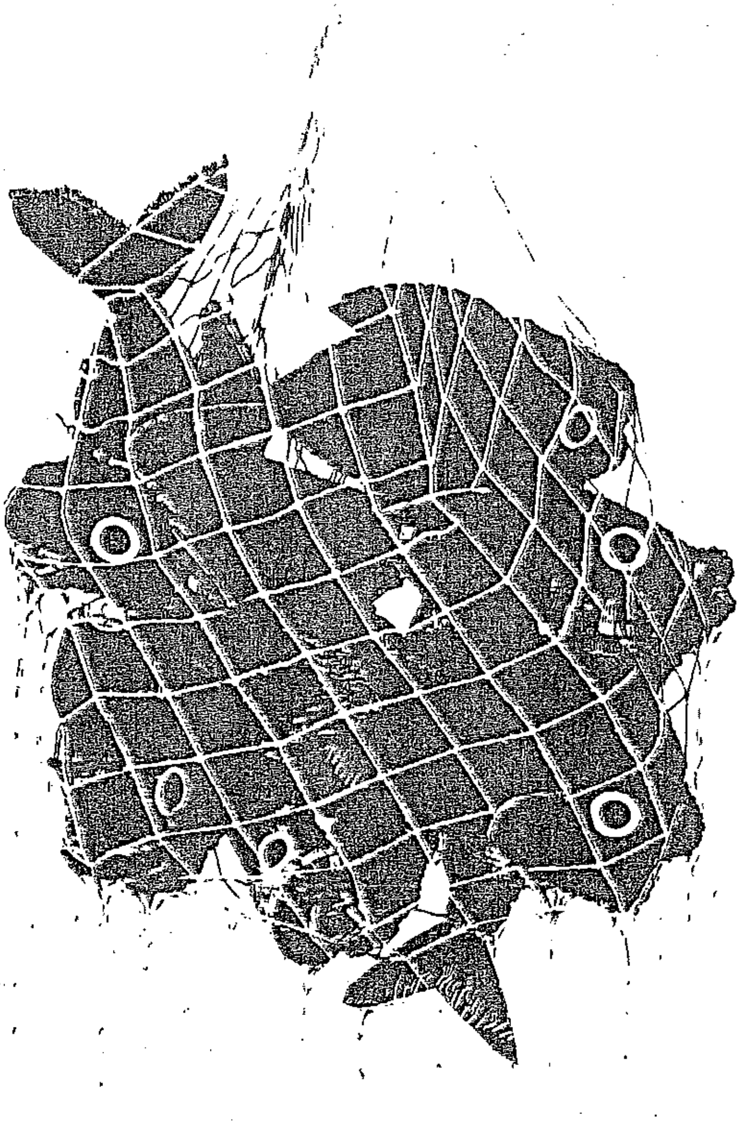
Analysis of Exploited Fish Populations

Edited by

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 options and 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.

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. 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 perhaps 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 habitat and biota may be caused by recreational fishing, commercial fishing, industrial activities, agricultural activities, or domestic activities. In short, nearly any human or societal activity may affect a fishery.

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, including fishing, 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, etc., 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.

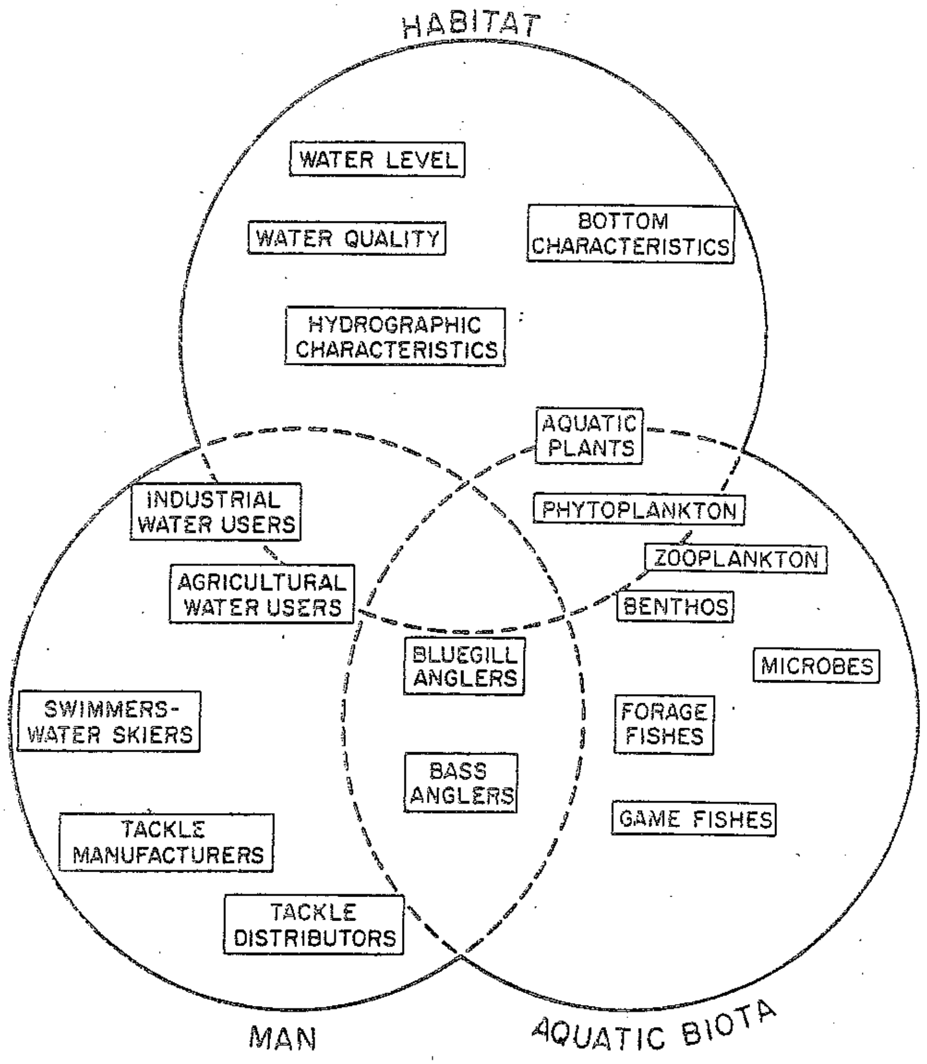

Figure I-1. Graphical model of a generalized sport fishery. Only major system components are included.

The human elements of fisheries were related quantitatively to fish population response for the first time in the initial decades of the 20th century (Russell 1931, Cushing 1968).

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

Expanding Russells' ideas to some degree, a more contemporary theory of fisheries management has been postulated (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:

$$Q_{MAX} = f(X_1, X_2, \ldots X_m \mid Y_1, Y_2, \ldots Y_n)$$

where Q_{MAX} is the maximization of societal benefits. The X's are the "decision variables" and include those things the manager can control. The Y's are the "constraints" and are not under the control of the manager (or are 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, haitat, 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 largely uncontrollable. A manager can do very little to substantially 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 and habitat destruction.
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 of the fisheries system. Man is the reason for performing the management activities 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, as well as economics, engineering, and others.

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 some of the major contributing disciplines.

Biology, obviously, contributes heavily to fisheries science. Biological information on the life history and physiological requirements of different organisms is needed. Simple questions such as "when do the species of interest spawn?" must be answered. Topics of interest within biology are ecology, behavior, morphology, and taxonomy.

Mathematics is an integral part of modern fisheries science. It has 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 estimates of stock abundance and potential yield 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 highly necessary to many areas of fisheries science. Interaction with engineers can serve to enhance, protect, or create habitats 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 analyses 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 all management agencies are conceived, initiated, budgeted, and governed. Problems with politics include conflicts between governmental 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. All 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 contributor. Computers can perform many elaborate 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 largely 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 concepts of systems analysis and decision analysis. It will be evident as the reader proceeds through the chapters the extent to which the various disciplines have contributed to fisheries science.

Further Reading

Cushing, D. H. 1968. Fisheries biology, a study of population dynamics. The University of Wisconsin Press, Madison. 200 pp.

Gulland, J. A. 1974. The management of marine fisheries. The University of Washington Press, Seattle. 198 pp.

Lackey, R. T. 1974. Introductory fisheries science. Sea Grant Program, Virginia Polytechnic Institute and State University, Blacksburg. 280 pp.

Lackey, R. T. 1975. Recreational fisheries management and ecosystem modeling. publ. VPI-FWS-4-75, Virginia Polytechnic Institute and State University. 44 pp.

Russell, E. S. 1931. Some theoretical considerations on the "overfishing" problem. J. Cons. Intern. Explor. Mer. 6(1):3-20.

CHAPTER TWO

STOCK IDENTIFICATION*

Concepts

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 delineated 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

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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 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 strictly 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 population complex 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 a hypothetical warmwater impoundment with four centrachid 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 confirm 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 a unit stock as a manageable portion of the target fish population remains the most practical definition in marine fisheries, and it is especially appropriate in freshwater recreational fisheries.

Identification

Numerous techniques have been developed for delineating stocks of fish. Some methods potentially 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, but 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 delineate 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 purposals based on food and habitat preferences. The population of Snake River cutthroat was the most acceptable from the anglers' point of view because of its preference for feeding on terrestrial and surface insects, thereby making it more vulnerable. The Pikes Peak origin cutthroat trout perferred 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 distribtuion, 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 they are 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 single morphological feature will allow fish stocks to be delimited as is the case for herring (*Culpea 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 culpeaformis) 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 problems 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 of each stock. Often the ranges in values overlap.

4. If the fisheries in two adjacent areas have similar catch and effort records, it is good evidence that only 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° if one stock only is present (Fig. II-2).

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

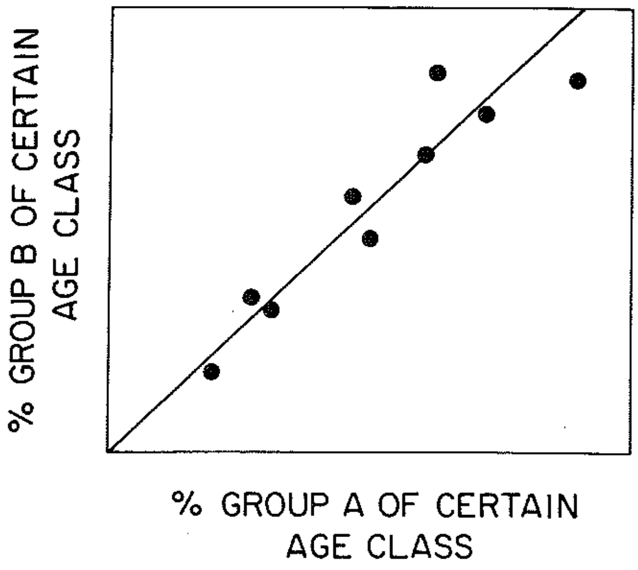

Figure II-1. Graph of the percentage of the population in a fishery versus the percentage of the population in another fishery. If the line deviates from 45°, two or more stocks may be involved.

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 may be one of the most reliable method of distinguishing stocks of fish. This method has confirmed the conclusions drawn from earlier attempts at delineating 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

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 such as the North Atlantic cod fishery, considerable time and effort has been directed at delineating 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 becomes 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 as a genetically 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 typically 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 purpose 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.

Further Reading

Averett, R. C., and F. A. Espinosa, Jr. 1968. Site selection and time of spawning of two groups of Kokanee in Odel Lake, Oregon. J. Wildlife Management 32(1):76-81.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Systematic Zoology 10:105-117.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Bd. Can. 29(6):639-671.

Calaprice, J. R., and J. E. Cushing. 1967. A serological analysis of three populations of golden trout, _Salmo aquabonito_ Jordan. California Fish and Game 53(4):273-281.

Clemens, H. B., and G. A. Flittner, 1969. Blue-fin tuna migrate across the Pacific Ocean. California Fish and Game 55(2):132-135.

Cushing, D. H. 1968. Fisheries biology, a study in population dynamics. University of Wisconsin Press, Madison. 200 pp.

Fenderson, O. C. 1964. Evidence of subpopulations of lake whitefish, _Coregonus clupeaformis_, involving a dwarfted form. Trans. Am. Fish. Soc. 93(1):77-94.

Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. Rome, FAO. FAO Manuals in Fisheries Science No. 4.

Gulland, J. A. 1974. The management of marine fisheries. University of Washington Press, Seattle. 190 pp.

Ingram, V. M. 1960. The gentic control of protein structure. Pages 65-176 _in_ H. E. Sutton (ed.). Genetics. Josiah Macy, Jr. Foundation, New York.

Lackey, Robert T. 1974. Introductory fisheries science. Sea Grant Program, Virginia Polytechnic Institute and State University, Blacksburg. 280 pp.

Lewis, Robert Minturn. 1957. Comparative study of populations of the striped bass. U.S. Fish and Wildlife Serv. Spec. Sci. Rep. Fish. 204 pp.

Lux, F. E., A. E. Peterson, Jr., and R. F. Hutton. 1970. Geographical variation in fin ray number in winter flounder, _Pseudopleuronectes americanus_ (Walbaum) of Massachusetts. Trans. Am. Fish. Soc. 99(3): 483-488.

McAfee, J. D. 1967. Lahontan cutthroat trout. Pages 225-231 _in_ Alex Calhoun ed. Inland fisheries management. Calif. Dept. Fish and Game. 546 pp.

Messieh, S. N. 1972. Use of otoliths in identifying herring stocks in southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Bd. Can. 29(8):113-118.

Morgan, R. P., II, T. S. Y. Koo, and G. E. Grantz. 1973. Electrophoretic determination of populations of striped bass Morone saxatilis, in the Upper Chesapeake Bay. Trans. Am. Fish. Soc. 102(1):21-32.

Northcote, T. G., S. N. Williscroft, and H. Tsuyuki. 1970. Meristic and lactase dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. J. Fish. Res. Bd. Can. 27(11):1987-1995.

Nyman, O. L., and J. H. C. Pippy. 1972. Differences in Atlantic salmon, Salmo salar, from North America and Europe. J. Fish. Res. Bd. Can. 29(2): 117-185.

Raleigh, R. F., and D. W. Chapman. 1971. Genetic control in lakewood migrations of cutthroat fry. Trans. Am. Fish. Soc. 100(1):33-40.

Ridgeway, George J., Stuart W. Sherburne, and Robert D. Lewis. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99(1):147-151.

Sinderman, C. J., and D. F. Maris. 1959. A major blood group system in Atlantic sea herring. Copei (3):288-232.

Smith, Albert C., and Harold B. Clemens. 1973. A population study by proteins from the nucleus of bluefin tuna eye lens. Trans. Am. Fish. Soc. 102(3): 578-583.

Trojnar, J. R., and R. J. Behnke. 1974. Management implications of ecological segregation between two introduced populations of cutthroat trout in a small Colorado Lake. Trans. Am. Fish. Soc. 103(3):423-430.

Vincent, R. E. 1960. Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchell). Trans. Am. Fish. Soc. 89:35-52.

Vrooman, A. M. 1964. Serologically differentiated subpopulations of Pacific sardine, Sardinops caerula. J. Fish. Res. Bd. Can. 21(4):691-701.

Wilkins, N. P. 1968. Multiple haemoglobins of the Atlantic salmon (Salmo salar). J. Fish. Res. Bd. Can. 25(12):2651-2663.

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 in a fish stock. One of the most important uses of abundance data is in estimating mortality rates, which in turn are reduced to exploitation rates. 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 here in order to concentrate on the application of the methods 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 all or some of the assumptions are not fully met. It is most important to identify the assumptions which are grossly violated and the degree or manner in which they are invalid.

The methods of estimating abundance discussed here are: 1) indices of adundance (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 estimators. The population dynamics symbols used in formulas throughout this book are listed in Table III-1. Formulas for calculating abundance are presented, but major emphasis is placed upon extracting the principles involved.

Table III-1. POPULATION DYNAMICS SYMBOLS

Symbol	Term
A	*Mortality rate (fraction) (often 1-S)
B	Biomass (general)
C	Catch of fish (number)
D	*Natural death rate (fraction)
E	*Exploitation rate (fraction)
F	*Fishing mortality rate (instantaneous)
G	*Growth rate (general)
K	*Growth rate (von Bertalannfy equation)
M	*Natural mortality rate (instantaneous)
N	Number of individuals in a stock (or population)
P	Biomass of fish in a stock
R	*Number of recruits (annual recruitment)
S	*Survival rate (fraction)
V	Virtual population estimate
Y	Yield (catch of fish in weight)
Z	*Total mortality rate (instantaneous)
e	Natural log base
f	Fishing effort
ℓ	Length of individual fish
ℓ_c	Length of first capture
m	Number of fish marked
n	Sample size
q	Catchability coefficient (F/f)
r	Number of fish recaptured
t	Time
t_c	Time at first capture
w	Weight of individual fish
w_c	Weight of first capture

*Rate estimators

Indices of Abundance

In many 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 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 index of abundance. The basic assumption is that C/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 amount of gear, as long as f is measured in the same units. Creel data can be used in many ways to express C/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.

Direct Enumeration Methods

Direct enumeration is one of the best and simplest techniques for estimating abundance. It requires counting all or a selected portion of the population. This method, although highly preferred, is of limited value because it can only be utilized when the total population may be confined sufficiently to make an actual count of the number 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 can be improved by providing a light colored stream bottom. Where fishways have been constructed, salmon can be easily counted at the exit, or a television camera and video-tape equipment can be installed in the fishway. 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. If a portion of the population is counted, the total population can be projected from these data. Towers on the banks of salmon streams are usually not manned continuously, rather, counting periods of 10 or 15 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, and the results of sampling these stratified areas can be projected to the total population. Reservoir cove sampling may be considered a type of partial count. In this method, coves 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 N_1, N_2, N_3 ... N_a corresponding to subspaces 1, 2, 3 ... a. Then:

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

and

$$\text{var}\ (N) = \frac{A^2 - aA}{a}\ \text{var}\ (N_i)$$

where

$$\text{var}\ (Ni) = \frac{a \sum_{i=1}^{a} N_i^2 - (\sum_{i=1}^{a} N_i)^2}{a(a-1)}$$

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:

$$a_1 = 30$$
$$a_2 = 40$$
$$a_3 = 25$$
$$a_4 = 15$$
$$a_5 = 35$$

then

$$N = (25/5)\ (30 + 40 + 25 + 15 + 35)$$
$$N = 725$$

The estimated variance of N is calculated as follows:

$$\text{var}\ (N_i) = \frac{5[30^2 + 40^2 + 25^2 + 15^2 + 35^2] - [30 + 40 + 25 + 15 + 35]^2}{5(4)}$$
$$\text{var}\ (N_i) = 92.5$$

then

$$\text{var}\ (N) = \frac{(25)^2 - 5(25)}{5}\ (92.5)$$
$$\text{var}\ (N) - 9250$$

Correlated Methods

The life history of a fish may be such that some closely related (correlated) sub-adult population can 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 forecast the size of salmon runs using a correlated method or index. Sometimes this method can only provide 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 also for planning and regulatory decision-making. Pink salmon forecasts, for example, can be based on the relationship between pre-emergent fry abundance and subsequent adult return. The forecast of the 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. 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	Y (Year)	XY	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

$\overline{X} = 103.04$

$\overline{Y} = 9.34$

$$\beta = \frac{(\Sigma XY) - (\Sigma X)\ (\Sigma Y)}{(\Sigma X^2) - (\Sigma X)^2} = 0.216$$

$\alpha = \overline{Y} - \beta \overline{X}$

$\alpha = 9.34 - 0.216\ (103.04)$

$\alpha = -12.92$

Thus

$\hat{Y} = -12.92 + 0.216X$

Current incomplete data include:

Brood Year	X	[Forecast] Y	(year)
1973	133.9	[16.0]	(1975)
1974	101.5	[9.0]	(1976)

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 cycle)

$$\hat{Y} = \alpha + \beta X$$

$$\hat{Y} = -12.92 + 0.216(133.9)$$

$$\hat{Y} = 16.00$$

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

$$S^2_{\hat{Y}} = \frac{\Sigma Y^2 - \frac{(\Sigma Y)^2}{n}}{n-2} \quad 1 + \frac{1}{n} + \frac{(X_i - \overline{X})^2}{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}$$

$$= 120.04$$

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

Indices of abundance have several advantages: 1) low cost for relatively 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 associated with partial count and correlation techniques.

Mark-Recapture Methods

Mark-recapture studies provide information on abundance and 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 methods.

Single Census

The simplest mark-recapture method is the single census estimator. The general method was developed by LaPlace to estimate the human population of France in the 1700's. Peterson (1869) used mark-recapture to estimate exploitation rate (E). Dahl (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 assumption 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 the same mortality as unmarked fish; (2) marked fish are caught at same rate as unmarked fish; (3) marks are not lost; (4) marked fish are randomly distributed <u>or</u> the sampling effort is random; and (5) recruitment is negligible or can be estimated. The simplest estimator is

$$\hat{N} = \frac{mC}{r}$$

Where: m = number of fish marked

C = the catch taken for census [total marked (m) and unmarked (C - m)]

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 anglers. Of these creeled fish, 157 were marked.

$m = 550$

$C = 8{,}720$

$r = 157$

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

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 and the manner in which they are captured. Confidence limits can generally be obtained by treating r as a Poisson or binomial variable and using a table [see Appendix II of Ricker (1975)].

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 Schumacher-Eschmeyer (1943) provided much of the mathematical basis for this estimator. 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
Σr_t = total recaptures during the experiment to day t.

C_t	M_t	C_tM_t	r_t	Σr_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

$$\hat{N} = \frac{\Sigma(C_tM_t)}{\Sigma r_t}$$

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

$$\hat{N} = \frac{\Sigma(C_t M_t)}{\Sigma r_t}$$

In practice, the worker would continue sampling until the confidence interval becomes narrow enough for the purposes of the analysis.

Multiple 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 is 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. In most cases, fish are not capture-prone or capture-shy and tend to avoid any type of sampling gear. Seber (1973) should be consulted for a detailed description of the method.

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 t = 1, ; and (3) estimates of the new relative abundances are made at 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 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 (4) 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:

N_1 = total number of fish (brook and brown trout, for example) in the population at $t = 1$

X = number (brook trout) added or removed between $t = 1$ and $t = 2$

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 $t = 2$

N_2 = total number of fish (brook and brown trout) in the population at $t = 2$

The two necessary simultaneous equations can be formed as follows:

$$p_2N_2 = p_1N_1 + X$$

$$N_2 = N_1 + X + Y$$

solving

$$\hat{N}_1 = \frac{X - p_2\ (X + Y)}{p_2 - p_1}$$

There are many possible applications to this method. One possibility 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 N_1 is found as follows:

$$\hat{N}_1 = \frac{-200 - 0.55\ (-230)}{0.55 - 0.70} = \frac{-73.5}{-0.15} = 490$$

$$\hat{N}_1 \text{ (brook trout)} = 343$$

$$\hat{N}_1 \text{ (brown trout)} = 147$$

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

Depletion Methods

The basic conditions required for application of this estimator (also called the Leslie, DeLury, or regression estimator) are that the population 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 when a substantial proportion 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. Variation in catch make this method unsatisfactory for many sport fisheries. 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 remains constant; (2) the population is totally available to sampling effort; (3) there is no natural mortality or recruitment; and (4) the fishing gear applied is constant in its effectiveness.

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 (ΣC_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.

$$C_t/f_t = qN_t \tag{1}$$

The population at the start of time t is equal to the original population less the cumulative catch ΣC.

$$N_t = N_o - \Sigma C \tag{2}$$

substituting into (1)

$$C_t/f = q(N_o - \Sigma C) \tag{3}$$

Equation 3 indicates that C/f plotted against ΣC has a slope of q. Also, the X axis intercept is an estimate of the original population N_o, since it represents ΣC 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).

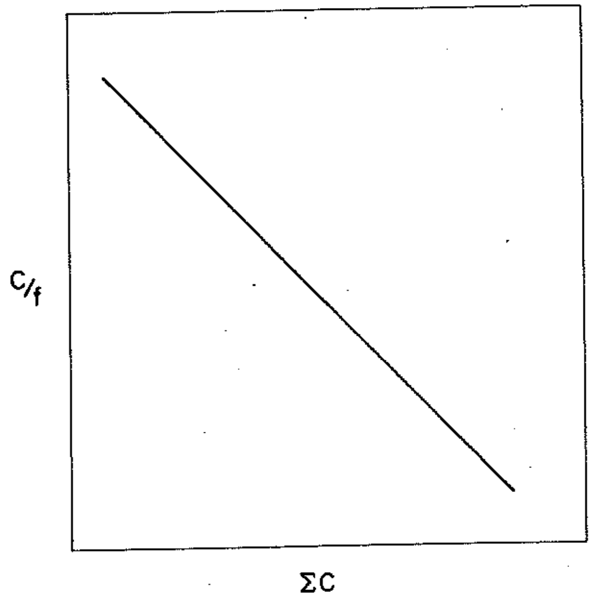

Figure III-1. Regression line calculated to describe the relation between catch per unit effort (C/f) and cumulative catch (ΣC). The X axis intercept gives estimate of abundance.

The following example shows table setup and calculations (from Ricker 1975).

Time Period	$\Sigma C(X)$	C_t/f_t (Y)	(XY)	(X^2)
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

$\Sigma x^2 = 1,846,194 - 3770^2/10 = 424,904$

$\Sigma y^2 = 57,062 - 710^2/10 = 6652$

$\Sigma xy = 223,519 - 3770\ (710/10) = -44,151$

β = slope = $-44151/424904 = -0.103908$

α = Intercept = $\dfrac{\underline{710 - (-0.103909)} \quad \underline{(3770)}}{10} = 110.17$

q = catchability = $+0.103908$

$$\hat{N}_o = \frac{\alpha}{q} = \frac{110.17}{0.103908} = 1060$$

Virtual Population Estimates

An estimate of population size 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 (simplified from Fry 1949 and Ricker 1975):

Year Class	III	IV	V	VI	Total Virtual Population	Year
1961	-	-	-	1665	5553	1967
1962	-	-	1371	1243	4764	1968
1963	-	1294	1199	1165	4753	1969
1964	1223	1193	1189	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, 4753 in 1969, etc. Exploitation rate can be calculated by

$$E_t(\max) = \frac{C_t}{V}$$

The actual population size 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 catch are $r_1 + r_2 + r_3 + \ldots$ then

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

Further Reading

Cushing, D. H. 1968. Fisheries biology - a study in population dynamics. University of Wisconsin Press, Madison. 200 pp.

DeLury, D. B. 1958. The estimation of population size by a marking and recapture procedure. J. Fish. Res. Bd. Can. 15(1):19-25.

Everhart, W. H., A. W. Eipper, and W. D. Youngs. 1975. Principles of fishery science. Cornell University Press, Ithaca, New York. 288 pp.

Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Manual in Fish. Sci. No. 4. Food and Agricultural Organization of the United Nations, Rome. 154 pp.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of Fish. Res. Bd. of Can. 382 pp.

Schnabel, Z. E. 1938. The estimation of the total fish population of a lake. Amer. Math. Mon. 45(6):348-352.

Schumacher, F. X., and R. W. Eschmeyer. 1943. The estimate of fish populations in lakes or ponds. J. Tenn. Acad. Sci. 18(3):228-249.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Charles Griffin and Co., Ltd., London. 506 pp.

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

Annual Mortality Rates

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

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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 (A or 1-S), its counterpart, are determined by a comparison of the numbers of a cohort or group of cohorts alive at successive ages:

$$S = \frac{N_{t+1}}{N_t}$$

The annual 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 and N = abundance:

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

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

The utility of the definitions of annual mortality rates are distinctly limited because the rates E and D defined in this manner ($A = E + D$) 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 cause of death will occur during the period, creating a situation where the two causes of death are mutually exclusive (Regier and Robson 1967).

Instantaneous Mortality Rates

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 total 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 Z equal to the negative natural logarithm of the complement of the annual mortality rate (-ln S). 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:

$$dN/_{dt} = -ZN$$

Thus, the rate of change of a cohort or year-class with time is proportional to the number present. The negative sign means numbers are declining. Rearranging,

$$dN/_{dt} = -ZN$$

$$dN/_{N} = -Z\ dt$$

Integration of the equation yields,

$$\ln \frac{N_{t+1}}{N_t} = -Zt \qquad \text{or} \qquad \ln S = -Zt$$

$$\frac{N_{t+1}}{N_t} = e^{-Z} \qquad\qquad S = e^{-Z}$$

$$N_{t+1} = N_t e^{-Z} \qquad\qquad Z = -\ln S$$

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

In practice, sources of mortality are usually divided into the two categories, fishing (F) and natural (M) mortality. The separation of total mortality into these two components becomes a matter of prime concern when predicting the effect of altering fishing intensity (f).

The frequency of encounters between fish and gear will be proportional to the product of fishing intensity and the abundance of fish. A certain fraction of these encounters will result in capture:

$$dN/_{dt} = -FN$$

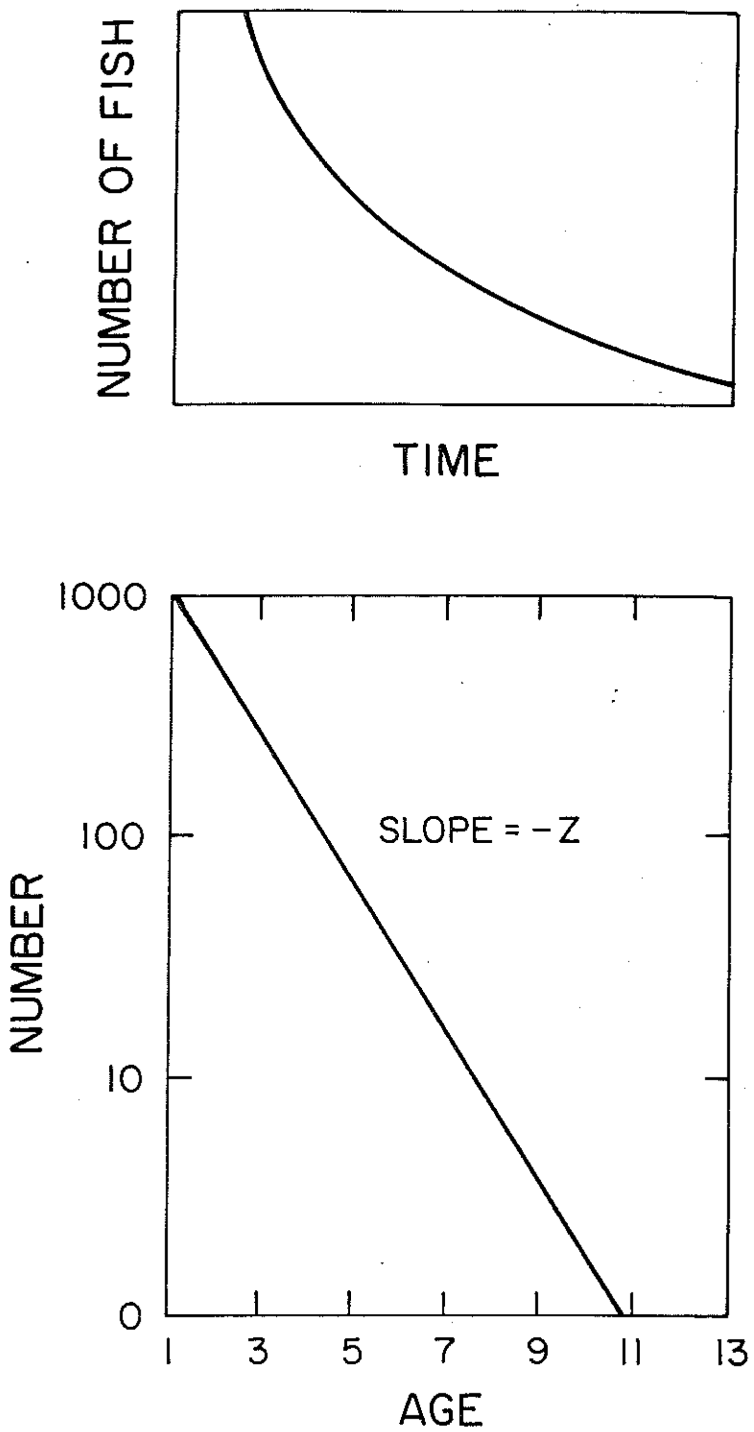

Figure IV-1: Upper - Relationship of the number of fish with time. Lower - Age-frequency distribution resulting from 50% survival and constant recruitment of 1,000 individuals per year (from Everhart, Eipper, and Youngs, 1975).

The instantaneous rate of fishing mortality (F) is proportional to the amount of gear or the effort expended (f). If q is a constant, then:

$$F = q\ f$$

When fishing and natural mortality are distributed proportionately over the year, F might also be calculated by:

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

For these models we assume that the catchability coefficient (q) is constant for fish between age at first capture (t_o) and the end of the life span, and that fishing effort (f) 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 large and small fish are distributed differently and also because of size selection inherent in gear; i.e., the larger the mesh, the larger and older the fish at the time of first 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. Fishing where the density of fish 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 instantaneous rate of natural mortality (M) at any time depends on the number of fish present, such that:

$$dN/_{dt} = -\ M\ N$$

Natural mortality 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.

It is often assumed that the rate of natural mortality is constant. If so, the maximum life-span of a cohort 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 the natural mortality rate, there is also the possibility of its changing suddenly at one or more stages during the life of a cohort. Intrinsic differences in the susceptibility to mortality factors leads to the tendency for more vulnerable individuals to die first, causing a decrease in the rate of natural mortality with age as only the more hardy survive (Beverton and Holt 1957).

Estimating Instantaneous Mortality Rate

Instantaneous mortality may be calculated by two approaches: (1) successive ages; and (2) catch curves.

Estimating Mortality Rate (Z) by Successive Ages

An estimate of Z can be determined based on the derivation of the instantaneous mortality rate ($Z = -\ln S$). If we have estimates of the average abundance of fish over some time interval:

$$N_t \text{ and } N_{t+1}$$

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

$$S = \frac{N_{t+1}}{N_t}$$

Either actual or relative abundance estimates may be used in calculations. The population is assumed to be in a steady state (both recruitment and mortality are constant). An example of the computation of S from fin whale "age composition" data is as follows (after Ricker 1975):

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,

$N_t = 24.1$ and $N_{t+1} = 14.1$

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

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 Instantaneous Mortality Rate (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 (S) has to be examined (Ricker 1975). A series of catches per unit effort ($^C/_f$) plotted against time form a catch curve (Figure IV-2). A catch curve is characterized by an ascending arm of incompletely recruited age classes. On a logarithmic scale, the descending arm of a catch curve is usually a straight line with a slope equal to -Z.

A catch curve provides 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).

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 1 and at that age's corresponding mean length on curve 2. This method of computation suffers from a serious limitation: it is useful only where the increase in the length of a fish is a constant number of units per year (Ricker 1975).

Very rarely do we have estimates of the actual abundance of fish at discrete points in time, nor will Z remain constant. To assume that $^C/_f$ is an index of abundance (N) is equivalent to assuming that the total amount of effort (f) is an index of F. While in some fisheries, fluctuations

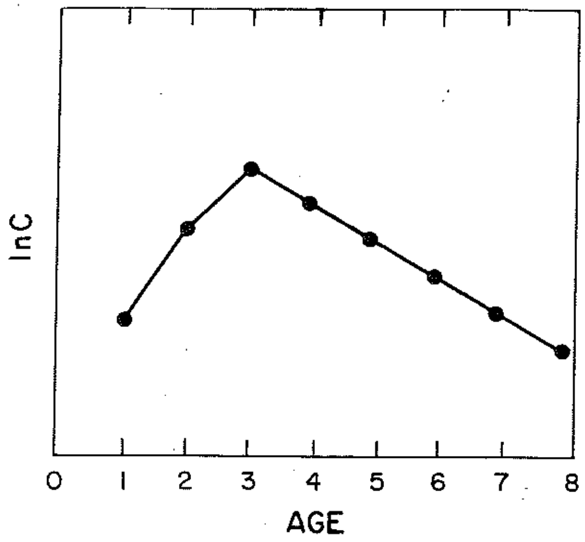

Figure IV-2. Catch curve. Ascending arm represents incompletely recruited age classes; descending arm represents fully recruited age classes.

in catches per unit effort may follow precisely fluctuations in abundance, very often the major cause of 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 left leg and a narrow sharp dome are the result of recruitment occurring over few age groups.

Straightness of the right limb of a catch curve indicates a uniform survival rate of 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 1948, Royce 1972).

The effort used in a fishery can vary from year to year; similar changes in the rate of natural mortality may also occur at times. The effects of these changes are graphically represented in Figure IV-3. Curve 1 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 2. 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 3 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. Curve 4 is from the new, balanced population, having existed for 18 years at the lower survival rate. The curve is similar to 1, but with a steeper slope (Ricker 1948, 1975).

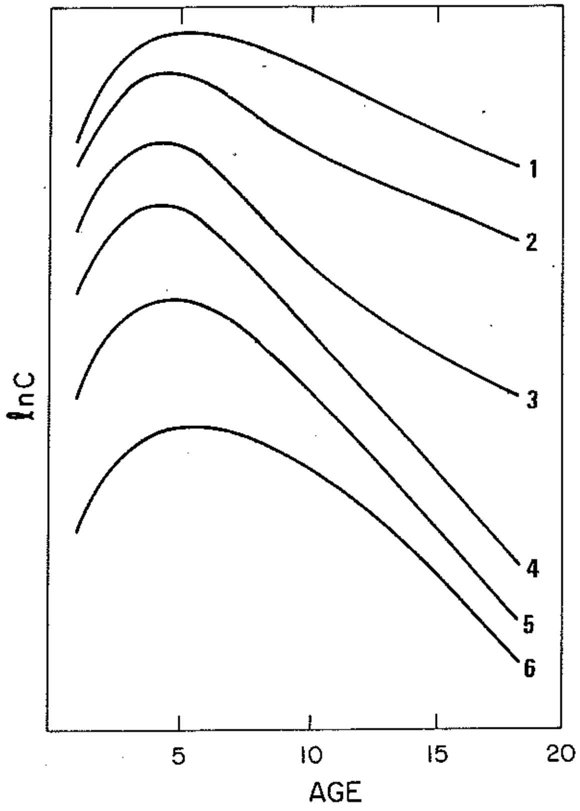

Figure IV-3. Catch curves illustrating changes in rate of fishing with time. In every instance recruitment is complete following the first six ages shown, and the instantaneous rate of natural mortality is the same for all ages and years. [1 = constant rate of fishing. 2 = rate of fishing has increased during the preceding six years. 3 = five years after 2, with rate of fishing stabilized. 4 = balanced curve for a constant rate of fishing. 5 = rate of fishing has decreased during the preceding six years. 6 = five years after 5, with rate of fishing stabilized (from Ricker 1948, 1975).]

In curves 1 through 4, fishing mortality (F) was increasing, and with constant natural mortality (M), total mortality (Z) increased also. These circumstances might commonly describe the initial exploitation of a fish population. With development the catch will begin to decrease, so, if F decreases with M remaining constant, Z will decrease also. This is the situation which produced curves 5 and 6, where the quantitative changes are the same as for 2 and 3, but in an opposite direction. The outer limb of 5 represents the former survival rate, again exhibiting a time lag. Curve 6, from catch data eleven years after the increase in survival rate, and five years under constant such survival, estimates with its outer end, again the former survival rate. This curve has no current estimate of the survival rate for it has no inflection point (Ricker 1948, 1975).

In summary, changes in the instantaneous rate of fishing mortality result in curved right limbs of the catch curve, convex when F decreases, and concave when F increases. The point of maximum slope on the right arm provides an estimate of current survival rate, though subject to a time lag (Ricker 1948, 1975).

Estimating Instantaneous Rate of Fishing Mortality (F)

Instantaneous rate of fishing mortality (F) and exploitation rate (E) are related in the following way when fishing and natural mortality are distributed proportionately with the year:

$$\frac{F}{Z} = \frac{E}{A}$$

Given an estimate of E, F can be calculated. Exploitation rate (E) can be derived in two basic ways.

1. Estimating Exploitation Rate (E) by Catch and Abundance data

By definition, the following relationship holds true:

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

where

C = catch

N = abundance

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 density of fish in the fished area should be greater then the average density, leading to an underestimate of the fishing mortality (Gulland 1973).

2. Estimating Exploitation Rate (E) with Tagging Data

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

then $E = \frac{r}{m}$

This method assumes no natural mortality nor losses of the the marked population of any kind (Beverton and Holt 1957, Gulland 1973).

Estimating Instantaneous Rate of Natural Mortality (M)

The instantaneous rate of natural mortality is nearly always estimated as 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, but this is the rare case.

Changes in Z can be related quantitatively to changes in fishing effort (F):

$$\begin{array}{ll} \text{if} & Z = F + M \\ \text{and} & F = q\ f \\ \text{then} & Z = qf + M \end{array}$$

If q is constant, then M changes with changes in f and Z. A plot of Z against f produces a line whose slope is q and intercept M (Figure IV-4) (Gulland 1972, Royce 1972). A time lag is possible, allowing for the estimation of some previous natural mortality rate when using values of two successive year-classes at a 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).

An approximation of the value of the rate of natural mortality can be gauged from the growth pattern of the species concerned. Fish which approach their ultimate length quickly are likely to have a high natural mortality rate, whereas fish which grow slowly are likely to have a low natural mortality rate. This estimate is not precise, but is often most useful in the early stages of studying a fishery and in judging which cause of mortality (F or M) is likely to be the dominant element in total mortality (Gulland 1973).

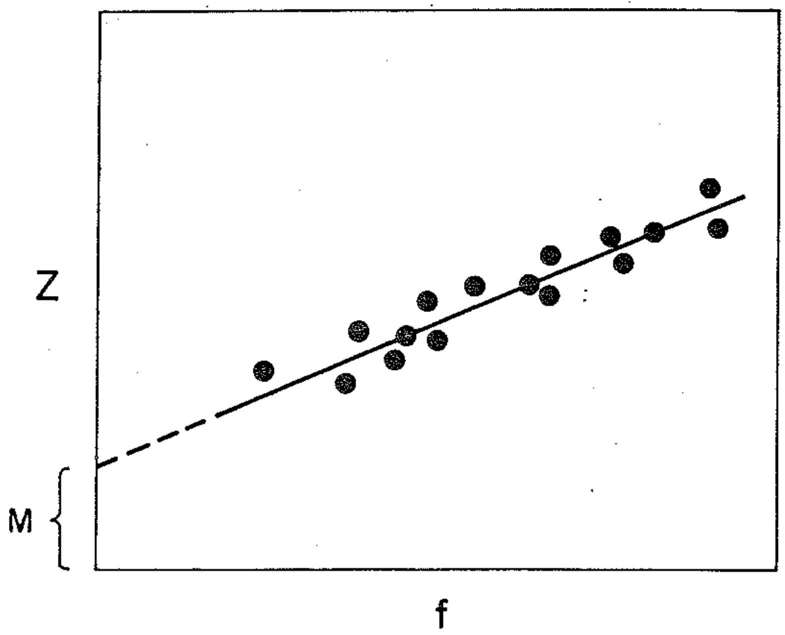

Figure IV-4. Total instantaneous mortality (Z) versus fishing effort (f) produces a line with a slope q and intercept M (instantaneous natural mortality).

Functional Value of E and F

Manipulating E is one of the most useful tools in fisheries management. When fishing and natural mortality are distributed proportionately within the year:

$$\frac{F}{Z} = \frac{E}{A}$$

A manager could conceivably adjust E and then predict the effect on F. And since

$$F = qf \quad \text{when } q \text{ is constant}$$

fishing pressure (f) could be adjusted to provide the desired level of fishing mortality (F).

Causes of Mortality

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 (Paling 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 critical stage may coincide with the exhaustion of the yolk-sac when the larvae, for the first time, become dependent on their 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 unwell 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 (Paling 1968). This is especially true when man is considered to be the 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. While most fish bear parasites, it is usually when fish become influenced by unfavorable environmental conditions or subjected to physical damage that the activities of 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 (Paling 1968).

There are many substances and a wide range of conditions which are known to cause pollution. Sources include industry, agriculture, and mining. Fish mortalities due to population usually result from sudden discharge of one or more toxic substances into 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, Paling 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 under-nutrition, unfavorable environmental conditions, loss of condition following spawning, social stress, and others (Paling 1968).

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

Further Reading

Backiel, T., and E. D. Le Cren. 1967. Some density relationships for fish population parameters. Pages 261-293 in S. D. Gerking (ed.) The biological basis of freshwater fish population. Blackwell Scientific Publications, Oxford.

Beverton, R. J. H., and S. J. Holt. 1957. On the dymanics of exploited fish population. Her Majesty's Stationery Office, London. 533 p.

Everhart, W. H., A. W. Eipper, and W. D. Youngs. 1975. Principles of fishery science. Cornell University Press, Ithaca. 288 p.

Gulland, John A. 1972. Population dynamics of world fisheries. University of Washington, Seattle. 336 p.

________________. 1973. Manual of methods for fish stock assessment. Part 1. Fish population analysis. F.A.O., Rome. 154 p.

Krebs, C. J. 1972. Ecology. Harper and Row, New York. 694 p.

Murphy, Garth I. 1966. Population dynamics and population estimation. Pages 1-17 in Alex Calhoun (ed.). Inland fisheries management. Department of Fish and Game, State of California. 546 p.

Odum, E. P. 1971. Fundamentals of ecology. 3rd ed. W. B. Saunders Company, Philadelphia. 574 p.

Paling, John E. 1968. Causes of mortality. Pages 226-235 in W. E. Ricker (ed.) Methods for assessment of fish population in fresh waters. Blackwell Scientific Publications, Oxford, England.

Regier, H. A., and D. S. Robson. 1967. Estimating population number and mortality rates. Pages 31-66 in S. D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Ricker, W. E. 1948. Methods of estimating vital statistics of fish populations. Sci. Series No. 15, Indiana University. Bloomington, Indiana. 101 p.

_____________. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of the Fisheries Research Board of Canada. Ottawa. 382 p.

Royce, W. F. 1972. Introduction to the fishery sciences. Academic Press, New York. 351 p.

CHAPTER FIVE

GROWTH*

Concepts

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 different 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.

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The importance of growth estimates in population dynamics is evident. Growth rate affects when fish first breed (maturity), age composition of the stock (recruitment into the stock), 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 a theoretical maximum length, ℓ_∞. 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_∞. These changes in size of fish have been expressed in three ways:

1. Absolute Growth

Absolute growth rate is the increment in growth over a given year:

$$\ell_2 - \ell_1 \text{ or } w_2 - w_1$$

where w_1 and w_2 = weight at time t=1 and t=2

ℓ_1 and ℓ_2 = length at time t=1 and t=2

2. Relative Rate of Increase

The relative rate of increase in fish size is the proportional increase (usually expressed as a percent) over a given year:

$$\frac{\ell_2 - \ell_1}{\ell_1} \text{ or } \frac{w_2 - w_1}{w_1}$$

3. Instantaneous Rate of Increase

The instantaneous rate of increase in fish growth is:

$$\ln \ell_2 - \ln \ell_1 \text{ or } \ln w_2 - \ln w_1$$

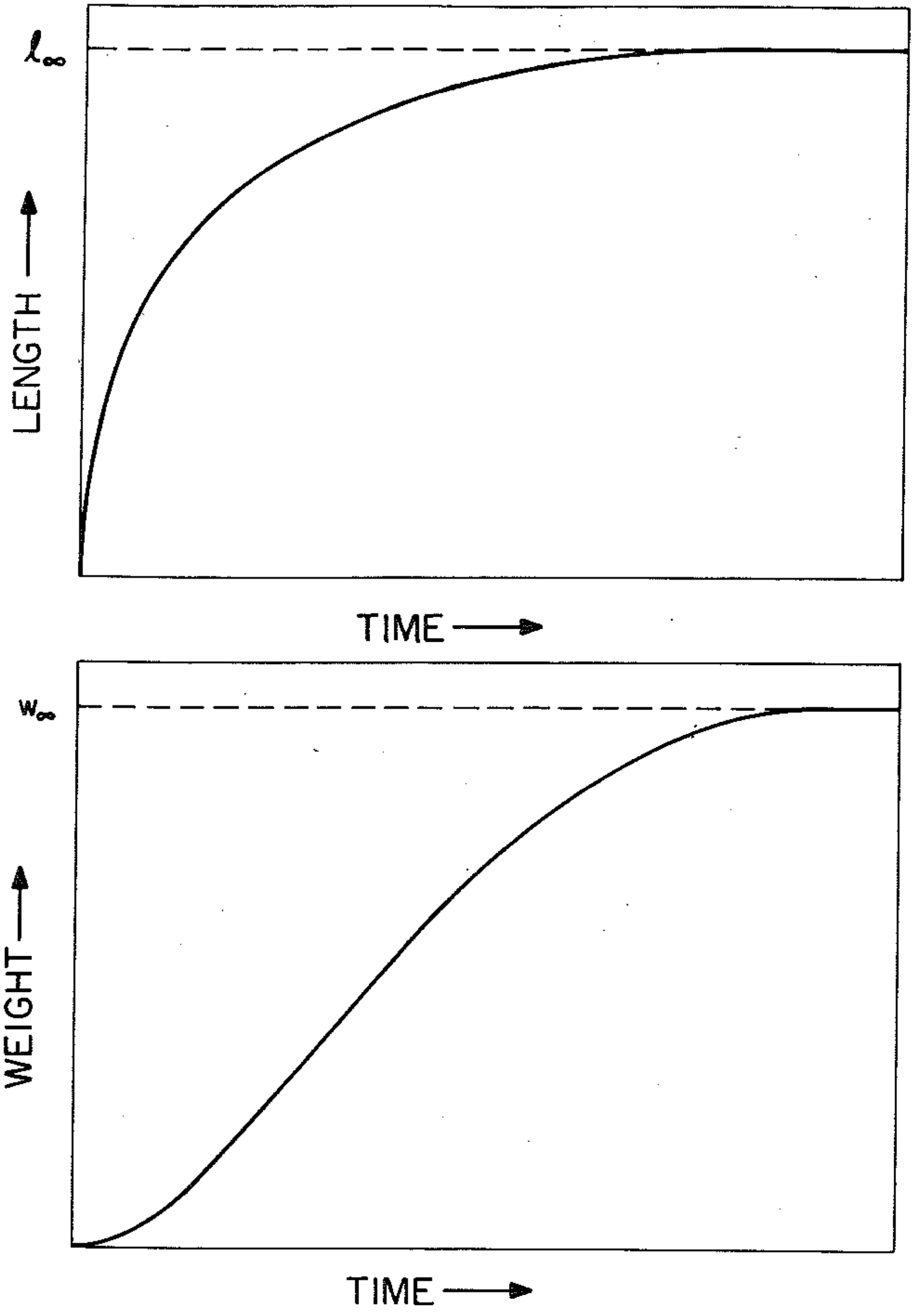

Figure V-1. (a) Growth in fish length plotted against time. [ℓ_∞ = maximum length attainable]

(b) Growth in fish weight plotted against time. [w_∞ = maximum weight attainable]

Weight of fish varies as a power of length:

$w = \alpha \ell^{\beta}$, where α and β are constants.

If the value of β is equal to three, the growth is said to be isometric; otherwise it is allometric. Isometric growth would indicate a fish having constant body form and specific gravity. Allometric growth is indicated by β greater or less than 3 and implies that body form does change with the length of the fish.

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 structures.

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

$$\ell_x = \ell_y \frac{T_x}{T_y}$$

where ℓ_x = length of fish at age x

ℓ_y = length of fish at present age

T_x = length of scale to annulus x

T_y = length of scale to present edge (present age)

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. 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 fish or population may be compared to others by use of the condition factor, or coefficient of condition, CF, where CF = w/ℓ^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 have little predictive value. The more sophisticated models require large amounts of and are called upon to forecast possible changes in fish populations 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. 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 as reasonable as possible. 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 length or weight of fish at a future point in time. This model expresses change in length, ℓ_t, over time as a function of the maximum length, ℓ_∞, and a growth coefficient, K. The equation is most commonly stated as:

$$\ell_t = \ell_\infty[1-e^{-K(t-t_o)}],$$

Assuming isometric growth, the growth equation stated in terms of weight (w_t) is:

$$w_t = w_\infty[1-e^{-K(t-t_o)}]^3$$

Values for K, ℓ_∞(or w_∞), and t_o may be obtained by plotting length at t+1 (y axis) against length at t (x axis) for each successive age (Fig. V-2) (Walford 1946).

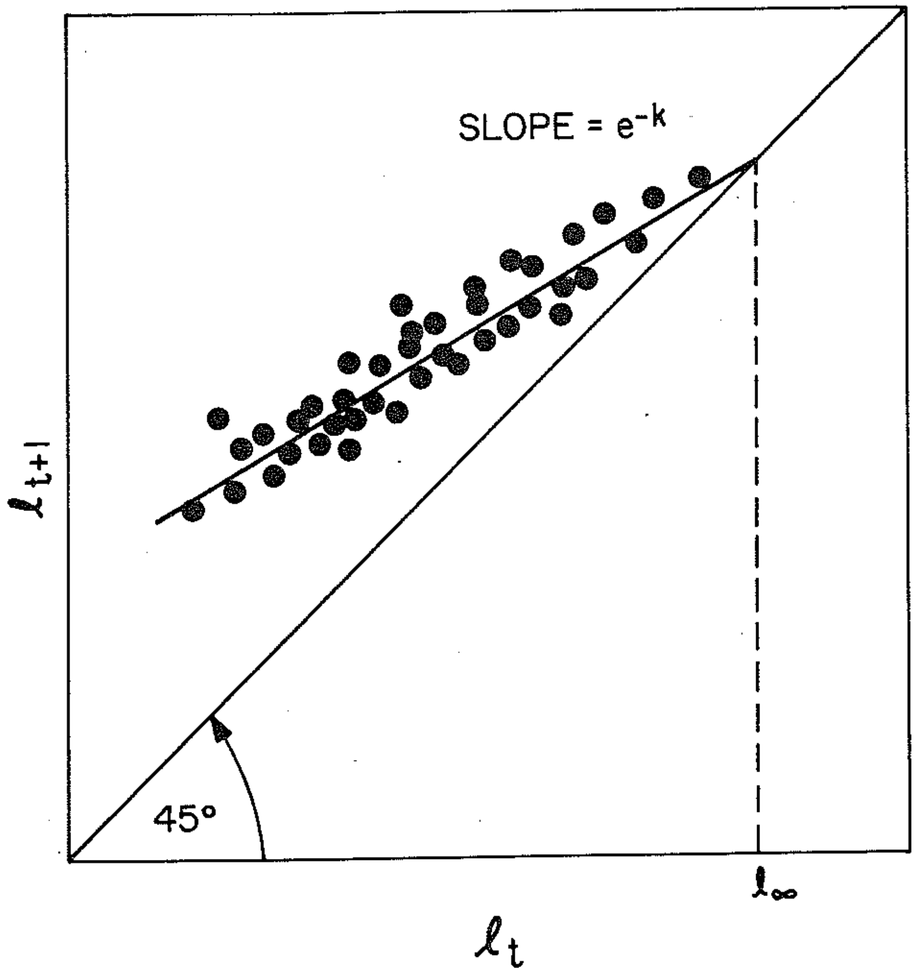

Figure V-2. Walford plot of annual increment in fish length. Length at time t plotted against length at time t + 1 [ℓ_∞= maximum length attainable]. The 45° line indicated the line of equality between ℓ_t and ℓ_{t+1}.

Taking the natural log of the von Bertalanffy equation and rearranging

$$\ell_t = \ell_\infty [1-e^{-K(t-t_o)}]$$

$$\ln \ell(\ell_\infty - \ell_t) = \ln \ell_\infty + Kt_o - Kt$$

which may be plotted and should form a straight line. Plotting the natural log of $\ell_\infty - \ell_t$ against age t (Fig. V-3), provides a slope of -K and an intercept (α) equal to $\ln\ell_\infty + Kt_o$. A value of ℓ_∞ 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_o:

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

Other mathematical descriptions of growth have been developed. For a review of these techniques refer to Ricker (1975) or Gulland (1969).

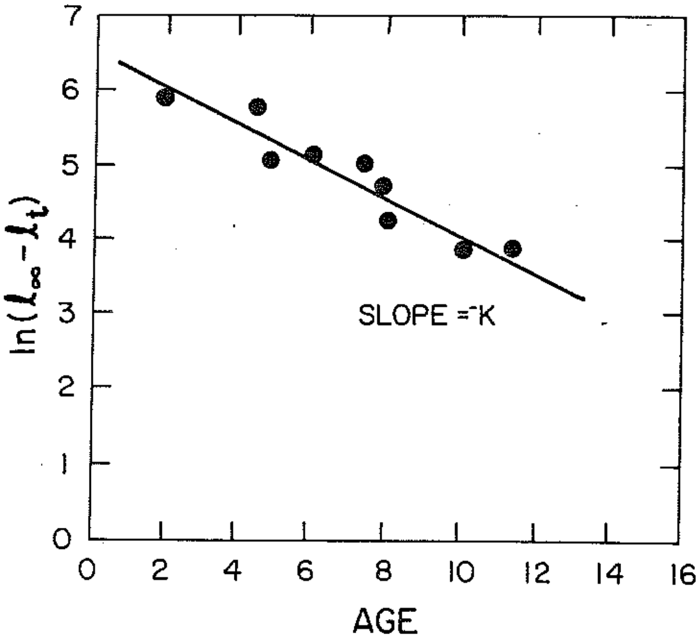

Figure V-3. Plot of $\ln(\ell_\infty - \ell_t)$ against age in years. Line shows fit of ℓ_∞ and K for the von Bertalanffy growth equation.

The questions 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 rate at a certain fish size or to advertise for commercial angling, then it may be necessary to estimate the size and rate of growth of individuals in 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 fishing pressure on a possibly under-exploited population. 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 analyses 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 ℓ_∞, as well as K and t_o, 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. However, even though the analytical capability is very sophisticated, the fisheries analyst should always carefully select the conceptual model most appropriate to the problem at hand.

Further Reading

Abramson, N. J. 1971. Computer programs for fish stock assessment. FAO (Food Agric. Organ, U.N.) Fish. Tech. Pap. 101:1-154.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10(2):181-213.

Coble, D. W. 1966. Dependence of total annual growth in yellow perch on temperature. J. Fish. Res. Bd. Can. 23(1):15-20.

Gerking, S. D. 1965. Two computer programs for age and growth studies. Prog. Fish-Cult. 27(2):59-66.

Hile, R. 1970. Body-scale relation and calculation of growth in fishes. Trans. Am. Fish. Soc. 99(3):468-474.

Menshutkin, V. V., and Y. U. Kislyakov. 1967. Modeling of a population of commercial fish with calculation of the variable growth rate. Zool. Zh. 46(6):805-810. Dist. by Div. Fish. Res., Bur. Sport Fish. and Wildl., Washington.

Paloheimo, J. E., and L. M. Dickie. 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Bd. Can. 22(2):521-542.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191:382 p.

Stevens, W. L. 1951. Asympototic regression. Biometrics 7(3):247-267.

Walford, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90(2):141-147

Weatherley, A. H. 1972. Growth and ecology of fish populations. Academic Press, Inc., London. 293 p.

CHAPTER SIX

RECRUITMENT*

Recruitment is typically defined as the addition of new members to the population 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 that portion of the population open to 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.

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 for fisheries managers. As the annual

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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 (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.

A number of factors affect recruitment, including size of the spawning stock, environmental factors, predation, and competition. These factors can be categorized as either <u>density-independent</u> or <u>density-dependent</u>. Density-independent factors act in a manner unrelated to population level. Pollution, floods, and water temperature act independent of population level. A fisheries manager must often handle these as probabilistic or stochastic events. Density-dependent factors are related to population level or ecological interrelationships. Competition, predation, and disease may be related to population level and can be considered density-dependent factors. The desire and need to know the structure and function of the recruitment process, especially for improving predictive capabilities, has led to development of stock-recruitment models.

Ricker Model

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. For this condition to exist, the population must be under some natural controls. Ricker (1954) hypothesized this regulator to be density-dependent mortality which had its major impact during the early life stages of the individual fish. No such regulator is pronounced in the adult stages, although growth rate probably does change somewhat as a density-dependent function. Regulatory mortality acts as a compensatory mechanism, with greatest effect at high population levels and little effect at low population levels. Such compensatory mechanisms might include prevention of breeding due to a limited number of breeding sites; 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 (Blaxter 1969); or predation on immature fish (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 density-independent 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:

$$R/R_r = P/P_r \quad e^{(P_r/P_m)\,(1-P/P_r)}$$

where:

R = recruitment
R_r = recruitment at the replacement point of stock, P_r
P = stock
P_m = the stock at which maximum recruitment is found
$P_r = R_r$ (by definition)

If $\alpha = (P/P_r)$ and $\beta = (P_r/P_m)$, then the expression may be rewritten,

$$P/P_r = \alpha\ e^{\beta(1-\alpha)}.$$

The 45° bisector in Figure VI-1 is significant because 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 often 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 salmon 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 once.

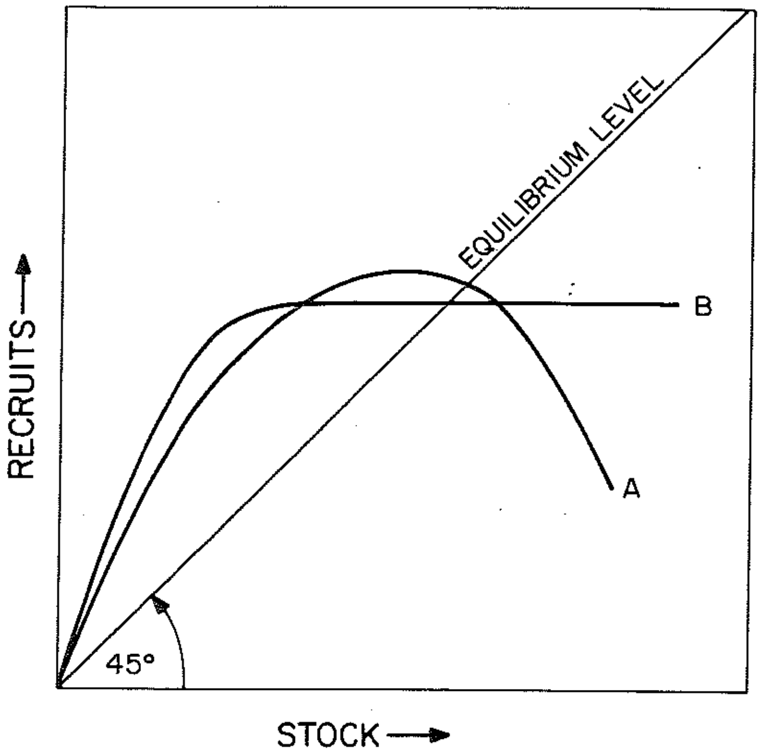

Figure VI-1. The two classical stock-recruitment curves: A, the Ricker curve; and B, the Beverton-Holt curve.

Beverton-Holt Model

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

$$^{dN}/_{dt} = (u_1 + u_2N)N$$

where.

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 asympotic (Fig. VI-1) rather than domed, as in the Ricker curves. The former imply that recruitment is in equilibrium with 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 density-independent 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 (see next page).

Using the mutiple regression model

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

a prediction of R and a measure of the variance accounted for by the three independent variables can be computed. Extensive data are required in order to apply regression techniques.

Year	Bass Recruitment	Stock Size	Day Water Reached 65°F	Crappie Stock Level
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

Limitations of Classical Models

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. 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 than when new recruit spawners predominate the egg producers. Thus, high stock numbers is no reproductive safeguard because 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; 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 magnitude (e.g. some herring) (Cushing 1973). Year to year differences in environment characteristics may result in reproduction fluctuations much greater than any associated with variations in stock density.

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 age-classes, 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 sudden and dramatic changes in recruitment in some stocks, and the inability to predict changes mediated by environmental influences led Cushing 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 smallmouth bass, walleye, and northern pike (Clepper 1975). 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 might be observed to exert their influence on recruitment through alteration in the amplitude and timing of freshwater production cycles to the critical period of larvae feeding and growth.

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 large sized prey, from insects to fish and crayfish. High larval mortalities linked to reduce growth as a result of reduced food availability have often been reported (Hassler 1970, Clepper 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). For this reason, estimates of larval or fry abundance by seining or trawling often yield a high correlation with year-class strength.

Variations in year-class strength for a given species may extend to all of the lakes or streams in one geographical area and such variations may also extend over several fish families within any one water body. This suggests that some general meterological phenomenon might be the controlling factor, again, 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.

Further Reading

Backiel, T., and E. B. LeCren. 1967. Some density relationships for fish population parameters. Pages 261-293 in S. D. Gerking (ed.). The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Bennett, G. W. 1970. Management of lakes and ponds. Van Nostrand Reinhold Co., Cincinnati. 375 p.

Blaxter, J. H. S. 1969. Development: eggs and larvae. Pages 177-252 in W. D. Hoar and D. J. Randall (ed.). Fish physiology. III. Reproduction and growth, bioluminescence, pigments, and poisons, Academic Press, New York.

Clepper, H. (ed.). 1975. Blackbass biology and management. Sport Fishing Institute, Washington, DC. 534 pp.

Cushing, D. H. 1968. Fisheries biology. University of Wisconsin Press, Madison. 200 p.

_______________. 1973. Recruitment and parent stock in fishes. Washington Sea Grant Program and University of Washington, Seattle. 197 p.

________________. 1974. The possible density dependence of larval mortality and adult mortality in fishes. Pages 103-111 in J. H. S. Blaxter (ed.). The early life history of fishes. Springer-Verlag, Heidelberg.

Everhart, W. H., A. W. Eipper, and W. D. Youngs. 1975. Principles of fishery science. Cornell University Press, Ithaca. 288 p.

Gulland, J. A. 1967. The effects of fishing on the production and catches of fish. Pages 399-415 in S. D. Gerking (ed.). The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

________________. 1974. The management of marine fisheries. University of Washington Press, Seattle. 198 p.

Hassler, T. F. 1970. Environmental influences on early development and year-class strength of northern pike in Lakes Oahe and Sharpe, South Dakota. Trans. Am. Fish. Soc. 99(2):369-375.

Maloney, J. E., and F. H. Johnson. 1955. Life histories and interrelationships of walleye and yellow perch, especially during their first summer in two Minnesota lakes. Trans. Am. Fish. Soc. 85:191-202.

Ponomarkenko, V. P. 1973. On a probable relation between age composition of spawning stock and abundance of the year-classes of cod in the Barents Sea. Pages 69-76 in B. B. Parrish (ed.). Fish stocks and recruitment. Rapp. Proc. Verb. Cons. Int. Explor. Mer. 164.

Priegel, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. Wisc. Dept. Nat. Res. Tech. Bull. #45, Madison. 105 p.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11(5): 559-623.

________________. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191, 382 p.

Slobodkin, L. B. 1973. Summary and discussion of the symposium. Pages 7-14 in B. B. Parrish (ed.). Fish stocks and recruitment Rapp. Roc. Verb. Cons. Int. Explor. Mer. 164.

Summerfelt, R. C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 295-305 in H. Clepper (ed.). Black bass biology and management. Sport Fishing Institute, Washington, D.C.

CHAPTER SEVEN

PREDICTING YIELD*

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 usually have higher predictive power and provide greater insight into the dynamics of a population, but require more data. Model selection is, therefore, of primary importance because it determines the data requirements.

A useful and reliable yield prediction model must 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 uncertainty. Model formulation should ideally 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 understood populations. Certain management situations demand that only the approximate magnitude of change in 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 collecting insufficient or superfluous data. It is important that the selected model fulfills the

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stated management objectives, and that the model chosen is the simplest alternative which meets these objectives. 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 practices. Yield models can be grouped into five categories: (1) 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) 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) 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) trophic dynamic models, which elucidate trophic level interactions by use of functional notation and the simultaneous solution of sets of resulting differential equations; and (5) multidisciplinary multi-stage decision models, which extend yield predicting capabilities of management to allocating of catch and maximizing 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 structure, 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 a complex system. When only a minimum amount of data are 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 be determined with statistical reliability, including the potential yield.

Fish production (or yield) is affected by three environmental influences: morphometric, edaphic, and climatic conditions. Thus, physical characteristics, such as lake area, mean depth, maximum depth, flushing time, and shoreline development; physicochemical characteristics, such as total dissolved oxygen level 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 in production.

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 morphoedaphic index are: (1) relatively homogeneous climatic conditions; (2) fairly constant ionic rations; (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 homogeneous 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 decisions and planning. In commercial fisheries, such as Lake Nasser, a more gradual and deliberate succession of exploitation can be accomplished by using the morphoedaphic model as a first approximation technique.

The morphoedaphic index constitutes a yield 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 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_1

P_1 = Total biomass of stock at t_o

R = Addition of biomass from recruitment

g = Addition of biomass from growth

m = Loss of biomass from natural mortality

C = Biomass of the annual catch

Factors which affect the level of a population are highly interdependent. The surplus yield model provides an adequate summary 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 with catch per unit effort data used to estimate stock size and instantaneous fishing mortality rate measured by total fishing effort (Schaefer 1954). This model formulation requires a long series of such catch and effort data, but 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 surplus yield model is based on 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. 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 (P_∞ and often defined as "carrying capacity").

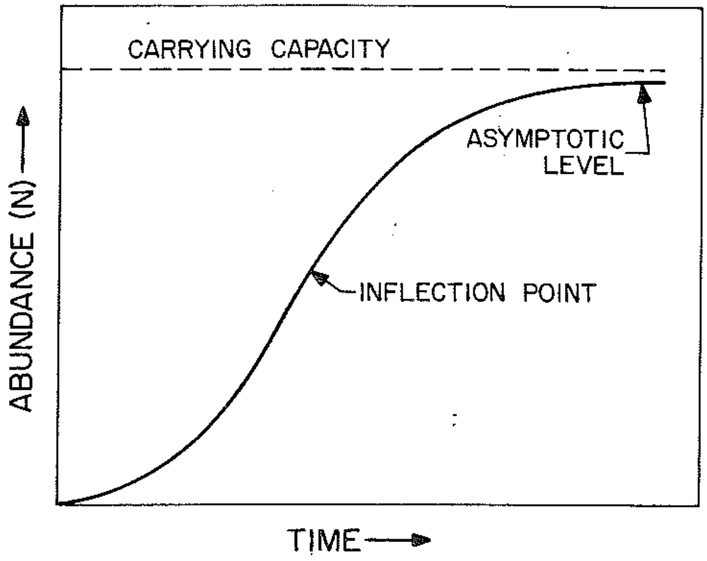


Figure VII-1. Sigmoid growth curve of abundance (N) versus time, the basis of the surplus yield model.

Yield from a fish population is a function of the population abundance and total fishing effort; therefore, under equilibrium conditions population size is a function of effort (Fig. VII-2). The highest yield occurs where the slope equal zero on the logistic curve, which corresponds to a population size one-half that of the original, unexploited stock. Further increases in fishing effort product a decrease in equilibrium yield, and a condition of overfishing.

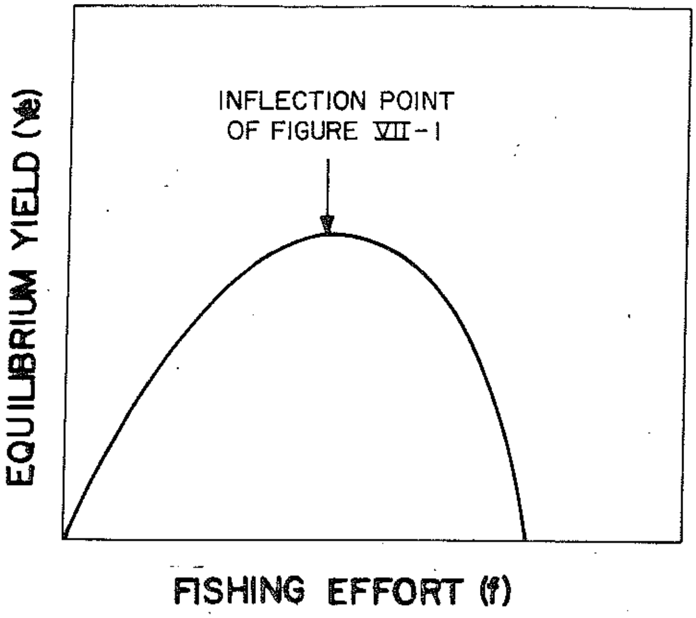


Figure VII-2. Equilibrium yield versus effort.

The assumptions inherent in the logistic model are: (1) population abundance is the only factor causing variation in the annual natural rate of population increase; (2) all fundamental rate parameters of the population can be combined to produce a simple functional relationship between the rate of stock 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 level; and (6) a symmetrical relationship exists between yield and effort (i.e., catchability is constant). The first four assumptions form the basic framework under which the model was developed, provide the logic for the simplicity of the model, and are often reasonable first approximations of a complex ecosystem. Many modifications of the surplus yield model have been developed. These modifications are based on different shapes of the growth curve described in Figure VII-1. The reader is referred to Fox (1970), Gulland (1972), or Ricker (1975) for further descriptions.

Surplus yield models are particularly valuable in the early stages of an investigation 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. 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 would be 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, therefore, an expression of yield, which is proportional to the total potential yield from the stock, and no attempt is usually 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

N = the number of fish in the stock

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 that (1) fish die once and only once, and (2) 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 relationships of growth, mortality, and recruitment to abundance can be described by 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 because it permits realistic simulation of growth and mortality when these cannot be expressed as simple functions of age. 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 pressure and age at entry into the stock. The Ricker model, 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. For example, 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 expressed as mathematical functions, which are integrated over all age classes. Chapter 9 provides a more detailed description of the mathematical development of the stock-recruitment relationship.

Trophic Dynamic Models

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

The degree of model complexity required to establish and express basic interrelationships of any ecosystem requires that simpler models (surplus yield, dynamic pond, etc.) should first be explored and evaluated before proceeding to more elaborate models typical of the trophic dynamic approach. Many empirical values of coefficients for complex models cannot be approximated with current knowledge and many mathematical equations are at best only crude approximations of the behavior of aquatic ecosystems. For example, 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 insight into the system's behavior, and, at times, in a reliable empirical model.

As in most modeling efforts, ecosystem components should 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-assisted procedures. Lackey and Zuboy (1975) constructed a simple model which accounted for interspecific competition and predation based on the spawning sequence of three fish species. This model used species interrelationships to create a set of differential equations. Walter and Hoagman (1971) developed a general multi-species model which could be used on the Great Lakes and could account for as many variables as the user wanted to consider. Plant et al (1973) modeled the biological, physical, and management components of the Cayuga Lake fishery. Effects of various fishing rates were then examined by varying instantaneous fishing mortality rate. 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. Currently, the primary advantages of trophic dynamic models are to identify data needs and guide future studies, and to provide insights into the processes of the ecosystem. Chapter 9 provides a more detailed example of the mathematical development necessary to develop trophic dynamic models.

Multidisciplinary Decision Models

This final group of models is aimed at extending the yield predicting capabilities of management to allocating catch, maximizing value, and in general, achieving any specific management objective. These models merge economic factors with the biological factors controlling 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. Multidisciplinary decision 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 generally apply best to single species fisheries as found in marine fisheries and only sometimes in freshwater.

Further Reading

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Min. Agric. Fish and Food (U.K.) Fish Invest. Ser. II 19, 533 p.

Fox, William, W., Jr. 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99(1):80-88.

____________________. 1971. Random variability and parameter estimation for the generalized production model. Fish. Bull. 69(3):569-580.

Gulland, John A. 1972. Population dynamics of world fisheries. Washington Sea Grant Program, Univ. of Wash. - Seattle, 336 p.

____________________, and L. K. Boerema. 1973. Scientific advice on catch levels. Fish. Bull. 71(2):325-335.

Jensen, A. L. 1973. Relation between simple dynamic pool and surplus production models for yield from a fishery. J. Fish. Res. Bd. Can. 30:998-1002.

Lackey, Robert T., and James R. Zuboy. 1975. A computer simulation model of a multispecies centrachid population complex. Va. J. Sci. 26(1):13-19.

Parrish, James D. 1975. Marine trophic interactions by dynamic simulation of fish species. Fish. Bull. 73(4):695-716.

Paulik, G. J., and W. H. Bayliff. 1967. A generalized computer program for the Ricker model of equilibrium yield per recruitment. J. Fish. Res. Bd. Can. 24(2):249-259.

Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock production model. Inter-Amer. Trop. Tuna Comm. Bull. 14:421-496.

Plant, R., R. Lance, and W. D. Youngs. 1973. Computer simulation of trophic level interrelationships in Cayuga Lake. Cornell Univ. Water Res. Mar. Sci. Center, Tech. Rep. 69, 26 p.

Rawson, D. S. 1952. Mean depth and the fish production of large lakes. Ecology 33:513-521.

Ricker, W. E. 1958. Maximum sustained yields from fluctuating evironments and mixed stocks. J. Fish. Res. Bd. Can. 15(5):991-1006.

______________. 1975. Computation and interpretation of biological statistics of fish populations. Information Canada, Ottawa, Canada, 382 p.

Rothschild, Brian J., and James W. Balsiger. 1971. A linear programming solution to salmon management. Fish. Bull. 69(1):117-140.

Ryder, R. A. 1965. A method for estimating the potential fish production of North-temperate lakes. Trans. Am. Fish. Soc. 94(3):214-218.

______________, S. R. Kerr, K. H. Loftus, and H. A. Reiger. 1974. The morphoedaphic index, a fish yield estimator - review and evaluation. J. Fish. Res. Bd. Can. 31(5):663-688.

______________, and H. F. Henderson. 1975. Estimates of potential fish yield for the Nasser Reservoir, Arab Republic of Egypt. J. Fish. Res. Bd. Can. 32(11):2137-2151.

Saila, Saul B., and James D. Parrish. 1972. Exploitation effects upon interspecific relationships in marine ecosystems. Fish. Bull. 70(2): 393-393.

Schaefer, M. D. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Amer. Trop. Tuna Comm. Bull. 1:27-56.

Silliman, R. P. 1971. Advantages and limitations of "simple" fisheries models in light of laboratory experiments. J. Fish. Res. Bd. Can. 28(8): 1211-1214.

Walter, G. G. 1973. Delay-differential equation models for fisheries. J. Fish. Res. Bd. Can. 30(7):939-945.

______________. 1975. Graphical methods for estimating parameters in simple models of fisheries. J. Fish. Res. Bd. Can. 32(11):2163-2168.

______________, and W. Hoagman. 1971. Mathematical models for estimating changes in fish populations with applications to Green Bay. 14th Conf. Great Lakes. Res. 170-184.

Walters, C. J. 1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98(3):505-512.

CHAPTER EIGHT

SYSTEMS ANALYSIS

Concepts

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 utilize 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 rate (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:

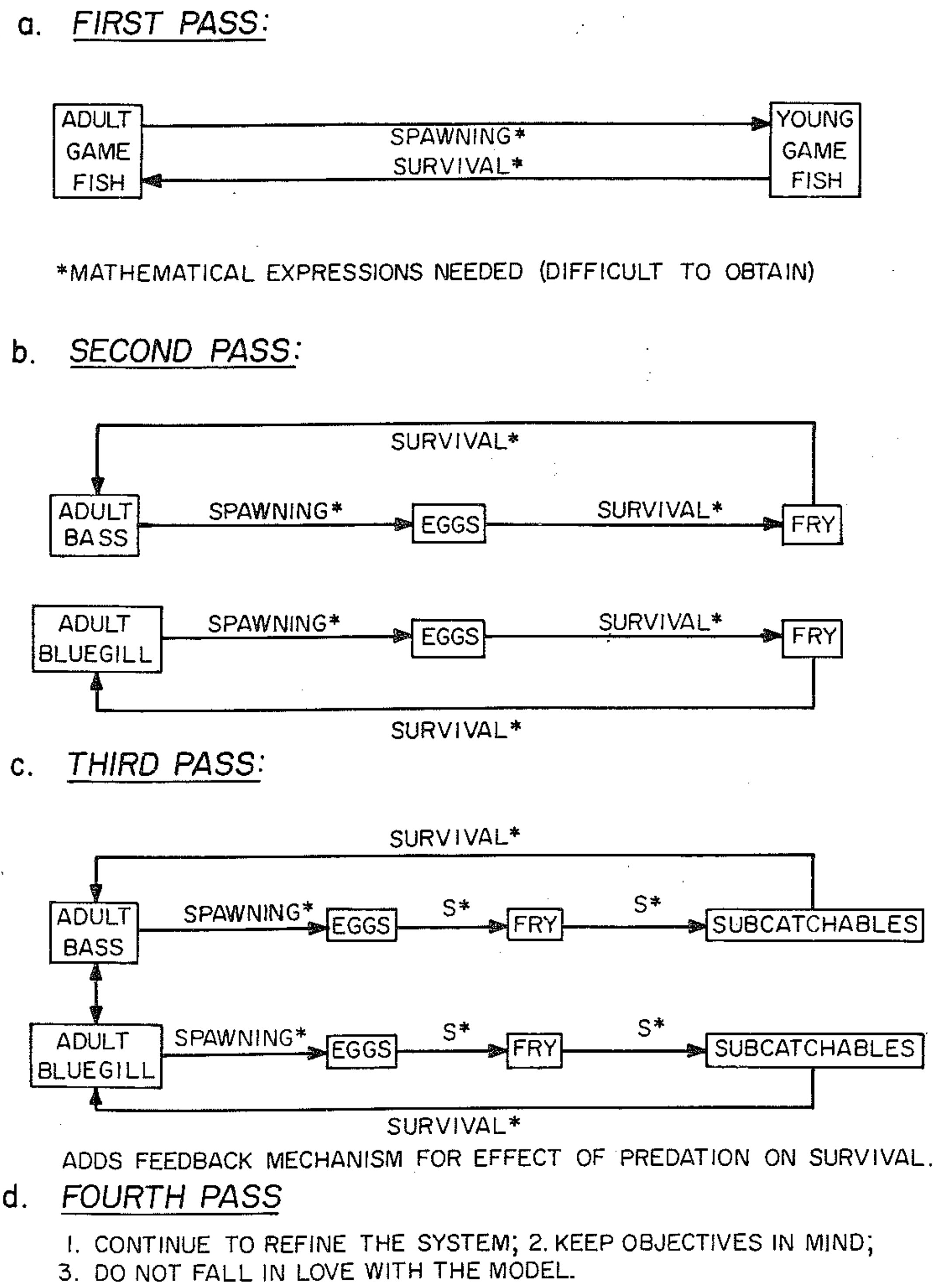


Figure VIII-1. Example of the steps in conceptualizing a model of the interaction between population levels of adult and young game fish.

Multiple Regression Analysis

Multiple regression analysis relates simultaneous changes in several independent variables (ecosystem components) to changes in a dependent variable (defined objectives). For example, the catch (C_t) 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:

C_{t-1} = Catch of year class i in year t-1

f_t = Fishing effort expended to catch all year classes in year t

f_{t-1} = Fishing effort expended to catch all year classes in year t-1

α, β, λ, and δ are regression coefficients; ε is "error"

Correlation Analysis

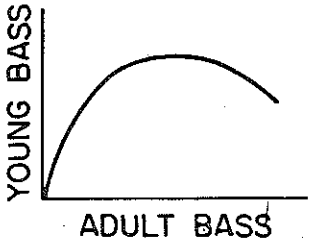
Correlation analysis differs from regression analysis in that the functional relationship of one variable to another is not considered. There is no distinction between dependent and independent variables in correlation analysis. Multiple correlation analysis measures the amount to which variables co-vary. 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 linear covariance is zero.

After the interrelationship 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 developed 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

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. The catch in biomass (C) could be described by the equation:

$$\frac{dC}{dt} = F\, N_t\, W_t$$

where:

W_t = Average weight of fish of age t
F = Instantaneous fishing mortality rate
N_t = Number of fish (age t) alive in a typical year class

continuing with the mathematical development

$$C_t = N_t\, W_t\, (A)^t\, \frac{F}{Z}$$

where,

A = Annual total mortality
Z = Instantaneous total mortality rate

This is an example of a rather simple model, but the mathematical interrelationships 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 handling 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 reducing 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 in solving 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 natural resource management, statistics, mathematics, and computer programming.

Coupled with the wide acceptance of systems analysis, natural 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 we can 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.

Computer Use

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 that 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 usage 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 computer-implemented 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 natural 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.

Further Reading

Gulland, John A. 1972. Population dynamics of world fisheries. Univ. Washington, Sea Grant Program, WSG 72-1, 336 p.

Patten, Bernard C. 1969. Ecological systems analysis and fisheries science. Trans. Amer. Fish. Soc. 98(3):570-581.

Rothschild, Brian J. 1971. A systems view of fishery management with some notes on the tuna fisheries. FAO Fisheries Technical Paper No. 106, 33 p.

Van Dyne, George M. Editor. 1969. The ecosystem concept in natural resource management. Academic Press, New York. 383 p.

CHAPTER NINE

DECISION ANALYSIS

Management Objectives

Objectives are the key components of management decision-making. The quality of a management decision is based upon the degree to which the decision leads to reaching management objectives. Objectives serve numerous purposes or functions in fisheries management. 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 priorities of managers.

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 aims 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 measurable. 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 components it affects, then it is likely not to be realized. The agreement of the various components of the public and professional sectors is difficult to achieve.

4. In most cases management objectives are conceptually simple, but technically difficult to formalize. For example, it may be conceptually very easy to maintain the quality of panfish fishing in a lake by limiting harvest of top carnivores, but problems with instituting and enforcing harvest restrictions on the carnivores may be very difficult to accomplish.

Selecting 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 natural 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 selecting 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 of these objectives could interfere with the objectives of other fisheries managers, or forestry, wildlife, agriculture, or recreation interests. Clearly, developing an interface between all competing uses of a resource is quite difficult.

Management Strategy

The basic strategy associated with fisheries management objectives is optimization of some aspects of the resource system. 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 (see Chapter 1 for additional discussion):

$$Q_{MAX} = f\ (X_1, X_2, \ldots X_m \mid Y_1, Y_2, \ldots Y_n)$$

where:

Q is the social benefit 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 and quantification of the system involved, as well as the array of decision variables and constraints encountered. Numerous analytical 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 here with their advantages and disadvantages.

Stock-Recruitment Strategy

Assume that our management objective is MSY (maximum sustained yield) from 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.

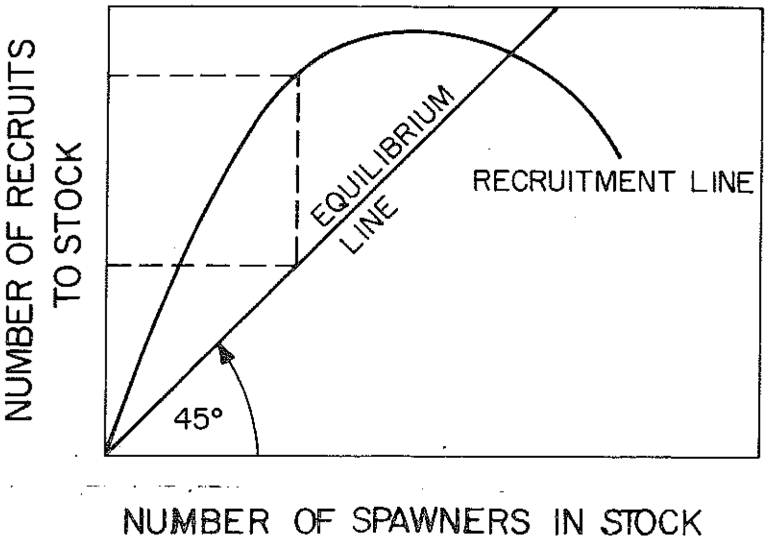


Figure IX-1. Stock recruitment model expressing the relation between density of spawners and density of recruits

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 due to density dependent 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. See Chapter 6 for further development of the model.

Regression Prediction Strategy

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

$$C_t = \alpha + \beta C_{t-1} + \upsilon f_{t-1} + \delta f_t + \varepsilon$$

where,

C_t = Catch in year t
C_{t-1} = Catch in year t-1
f_t = Fishing effort in year t
f_{t-1} = Fishing effort in year t-1
ε = Unaccounted for variation
α, β, υ, and δ 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. Selecting the independent factors (C_t, C_{t-1}, f, and f_{t-1}) is often difficult to practice. Such parameters as total dissolved solids, water temperature, barometric pressure, and average lake depth have also 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) density dependent 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 (ε) may always, even with a highly complex model, account for most of the variation.

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 7. 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,

$$\frac{dN}{dt} = -ZN_t$$

And,

$$\int_{t_c}^{t_\infty} dN = \int -ZN_t dt$$

$$N_t = N_o e^{-Z\Delta t}$$

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

$$N_t = Re^{-ZWt}$$

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

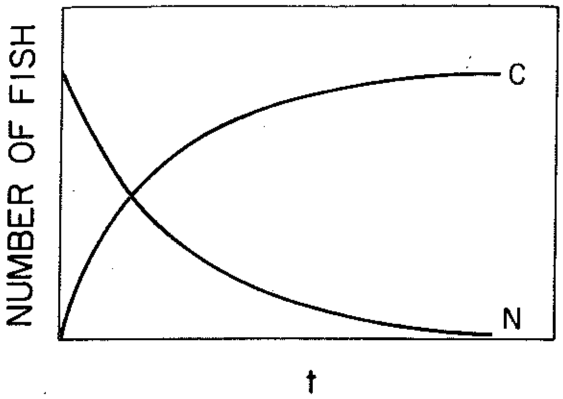


Figure IX-2. Relation between fish harvest (C) from a stock and the stock abundance (N) over time.

Then,

$$\frac{dC}{dt} = FN_t$$

And,

$$\int_{t_c}^{t_\infty} dC = \int FN_t dt$$

$$C_t = \int_{t_c}^{t_\infty} FN_t dt$$

But,

$$N_t = N_o e^{-Zt} = Re^{-Zt} \qquad (\text{if } \Delta t = 1)$$

Then,

$$C = \int_{t_c}^{t_\infty} F \left[Re^{-Zt}\right] dt$$

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

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

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

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

can be reduced to

$$w_t = w_\infty\ [1 - e^{-K(t-t_o)}]^\beta$$

By adding the expression for w_t, C becomes Y and

$$Y = R[1-e^{-Zt}]\ \frac{F}{Z} \int_{t_c}^{t_\infty} K\ (w_\infty - w_t)dt$$

This equation for estimating Y is called a "yield equation" and is a mathematical statement of the "theory of fishing" (See Chapter 1).

The advantages of classical population dynamics as a strategy are: (1) the relatively simple conceptual basis; (2) there are often 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 reflect changes in population level.

Variable Environmental 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 model" 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

$$N_{ij} = N_{io}\ S_{i1}\ S_{i2}\ S_{i3}\ .\ .\ .\ .\ S_{ij}$$

where

N_{ij} = Number of bass in the ith year class surviving to the jth birthday

S_{in} = Probability of survival of individual bass in the ith year class from the n - 1 to the nth age

N_{io} = Number of bass in the ith year class that hatched

Since

E = Fraction of fish caught over a specified time (exploitation rate)

then

$$C_{ij} = E\ N_{ij}$$

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 extensive 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.

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.

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 efforts tend 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.

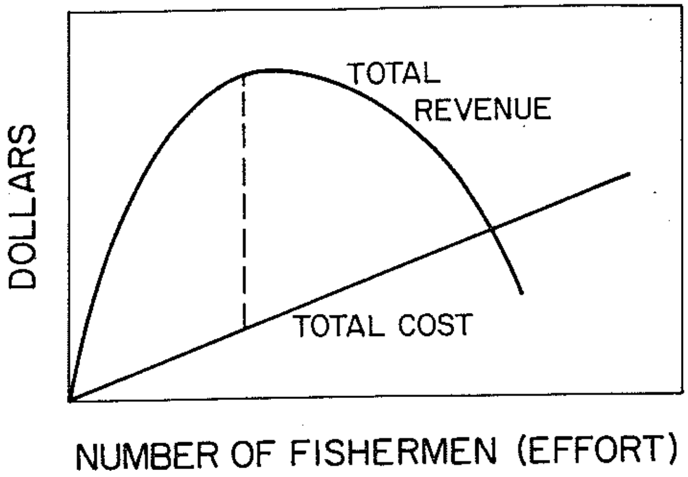


Figure IX-3. Relation between economic yield ($) and the amount of fishing effort on a particular stock.

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.

Management Benefit Unit Strategy

In all the previously discussed strategies, we measured fisheries 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 the 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.

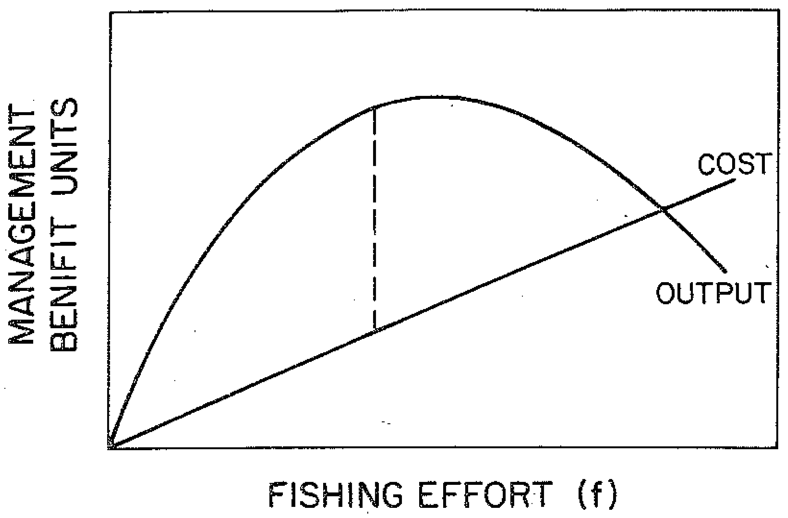


Figure IX-4. Relation between management benefit units, fishing effort, cost, and output from a fishery.

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 utilizing the various population parameters is an integral part of management strategies, whether they are highly mathematically oriented or based on logic and experience.

Further Reading

Clark, Colin W. 1976. Mathematical bioeconomics: the optimal management of renewable resources. John Wiley & Sons, New York, 352 p.

Powers, Joseph E., Robert T. Lackey, and James R. Zuboy. 1975. Decision-making in recreational fisheries management: an analysis. Trans. Am. Fish. Soc. 104(3):630-634.

Russell, Clifford S. Editor. 1975. Ecological modeling in a resource management framework. Resources for the Future, Washington, D.C. 394 p.

Von Bertalanffy, Ludwig. 1968. General system theory. George Braziller, NY. 299 p.

Watt, Kenneth E. F. 1968. Ecology and resource management. McGraw-Hill Book Company, New York. 450 p.