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An Argument Supporting the Reality of Compensation in Fish Populations and a Plea to Let Them Exercise It

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*Hope from him had almost drained;
His children all had been entrained.
The last striped bass in Hudson River
Gave a pained, convulsive shiver.*

*His civil rights had been infringed –
On intake screen he hung impinged.
But yet one chance to outwit fate:
"I think I still can compensate!"*

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INTRODUCTION

The concept of compensation is very important in assessing the impact of power plant operation on fish populations because compensation represents the capacity of a fish population to offset, in whole or in part, reductions in numbers caused by entrainment and impingement. Not everyone has rushed to embrace the concept, however. In fact, government regulatory agencies and their scientific staffs involved in power plant licensing proceedings have seemed reluctant to credit many fish populations with significant natural compensatory capacity and even more reluctant to make quantitative allowance for this capacity when evaluating power plant impact. An example, presented for its utility not as a criticism, is the original position of the U.S. Nuclear Regulatory Commission on Indian Point Unit 2 on the Hudson River in New York and later applied to the proposed Summit Power Station Units 1 and 2 in Delaware: "Examination of relevant information concerning striped bass populations has led the staff to conclude that density-dependent regulatory processes as described above are not operative in East Coast striped bass

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larval and juvenile populations, because the breeding stock is not sufficient to saturate the nursery areas to population levels at which such processes would be operative" (USAEC 1974, citing USAEC 1972). Some softening of this stand was reflected in the NRC staff's review of Indian Point Unit 3 (USNRC 1975) and its testimony for the Summit Power Station (Christensen et al. 1975) for which it was maintained that the fishery operates in a compensatory manner but that natural compensatory processes should not be relied on to a major extent to offset power plant impact in heavily fished populations.

By contrast, I have always maintained, as a general proposition, that some natural compensatory capacity must be recognized as a logical necessity; that general observation of natural populations, a wide range of specific scientific studies, and the prevailing concepts of the field of fishery management all support this view; and that the operation of compensation must be taken into account in order to make realistic decisions in management of fish populations, whatever the source of disturbance or impact. Most people seem to intuitively expect that killing some fish will reduce the size of the population — a proposition which seems logical enough but is not always true. Upon a little reflection, I would argue that it should be at least equally obvious that a sustained removal of fish from a population will eventually result in reduced natural death rate or increased reproduction by the remainder.

This paper presents an argument in favor of the reality of compensation in fish populations — it is not a balanced examination of pros and cons. The ideas, at first developed in the relative tranquility of an academic environment, have been shaped through a succession of regulatory agency hearings in which too much open-mindedness has seemed the short road to intellectual extinction. They are called "adversary" proceedings for good reason. Hence, while trying to be fair and logical, my main goal has been to make converts rather than compromises. Success has been limited, but I remain optimistic.

HISTORICAL DEVELOPMENT OF THE GENERAL CONCEPT

The term "compensation" refers to the tendency of populations of living organisms to experience (a) an increase in death rate or decrease in birth rate as they grow in density, thus establishing some ultimate upper limit, and (b) a decrease in death rate or increase in birth rate as population density declines, thus leading to stabilization before extinction, or even to an eventual return to higher numbers.

The concept arises directly from recognition that living organisms depend on resources such as food and space, which are available in limited amounts. When density of organisms is low, competition for resources is slight; when density is high, competition becomes intense to the disadvantage of survival or reproduction. It is also possible that large populations will attract greater

attention from predators, either because the latter congregate in the vicinity of a food source or reproduce more rapidly when prey is abundant or because predators become conditioned to seek the more abundant prey. Cannibalism also may contribute to compensation in some species because the large numbers of parents from which initially large broods arise also constitute a large pool of predators. The number of physical and biological forces that may play a role in compensation is very large, and the possible modes of operation are numerous and complex. As Cushing (1975, p. 237) states, "Any description of the phenomenon reveals the stability and leaves the possible mechanisms indistinct." This is not to say that no mechanisms of compensation can be identified; many indeed have been identified, and a number of examples will be cited in the following sections. However, of the number of mechanisms operating simultaneously (often with a high degree of interaction) and sequentially through the various life-history stages (with intensity of operation at each stage determined in part by the population density established in the preceding stage) only a few may be statistically verifiable during a single period of observation. Undoubtedly too, the operation of one mechanism under certain environmental conditions may preempt the operation of other potentially effective mechanisms.

Thus a common state of affairs is to observe a population's stability as generated by compensation and to estimate the compensatory capacity while being unable to explain all or even very many of the mechanisms involved. This latter limitation has not prevented scientists from developing highly successful management programs grounded on the reality of compensation, as will be shown.

Because compensation involves changes in birth rates or death rates in response to changes in population density, the biological processes involved are often termed "density dependent." Thus, a density-dependent increase in mortality rate might be expected to result from a substantial increase in population density. Strictly speaking, only processes that reduce population growth at high densities and increase growth at low densities — "direct density-dependent processes"* — are compensatory. Nevertheless, the term "density dependence" is often used synonymously with "compensation."

The concept of compensation has been long and widely accepted. In 1798 Thomas Malthus published his famous *Essay On The Principle Of Population* (Malthus 1798) in which he maintained that, when unchecked, a population increases in a geometrical ratio; that the increase is always up to the

*Mortality may also take an *inverse* density-dependent form; that is, the mortality rate decreases with an increase in population density. This could happen where very abundant prey "saturate" the capacity of a predator to capture them, thereby causing a smaller fraction of the prey to be caught when they are more abundant. Other types of "protection in numbers" would bring about the same result. Inverse density-dependent mortality is not synonymous with compensation.

limits of the means of subsistence; and that further increase is prevented by war, famine, pestilence, etc. He termed the processes involved in regulation of population size the "struggle for existence." His observations, based on human populations, clearly encompassed the compensatory concept that population growth declines as population size increases. The ideas presented by Malthus were not entirely new; for example, Machiavelli had realized 275 years earlier that human populations in some areas might increase beyond the limits of subsistence and be checked by want and disease. In 1835, Quetelet, a Belgian statistician, concluded that a population's resistance to growth increases in proportion to the square of the rate of population growth (Quetelet 1835). In 1838, Verhulst, a student of Quetelet, published a short essay developing an equation describing the course of population increases in proportion to population density; his equation generated the *S*-shaped population growth curve so familiar today, the logistic curve. Nearly 100 years later, this formulation of population growth was rediscovered by Pearl and Reed (1920) and was soon shown to describe the performance of such diverse organisms as yeast, protozoa, fruit flies, and man. Pearl recognized the importance of density-dependent mortality and reproduction: "In general there can be no question that this whole matter of influence of density of population, in all senses, upon biological phenomena, deserves a great deal more investigation than it has had. All indications are that it is one of the most significant elements in the biological, as distinguished from the physical, environment of organisms" (Pearl 1930, p. 145).

In the last four decades, the concept of compensation has been debated, refined, and amplified. A well-balanced review is presented by Krebs (1972, p. 269–288). Major contributions to our understanding have come from studies of insects, fishes, birds, and mammals. Despite the long history of the concept and its simple, almost intuitive basis, its explicit formulation and modern emphasis are usually attributed to the Australian entomologist Nicholson (1933). His inspiration was later referred to by another notable population ecologist (Haldane 1953) as "a blinding glimpse of the obvious."

Thus, the emergence of the concept of compensation can be traced over the past 450 years. It seems to have originated in observations of local human populations "struggling for existence" in the face of limited resources. The first formulations were crude and partially incorrect. It was Pearl's work in the 1930s that established the generality of compensation among diverse types of living organisms. Common to all these perceptions was the realization that populations possessed a potential to increase at a much more rapid pace than was realized, except possibly when they were so small that the resources upon which they depended were, for all practical purposes, infinite in extent. To appreciate the reality, pervasiveness, and imminence of the operation of compensation within a population, one should look first to this "biotic potential" as it is sometimes called and then envision as a population grows in size "the absorption of the potential increase by innumerable checks

(in the shape of mortality) . . . The survivors flourish by the deaths of their brothers and sisters, and the stable numbers must be the result of a fine control of mortality, perhaps a density-dependent one" (Cushing 1975).

Some feel for the magnitude of biotic potential can be gained by artificially simplifying the life history of a reasonably representative fish. The striped bass, which has inspired endless volumes of testimony in power plant hearings, serves as a useful example here. Assume that each fish spawns once in its lifetime at age 6; half are females, each producing 700,000 eggs; each fish reaches 457 mm in length; and all the eggs survive to become mature fish. These assumptions cause the biotic potential to be seriously underestimated since some females spawn at an earlier age and many live to spawn again at older ages. Beginning with one spawning pair, such a striped bass population would grow to astronomical numbers by the end of three generations (18 years). At the end of the third generation, all the fish laid end to end would encircle the earth at the equator 500,000,000 times or would stretch from the earth to the sun and back again 60,000 times. This is the biotic potential, which is increasingly suppressed by density-related mortality factors as a striped bass population grows from some minimal initial density toward an upper limit set by the carrying capacity of the environment. In 1879–1881, 435 striped bass were transplanted from the east coast to San Francisco Bay; within 20 years, annual catches were 500 tons (Merriman 1951). Under minimal densities, the population grew explosively; within a relatively short time, numbers became large enough that population growth leveled off. The innate capacity for growth is the foundation of the compensatory capacity possessed by striped bass.

Approaching population processes of fish in general from this perspective, one envisions an established population as one in which survival or reproduction (or both) have been vastly suppressed — precisely for the reason that the population has become large. The natural factors that operate to suppress the biotic potential are many and are complexly intertwined — availability of food, predators, disease, and physical factors such as temperature. Many of them (probably all of them under certain conditions) have greater suppressive effect when the population is large than when it is small. If some new effect that kills off part of the population is introduced, it reduces the suppressive effect of many factors in the population's environment. As a consequence, survival rate or reproductive rate becomes higher — the population *compensates* in part for the reduction in size. When something causes a population to either increase or decrease in size, there is a tendency for eventual return to average size when the perturbation is removed. "Populations do not usually become extinct or increase to infinity. This is what is loosely termed the 'balance of nature'" (Krebs 1972).

Rather than being a fragile living system then, the population typically is vigorous and resilient. This sense was captured admirably by that eminent interpreter of marine science, the late Rachel Carson, who, in describing the

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life of the seacoast, wrote, "Whenever the sea builds a new coast, waves of living creatures surge against it, seeking a foothold, establishing their colonies. And so we come to perceive life as a force as tangible as any of the physical realities of the sea, a force strong and purposeful, as incapable of being crushed or diverted from its ends as the rising tide" (Carson 1955).

The 10-year span from the mid-1960s to the mid-1970s has seen an impressive and timely increase in public awareness of environmental problems. With this awakening has come an accurate perception of the fragility of the ecosystem, which may seem at first to conflict with the description of life as a force "as incapable of being crushed or diverted from its ends as the rising tide." The apparent conflict is easily explained. Populations of most living organisms have little means of coping with wholesale destruction of environmental resources upon which they depend. If specific foods or narrow temperature ranges to which they are highly adapted are destroyed, the population perishes. Likewise, exposure to toxic substances such as the many organic compounds introduced into the environment by man, with which a natural population has no evolutionary experience, is likely to prove disastrous. Most of the current environmental awareness is built on public recognition of these two classes of problems — wholesale destruction of environmental resources and the release of exotic toxic substances. A third class of man-caused problems — the imposition on a population of increased mortality that takes a form similar to natural predation — has an entirely different effect on most species. This is the kind of impact to which the population has been adapted by thousands or millions of years of evolutionary experience. The agent of mortality — predatory fish, commercial or sport fishermen, or power plants — is an indifferent matter from the standpoint of population response. When the population is reduced in numbers, the survival rate or reproductive rate among the remaining members tends to increase; a compensating response is generated. This is the reality upon which successful management of agriculture, forestry, wildlife, and fisheries is carried on today. The population has a measurable and often impressive capacity to persist in a healthy state in the face of deliberate removals by man. Populations of most species, while fragile when deprived of basic life requirements or exposed to exotic toxicants, are robust in the face of this predation-type mortality.

A GENERAL CASE ARGUMENT

A formal argument for the general operation of compensation in animal populations can be developed as follows. It is generally observed that populations fluctuate within some more or less well-described bounds; that is, they neither increase without limit nor commonly decline to extinction during the normal time span of human observation.

A useful simplification is to represent a population as persisting at or near some average level of abundance or equilibrium level represented by K_0 (Fig. 1). As a generalization, the birth rate is expected to decline and the death rate to increase as a population becomes larger and larger. Linear relationships are used to simplify the illustration, even though the real relationships would almost certainly be nonlinear. Death rate would reflect the combination of natural deaths and any deaths imposed on the population by activities of man. In Fig. 1, the equilibrium population density, K_0 , is maintained, on the average, by the balance between the death rate (I_0 , representing the prevailing natural death rate plus a 0-level of man-caused deaths) and the birth-rate characteristic of the population at density K_0 . If a low level of man-induced mortality is added to the baseline natural mortality, the overall death rate would increase to a level I_L (Fig. 1). The population would then decline and the birth rate would consequently increase until a new equilibrium density had been reached (K_L) at which the birth rate equaled the new death rate I_L . Imposition of a still higher man-induced mortality would increase the total death rate to I_H , and the population would equilibrate eventually at a still lower average density K_H . Thus, one can think of the population as fluctuating through time around some average level of abundance determined by the overall death rate (Fig. 2). For a 0-level man-induced environmental

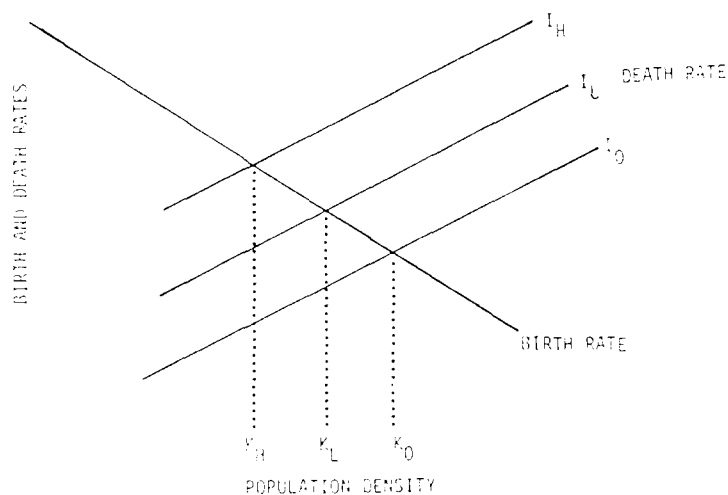


Fig. 1. Relationship of birth rates and death rates to population density. The death rate I_0 and the population density K_0 represent zero environmental impact; the death rate I_L and the corresponding population density K_L represent a low level of environmental impact superimposed on a fish population; the death rate I_H and the corresponding population density K_H represent a fish population subjected to a high level of environmental impact. In each case, the population equilibrates at that density at which the birth rate and death rate are equal.

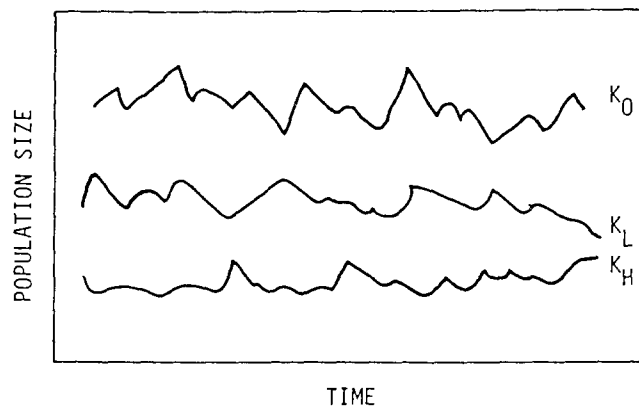


Fig. 2. Hypothetical population histories corresponding to zero, low, and high levels of environmental impact represented in Fig. 1.

impact, this would be a population density K_0 ; for a low level of environmental impact, a population density K_L ; and for a high level of environmental impact, a still lower population density K_H .

This example was chosen to illustrate as simply as possible the relationship among death rate, birth rate, and average population density where compensation is operative. The increase in total mortality depicted in this example could have been offset at lower population levels by an increase in survival among members of the population not killed by the man-induced impact rather than by the increase in birth rate; the principle would be the same.

Referring again to the example in Fig. 1, the initial condition postulated is a population fluctuating around an average equilibrium level K_0 ; for this population, the birth rate (b) and death rate (d) on the average are equal. Thus, the rate of population increase (r) is 0:

$$r = b - d = 0.$$

When the population is first subjected to additional mortality (no matter how slight) caused by man, the death rate is increased and exceeds the birth rate. The population's rate of growth (r) becomes negative — that is, the population declines in numbers:

$$b - d < 0.$$

If the increment of mortality is sustained, the population eventually will dwindle to extinction unless the birth rate increases or the natural mortality rate decreases sufficiently to allow the overall birth and death rates to again become equal. This would be true if the removal is sustained over a long enough period, even if only a single organism per year is killed over and above

the pre-impact natural mortality rate. Therefore, every population that is subjected to sustained additional mortality through man's activities and does not become extinct must possess some compensatory capacity. The list from everyday observation is impressively long. Species of birds and mammals commonly killed along highways — raccoons, squirrels, skunks, deer, pheasants, woodpeckers, sparrows — must have some compensatory capacity, or the new predator, the automobile, by now would have pursued them far down the trail toward extinction. The same can be said for pest insects attacked with weapons ranging from rolled newspapers to organic chemicals. Any wild plant or animal harvested by man for sport or subsistence — and many have been pursued since antiquity — must have some form of compensatory capacity to have survived. However, this compensatory capacity is not unlimited, as proven by the extinction or near extinction of a number of species caused by man's predatory activity. Ecologists now understand that compensatory capacity is most limited in species having relatively low maximum reproductive rates.

Simulation models are valuable aids in making decisions about management of complex systems, such as fish populations, and a variety of models have been used to estimate power plant impacts. The compensation argument just developed finds support in the realistic exercise of such simulation models. If a fish population model is operated from an initial state representing a population at a stable equilibrium or one fluctuating around an average equilibrium level and if removal of a single additional fish per year is simulated over a long period, the population will dwindle to extinction unless compensatory processes are simulated as well. The extinction case clearly is not a realistic simulation of commonly observed population performance. Further, because populations incorporate negative feedback processes under completely natural conditions, it does not suffice to confine compensatory mechanisms to those accounted for by the activities of man — such as density-dependent fishing. The general case argument requires that some *natural* compensatory process be operative to represent realistically and logically the performance of a population of living organisms.

COMPENSATION IN FISH POPULATIONS

Both the historical development of the general concept of compensation and the formal argument presented above support the view that compensation is operative in fish populations. This section supports this view with three additional lines of evidence:

- The historical development of the concept is traced through its applications in fishery management, and the present-day consensus held by the world's leading fishery scientists is summarized.

- A selection of compensatory mechanisms that have been convincingly demonstrated to operate in fish populations is reviewed.
- A large number of cases, in which substantial levels of exploitation by sport or commercial fisheries have been sustained by fish populations without serious depletion, are cited.

History of the Concept of Compensation in Fisheries

Historically, the formal foundation of modern fish population dynamics was laid down in the mid-1930s. Picking up the thread of historical development of the concept of compensation with the rediscovery of the logistic curve by Pearl and Reed (1920), the first explicit application of the concept in this form to fisheries seems to have been in 1933 when a parallel between the sigmoid population growth form in yeast and growth in numbers in a fish stock was noted (Hjort, Jahn, and Ottestad 1933). The first formal application of the logistic to management problems in a major fish stock was Graham's (1935) application to the plaice stock of the North Sea.

The logistic and its various modifications such as the "Schaefer model" (Schaefer 1954) have since been applied to such important fisheries as the Antarctic blue whale (Chapman 1964), Icelandic cod (Gulland 1961), Pacific halibut (Schaefer 1954), and Icelandic haddock (Gulland (1961). "The development of the logistic curve in fisheries and in other fields implied that loss of stock with increased mortality was compensated by increased recruitment" (Cushing 1974, p. 237). Thus, since the publication of Graham's work in 1935, the concept of compensation clearly has been a basic tenet of scientific management for the world's major fish stocks.

Interpretation and application of the logistic curve to fishery management is conveniently summarized in a recent book, *The Management of Marine Fisheries*, by J. A. Gulland, an internationally noted scientist with the Food and Agricultural Organization of the United Nations (Gulland 1974, p. 68-86). He makes the following points about compensation from the basis of the logistic model:

Though the curves of Figures 3 and 10 and the model on which they are based are highly simplified descriptions of the changes in a fish stock under exploitation, they do illustrate most of the biological features important to fishery management. The first is that it is impossible to exploit a fish population without causing some change. This may seem obvious, but with the present day concern with the natural environment, and the desire to minimize ecological disturbance, there may be a feeling that a well-managed fishery should cause no changes, which is impossible . . . The second important point is almost the converse of this. That is, provided the catches are not too great, the decline in abundance is not continual. After a time

the population will reach a new equilibrium, at which the same catches can be maintained indefinitely year after year. Finally, if the stock is allowed to be depleted too far, though still without driving it to extinction, its productivity and the catches that can be taken will be reduced.

Ricker's commentary (1958, p. 250) on the same basic compensatory principle applied in fishery management is

The principal reasons for lessened surplus production at higher stock densities are three:

1. Near maximum stock density efficiency of reproduction is reduced, and quite commonly the actual number of recruits is less than at smaller densities. In the latter event, reducing the stock will increase recruitment.
2. When food supply is limited, food is less efficiently converted to fish flesh by a large stock than by a smaller one. Each fish of the larger stock gets less food individually, hence a larger fraction is used merely to maintain life, and a smaller fraction is used for growth.
3. An unfished stock tends to contain more older individuals, relatively, than a fished stock. This makes for decreased production in at least two ways: (a) Larger fish tend to eat larger foods, so an extra step may be inserted in the food pyramid, with consequent loss of efficiency of utilization of the basic food production. (b) Older fish convert a smaller fraction of the food they eat into new flesh — partly, at least, because mature fish annually divert much substance to maturing eggs and milt.

Under reasonably stable natural conditions, the net increase of an unfished stock is zero, at least on the average; its growth is balanced by natural deaths. Introducing a fishery increases production per unit of stock by one or more of the methods above and so creates a surplus which can be harvested. In these ways "a fishery, acting on a fish population, itself creates the production by which it is maintained" (Baranov). Notice that effects 1 and 3 above may often increase the *total* production of fish flesh by the population — it is not merely a question of diverting some of the existing production to the fishery, although that also occurs.

The logistic-type models have been used successfully in fishery management since their inception and are still used today, but they have long been recognized as embodying important basic principles in an over-simplified way. For example, they do not distinguish the contributions of growth of existing stock and recruitment of new individuals; they assume that the entire population is involved equally in compensatory response; they represent density-related changes in populations as occurring instantaneously and continuously.

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A very important advance in conceptualizing fish population dynamics in a more realistic way is Ricker's (1954) exposition of the problem of stock and recruitment. Ricker emphasized the compensatory nature of the numerical relationship between parent fish and the progeny they produced and the importance of the earlier life history stages in compensation, and he formulated a mathematic model embodying these concepts, which has been applied to major fish stocks throughout the world. Ricker's model operates on the same basic principles given in the formal argument presented earlier in this paper and implicit in the logistic model — but in a much more refined and realistic way. It is explained here in graphical form because of its usefulness in clarifying the compensatory responses of fish populations to new increments of mortality (e.g., fisheries, power plant operations, and pollution).

Consider a parent stock of fish and the stock of progeny that it produces, expressing both the parents and progeny in the same units of measurement. If the *rate* of future replacement of the present population is independent of the *size* of the population, the relationship between parental stock and progeny will be described by a 45° diagonal line as shown in Fig. 3 (replacement reproduction), and this will be referred to as a *density-independent* relationship between parents and progeny. If environmental conditions permit survival of a very large parental stock, that stock will produce a generation of progeny equal in size to itself; by the same token, if unfavorable environmental conditions reduce the parental stock to some very low

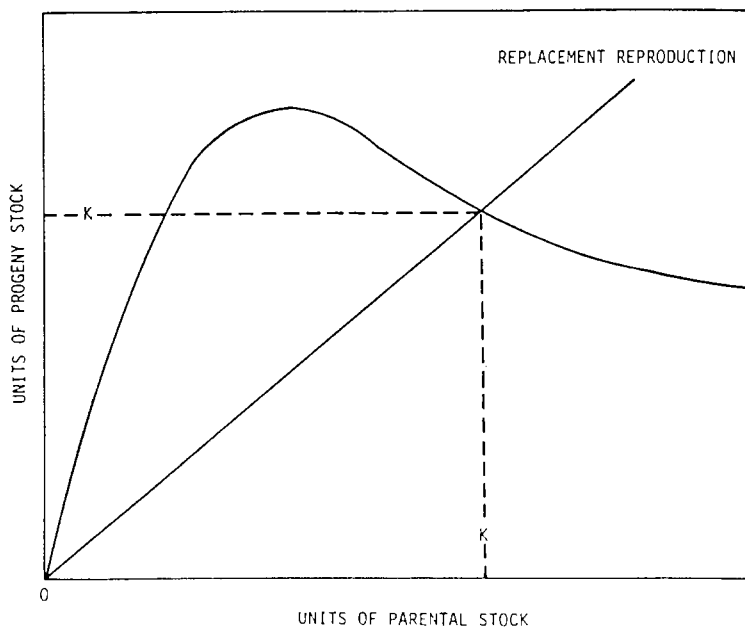


Fig. 3. Relationship between parental stock density and production of progeny for a hypothetical fish population.

density, it will produce again a generation of progeny equal to itself. Under these situations the size of the population could, by chance, increase without limit or dwindle to extinction; no compensatory process operates to increase the rate of population growth at low levels of density, thus deflecting it from decline to extinction, or to decrease the rate of population growth at very high levels of population density, thus deflecting it from unlimited expansion. To persist within some more or less well-defined limits of abundance, a fish stock must have some compensatory (density-dependent) processes.

The curve in Fig. 3 represents a density-dependent relationship between parental and progeny stocks. At very low levels of parental stock, the population tends to increase severalfold in the progeny generation. At point K, the parental stock is replaced by exactly the same size progeny stock (the reproduction curve intersects the 45° diagonal), and this density is the equilibrium point or replacement level of reproduction. If no environmental fluctuation deflects the stock from point K, it will remain perpetually at that density, exactly replacing itself over each succeeding generation. At densities above replacement reproduction, the parental stock will fail to replace itself and the population will decline back toward the equilibrium point. If stock density is deflected by environmental conditions below the equilibrium point, the parental stock will more than replace itself; that is, the population will tend to increase back toward replacement level over succeeding generations. At replacement level, the parental stock exactly replaces itself in the face of baseline natural mortality, producing no surplus progeny as a buffer against removal by an environmental impact such as power plant operation, a fishery, or pollution.

Figure 4 explores the situation in which an increment of mortality is imposed on the population of Fig. 3, thus deflecting it away from the replacement level of parental stock. Let us say, for example, that an amount of parental stock equal to the line segment cK is removed from the population before reproduction. The parental stock now consists of \overline{Oc} units, and this parental stock produces \overline{ca} units of progeny. At this stock density, the parents produce \overline{cb} units of offspring (sufficient to replace themselves) plus a surplus \overline{ab} , which may be removed by the fishery or killed by power plant operations or pollutional inputs but which still leaves the population equilibrated at a density \overline{Oc} . For this situation, the removal, \overline{ab} , from the population is about 28% of the progeny stock, \overline{ac} .

If an additional increment of removal is imposed on the stock (e.g., a total of \overline{de} units of progeny stock), the removal rate ($\overline{de}/\overline{df}$) will be 60% and the population will sustain this level of removal, equilibrating at a density \overline{Of} . To hold the stock at this reduced density, 60% average removal must be sustained. If this rate of removal is reduced, the parental stock will more than replace itself and succeeding generations will tend to increase until the population equilibrates once again at a higher level of density. A still higher percentage removal (70% [$\overline{gh}/\overline{gi}$] for example), if sustained, will reduce the population to the density \overline{Oi} .

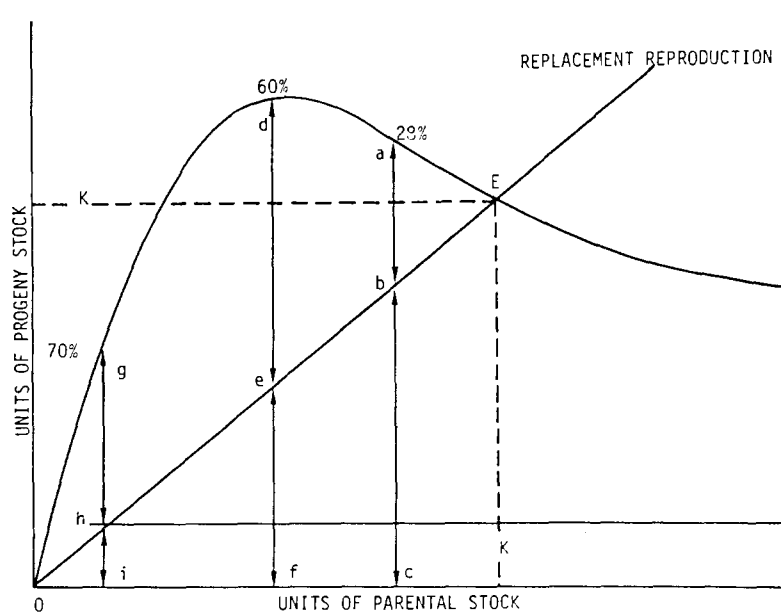


Fig. 4. Equilibrium exploitation rates for parent-progeny relationship of Fig. 3. (Equilibrium at c units of parental stock is maintained with an exploitation rate of 28%; a level of f units of stock by an exploitation rate of 60%; and a level of i units of stock by an exploitation rate of 70%.)

Two important points emerge. First, an increment of removal imposed on a fish stock drives the stock to a lower average density at which the population once again equilibrates, but the increment of mortality imposed and sustained does not drive the population into a steady downward spiral leading to severe depletion or extinction. This point was advanced earlier in summarizing compensation concepts from Gulland (1974) and Ricker (1958). Second, the rate of removal must be sustained from generation to generation if the stock is to be held at a reduced level of abundance; increasingly higher percentage removals must be sustained if the stock is to be driven to successively lower levels of density.

Cushing (1975, p. 238) states:

The equation relating recruitment to parent stock used initially by Ricker and later by Beverton and Holt is a convenient summary of present opinion on the natural regulation of numbers in a fish population. Recruitment depends on stock modulated by density-dependent mortality.

Gulland (1974, p. 101) also reflects on the widespread acceptance of this type of formulation of compensation:

Other curves could be derived with other assumptions, but so far for all stocks the observations of stock and recruitment, though often scattered, have been consistent with at least one of the theoretical curves.

To promote discussion of the present state of knowledge and of future research requirements in the face of the large post-war increase in global fishing intensity and problems in the world food supply, a symposium on fish stocks and recruitment was convened in 1970 by the International Council for the Exploration of the Sea, the International Commission for North Atlantic Fisheries, and the Food and Agricultural Organization of the United Nations. There were 82 participants from 20 countries. The published proceedings (Parrish 1973) recorded the following scientific opinions on the importance and prevalence of compensation or density dependence in fish populations:

When J. Tanner (1966) concluded after the analysis of density dependence in 111 different populations representing 71 species, "It is significant that the processes known to regulate vertebrate populations affect either reproduction or the survival of juveniles," he could have been reciting from the current litany of fisheries biology (Paulik 1973, p. 302).

The papers and discussions indicate that recruitment . . . in both marine and freshwater fish and shellfish populations is determined by a complex of density-dependent and density-independent factors. The former may act as the main source of control governing the form of the relationship between recruitment and spawning stock size (egg production), and the latter give rise to the well-known short-term, irregular fluctuations in recruitment characteristic of some teleost species having high fecundity. The papers and discussions indicate further that in most species for which detailed information is available these factors operate mainly during the early stages of development (i.e. between the egg and the end of the first year of life) so that year-class strength is determined and population control mechanisms for most fish stocks operate before the individuals enter the exploited phase" (Parrish 1973, p. 5).

It was the consensus of the meeting that density dependence does occur in all fish stocks at some point, and this is itself a major transition from earlier dogma. As R. Jones and Bowers pointed out, the precise age at which density becomes of major significance varies from stock to stock so that, for example, the plaice may have properties that are different from haddock. Plaice growth may be

density-regulated while they are in the plankton, and a relatively constant number may transform to the demersal habitat.

Dr. LeCren pointed out that freshwater species such as trout and salmon are really not very different in their fundamental biological machinery from the marine ones and that the same kind of density dependencies probably occur in marine and fresh water. The general acceptance of density dependence as relevant to all marine stocks is probably of great value since it avoids the nasty theoretical problem, specifically, that the absence of any density-dependent feedback system implies a random walk process in stock size which would predict much greater temporal variations in population size than are actually observed (Slobodkin 1973, p. 10).

Compensatory Mechanisms

As discussed earlier for animal populations in general, a wide range of environmental agents and compensatory mechanisms may be involved in the overall compensatory response generated by a fish population. Different mechanisms may operate at different levels of population density or under different environmental conditions, and the effect of one compensatory mechanism may preempt the activation of alternate mechanisms that are potentially available. A wide range of population processes also may play a significant role in the compensatory response. Furthermore, compensation may be masked statistically either by its own effectiveness, which may so stabilize some fish populations that observations on population processes at very different levels of density are hard to obtain, or by the imposition of a large amount of random variation in population parameters caused by density-independent factors. Thus, it is usually not profitable to focus on a single mechanism of compensation or on even a small complex of mechanisms to test the reality or extent of the phenomenon. However, this is not to say that the existence of such mechanisms is a matter of theory, speculation, or mystery; on the contrary, the compensatory operation of many different mechanisms and population processes has been proven in fish populations. The 17 examples in Table 1 drawn from the scientific literature provide a concrete understanding of the remarkable resilience of fish populations in the face of increases in mortality caused by man.

Capacity of Fish Populations to Withstand Mortality

While it is clear that the concepts in fisheries science were developed through experience with stocks subjected to exploitation by man, nothing explicit has yet been stated here about the degree of resiliency possessed by these stocks. Remaining unanswered are such questions as how large an

Table 1. Examples of the resiliency of fish populations to man-induced mortality

1. A dense population of perch in Lake Windermere was subjected to an extensive experimental fishery for five years (LeCren 1958); reduction of the population to 3% of its original density resulted in a fourfold increase in both mean weight and fecundity of adults.
2. Brown trout populations in a small Swedish lake were compared for six years before and six years during exploitation with gill nets and sport fishing gear (Lindstrom, Fagerstrom, and Gustafson 1970). Although mean size decreased, the individual growth rates (lengths) increased an average of 10.5% after exploitation.
3. Bluegills in three large Michigan ponds were subjected to annual reductions of 0, 60, and 90% in young-of-the-year during a five-year experiment (Beyerle and Williams 1972). Survival averaged 0.5, 8.1, and 12.2% respectively. Growth of fish in all three ponds was similar, evidently as the result of compensatory survival rates.
4. Commercial exploitation of plaice off the coast of Scotland increased greatly after 1956 (Bagenel 1963). Fecundity increased from 137,000 eggs per female in 1956-1957 to 157,000-161,000 eggs per female in 1958-1961. The data suggest that heavy fishing reduced the population size but that survivors had proportionately more food, resulting in higher fecundity.
5. Large brook trout in a Canadian lake were subjected to 90% experimental exploitation by gill nets (Smith 1956). Survival of planted fingerlings was two times that existing before gill netting of large trout. Although growth data are not easily interpreted, the growth rate of fingerlings appeared to have decreased after exploitation.
6. Data from seven brook trout populations were studied to compare fished and unfished populations (Jensen 1971). Fishing resulted in more young and fewer old fish. Increased age-specific fecundity compensated for increased mortality from fishing. Since fecundity increased with size, the data suggested that growth may be the most important variable in a fish population's adjustment to exploitation.
7. Reductions in numbers of adult pike were observed in Lake Windermere (Kipling and Frost 1969). There was a significant increase in eggs per gram of fish after the population density had been falling for several years, suggesting a compensatory response in fecundity.
8. Ciscoes in three Canadian lakes were subjected to varying degrees of exploitation (Miller 1950). Total mortality averaged 61 and 60% in two mildly exploited lakes and 70.5% in an unfished lake. Under moderate and then heavy exploitation, total mortality in one lake averaged 80 and 94% respectively. The comparison suggests that fishing mortality reduces natural mortality, but that the overall effect of moderate to heavy exploitation is an increase in total mortality.
9. Brook trout in a Wisconsin stream were subjected to varying amounts of sport fishing (McFadden 1961). There was a significant regression of natural mortality on angling mortality so that exploitation reduced natural mortality. Total mortality increased with exploitation, but there was a broad range in the number of spawners and size of the egg complement, which would result in adequate numbers of progeny.

Table 1 (continued)

10. Rainbow trout populations maintained by stocking were compared in five New Zealand lakes (Fish 1968). In three of the lakes supporting 7–18 fish per acre, growth in weight was two to three times that in two lakes supporting 31–35 fish per acre. The inverse relationship between number of trout and their average weight suggests that the lakes would produce large trout if the population were kept small.
11. Rainbow trout in a New Zealand lake were subjected to a sport fishery of increasing intensity for 14 years (Percival and Burnet 1963). The growth of two- and three-year-old fish was negatively correlated with population size. The data suggest that an increase in exploitation increases the survival rate of juveniles. The larger number of surviving juveniles resulted in a reduction in growth rate and maximum size of the fish.
12. Catch and escapement of an exploited sockeye salmon population were studied in Bristol Bay, Alaska (Mathisen 1969). Growth in length of smolts could be expressed as a negative exponential function of population density. A similar relationship exists for maturing salmon during their migration toward fresh water. Thus, as exploitation increases, the growth in individual fish increases.
13. Records of 111 animal populations representing 71 species were analyzed to determine the relationship between the rate of increase of a population and the population density (Tanner 1966). Of the seven fish species examined, Atlantic salmon, yellow perch, walleye, and northern pike showed a statistically significant negative correlation of population growth rate with population density; freshwater drum and goldeye showed a negative correlation and lake trout a positive correlation, but these were not statistically significant. The data strongly support the concept of a compensatory increase in survival and/or fecundity following reduction in the size of a population.
14. Populations of rainbow and brook trout were compared among New York ponds (Eipper 1964). Growth rates of both trout species were inversely related to population density.
15. The number of spawners was compared with the number of progeny for haddock, Pacific herring, and coho, sockeye, and pink salmon (Ricker 1954). The data suggest that the survival rate of progeny increases as the number of spawners decreases. Within limits, a reduction in spawners can also result in increased numbers of surviving progeny.
16. Plaice, haddock, sole, turbot, and cod in the North Sea were subjected to varying degrees of exploitation (Beverton and Holt 1957). Survival, particularly of plaice, was strongly inversely correlated with the size of the adult population.
17. The size of young sockeye salmon in a British Columbia lake was compared with population density for 11 years (Foerster 1944). There was a statistically significant negative correlation ($r = 0.82$) between the density of the lake population and the mean weight of migrants.

annual removal can be sustained, at what level of added mortality will the population be drastically reduced in numbers, at what level of added mortality will it be threatened with extinction, and what would constitute an intolerable or irreversible reduction of a fish population. As a foundation for responding to these questions from a basis of empirical evidence, the principles unfolded through the arguments and historical accounts previously presented are summarized as follows:

- An undisturbed or unexploited population (one at the maximum equilibrium level on the average) produces enough new individuals to just replace natural losses; there is no surplus production.
- A population, if it is to be held at maximum size, cannot be exposed to any additional mortality either from natural causes or from man's activities because, at maximum stock size, no surplus production is available to absorb an increment of mortality.
- At the opposite extreme, as a population approaches 0 size, surplus production approaches 0. In very small populations, the rate of surplus production per individual is very high; however, so few individuals are present that the overall rate of increase for the population is very low.
- Should exploitation or some other form of environmental impact occur, population size will be reduced. At levels of density lower than equilibrium, surplus production will be available to absorb the environmental impact while maintaining the population at the new but reduced level.
- Maximum surplus production occurs at some intermediate level of stock density.
- If an added mortality is large enough, population size will be reduced to a level at which the fish may become undesirably scarce, and the population may be vulnerable to accidental or even inevitable extinction and may be able to generate only a small surplus production for the benefit of man or as a cushion against further decline.

In ecological terms, the significance of an impact imposed by man on a fish population is not a matter of "good" or "bad" but rather a matter of one or more states of reality defined by the average level of abundance of the impacted stock and the magnitude of its surplus production. Increasing overall impact on the fish population decreases standing stock, increases resource utilization, causes maximum surplus production at an intermediate level of exploitation, and varies the potential for disposition of the surplus production as, for example, between fisheries and kills resulting from power generation. Because the objective of fisheries management is to maximize some form of productivity on a sustained basis (often the total weight of the fish harvested), identification of the fishing rate that will produce the greatest yield on a long-term basis has usually been emphasized. There has been no particular value attached to building up the population to maximum size.

Unlike esthetically valued species such as brightly feathered birds, fish are rarely accessible to the admiring gaze of the public and none has a reputation for song.

The emphasis on maximizing harvest has led to a wide range of historical experience with initially unexploited fish populations that have been subjected to harvest by sport and commercial fisheries and have persisted in a healthy ecological state despite increased overall mortality. This experience constitutes unassailable proof of the general operation of the phenomenon of compensation in fish populations. If the natural death rate had not declined or the birth rate increased as population density was reduced, the large removals by fishing would quickly have driven these populations to extinction.

In reviewing a substantial number of published estimates of exploitation rates (Table 2), it becomes clear that cases in which $\geq 25\%$ of the exploitable age classes in a population have been removed annually are common. The figures generally represent situations in which substantial exploitation has been underway for fairly long periods (usually for decades) and is continuing. Clearly then, many populations possess compensatory reserve sufficient to offset very substantial increments of man-induced mortality. The repeated removal of 25–50% of a fish population and the sustained reduction of abundance of the fish to a level well below the pre-fishing stock size, with hopes for survival of the stock dangling by the seemingly precarious conceptual thread of compensation, may at first seem a drastic proposition to the interested layman or the scientist lacking a background in scientific management of fisheries. However, such treatment, rather than being an extreme to which populations can at great peril be pushed, is a normal and ecologically sound treatment that permits fish stocks to operate at maximum productivity. Earlier management models (e.g., the logistic model) predicted that maximum sustained yield would be obtained at an average population level of 50% of the virgin stock. Current more flexible and realistic models (e.g., that of Ricker) indicate that, for the stock recruitment relationship characteristic of many important fish, maximum sustained yield would be obtained under exploitation rates of 25–75% and that the average equilibrium level of the populations at maximum sustained yield would be less than half the virgin stock level (Ricker 1958, p. 239, 268). The broad experience sampled in Table 2 confirms these management tenets, and the tenets provide a basis for assessing the limits within which fish populations can be managed safely by man. It is not suggested here that harvest of fish by fishermen and power plants up to the level of maximum sustained yield is socially desirable, but simply that it is ecologically safe.

Yield statistics from commercial and sport fisheries provide another reflection of the capacity of fish stocks to sustain themselves in the face of substantial man-induced mortalities. The relatively unproductive Great Lakes of North America have produced yields from 1 to 7 lb per acre per year; a

Table 2. Summary of published estimates of exploitation rates in fish populations

Name of species		Exploitation rate, %	Location	Reference
Scientific	Common			
<i>Alosa sapidissima</i>	American shad	25	Connecticut River, Conn.	Walburg 1960
<i>Amphiphetes rupestris</i>	Rock bass	16 24	Oliver Lake, Ind. Escanaba Lake, Wis., 1946-69	Gerking 1950 Kempinger et al. 1975
<i>Aplodinotus grunniens</i>	Freshwater drum	47 58 31	Upper Miss. River impoundments, 1944-48 Upper Miss. River impoundments, 1944-48 Upper Miss. River impoundments, 1944-48	Butler 1965 Butler 1965 Butler 1965
<i>Clupea harengus</i>	Atlantic herring	29 10 42 25	South coast, Ireland, 1906-36 South coast, Ireland, 1951-55 South coast, Ireland, 1956-60 South coast, Ireland, 1961-63	Burd and Bracken 1965 Burd and Bracken 1965 Burd and Bracken 1965 Burd and Bracken 1965
<i>Coregonus clupeaformis</i>		40 21	Georgina Bay, Lake Huron Lake Superior	Cucin and Rejcek 1965 Dryer 1964
<i>Cynoscion nebulosus</i>	Spotted seatrout	19	Pine Island, Fla., 1961	Iversen and Moffett 1962
<i>Esox lucius</i>	Northern pike	38 14 32-49 23 46 32 50 22-28	Fletcher Floodwater, Mich. Lake George, Minn. Grove Lake, Minn. Ball Club Lake, Minn. Escanaba Lake, Wis., 1946-69 Murphy Flowage, Wis. Wisconsin waters Grace Lake, Minn.	Christensen and Williams 1959 Groebner 1964 Groebner 1964 Johnson and Peterson 1955 Kempinger et al. 1975 Snow 1958 Threinen et al. 1966 Wesloh and Olson 1962
<i>Esox masquinongy</i>	Muskellunge	27 14-70	Escanaba Lake, Wis., 1946-69 Nogies Creek, Ont., 1952-60	Kempinger et al. 1975 Muir 1963
<i>Gadus morhua</i>	Atlantic cod	11 25	Gulf of St. Lawrence, 1949-52 Gulf of St. Lawrence, 1955-65	Palohelmo and Kohler 1968 Palohelmo and Kohler 1968

Table 2 (continued)

Name of species		Exploitation rate, %	Location	Reference
Scientific	Common			
<i>Hippoglossoides platessoides</i>	American plaice	31	Gulf of St. Lawrence	Powelles 1969
<i>Ictalurus nebulosus</i>	Brown bullhead	25	Shoe Lake, Ind.	Ricker 1945
<i>Ictalurus punctatus</i>	Channel catfish	30	Sacramento Valley, Calif.	McCannon and LaFauce 1961
<i>Lepomis gibbosus</i>	Pumpkinseed	29	Escanaba Lake, Wis., 1946-69	Kempinger et al. 1975
<i>Lepomis macrochirus</i>	Bluegill	25 35 42 15-20 36	Sugar Loaf Lake, Mich. Gordy Lake, Ind. Escanaba Lake, Wis., 1946-69 Muskellunge Lake, Ind. Spear Lake, Ind.	Cooper and Latta 1954 Gerking 1953 Kempinger et al. 1975 Ricker 1945 Ricker 1955
<i>Lepomis microlophus</i>	Redear sunfish	29 23	Gordy Lake, Ind. Muskellunge Lake, Ind.	Gerking 1953 Ricker 1945
<i>Micropterus dolomieu</i>	Smallmouth bass	05-18 22	Oneida Lake, N.Y. Wauwassee Point, Lake Michigan	Forney 1961 Latta 1963
<i>Micropterus salmoides</i>	Largemouth bass	17 36 20 20-48 14 11 12	Oliver Lake, Ind. Gordy Lake, Ind. Clear Lake, Calif. Southernland Res., Calif. Gladstone Lake, Minn. Browns Lake, Wis., 1953 Shoe Lake, Ind.	Gerking 1950 Gerking 1953 Kimsey 1957 LaFauce et al. 1964 Maloney et al. 1962 Mraz and Threinen 1957 Ricker 1945
<i>Perca flavescens</i>	Yellow perch	15	Escanaba Lake, Wis., 1946-69	Kempinger et al. 1975
<i>Pleuronectes platessa</i>	Plaice	49 33	North Sea, 1929-38 North Sea, 1950-64	Beverton and Holt 1957 Gulland 1968

Table 2 (continued)

Name of species		Exploitation rate, %	Location	Reference
Scientific	Common			
<i>Pomoxis nigromaculatus</i>	Black crappie	11 26 40	Oliver Lake, Ind. Escanaba Lake, Wis., 1946-69 Coast of Nigeria, 1961-62	Gerking 1953 Kempinger et al. 1975 Longhurst 1964
<i>Pseudotolithus typus</i> , <i>P. senegalensis</i>	Rainbow trout	13-17 20-26	New York streams New York Lakes	Hartman 1959 Hartman 1959
<i>Salmo gairdneri</i>	Atlantic salmon	66	Little Codroy River, Newfoundland, 1955-63	Murray 1968
<i>Salmo salar</i>	Brown trout	23	Sydenham River, Ont., 1966-67	Marshall and MacCrimmon 1970
<i>Salvelinus fontinalis</i>	Brook trout	59 19-75	Sydenham River, Ont., 1966-67 Lawrence Creek, Wis.	Marshall and MacCrimmon 1970 McLadden 1961
<i>Stizostedion vitreum</i>	Walleye	29 27 20-40 15-28 07 13 34 05	Escanaba Lake, Wis., 1946-69 Many Point Lake Minn. Escanaba Lake, Wis. Spirit Lake, Iowa Niipigon Bay, Lake Superior, 1955 Niipigon Bay, Lake Superior, 1956 Niipigon Bay, Lake Superior, 1957 Fole Lake, Mich.	Kempinger et al. 1975 Olson 1957 Patterson 1953, Niemuth et al. 1959 Rose 1947, 1955 Ryder 1968 Ryder 1968 Ryder 1968 Schmeler 1969
<i>Tilapia esculenta</i>		49 42 32 34	Lake Victoria, Africa, 1958-59 Lake Victoria, Africa, 1959 Lake Victoria, Africa, 1959-60 Lake Victoria, Africa, 1960	Garrod 1963 Garrod 1963 Garrod 1963 Garrod 1963

productive North Sea fishery has yielded about 27 lb per acre, Escanaba Lake in Wisconsin has yielded 4–41 lb per acre over a 24-year period (the overall average being 20 lb per acre), the Gulf of Mexico's fin-fish catch attributable to estuarine production has averaged about 50 lb per acre in recent years, and commercial fishing in Chesapeake Bay has yielded about 155 lb per acre. Clearly, these substantial removals would deplete fish populations rapidly were those populations unable to compensate through increased survival or reproduction rates.

Experience with the world's major stocks has proven both that they have the capacity to withstand impressively high levels of exploitation and produce a substantial surplus at population levels well below their pre-exploitation abundance, and that they have the ability to rebound to higher levels of abundance after being heavily exploited if fishing intensity is reduced. This is entirely in keeping with the concepts of population dynamics, and there is important empirical proof of this recovery capacity. Fishing reduced the plaice stock in the southern North Sea to one-third or one-half its original abundance, but relaxation of fishing during wartime rapidly doubled its size (Cushing 1975, p. 135). The Pacific halibut population decreased by a factor of 7 during a 20-year period of fishing, then increased in size when protected by a closed season (Fukuda 1962). A North Sea herring stock was reduced to one-tenth its previous abundance during a 12-year period and subsequently began to increase as a result of reduced fishing pressure (Cushing 1975, p. 136). Sturgeon fishing in the Amur River basin was banned for 12 years to restore overfished stocks; by the end of the ban, the proportion of sexually mature fish had increased sixfold and the average size and age of fish had increased as well – evidence of restoration of the stock (Krykhtin 1972). Similar examples are reported for the whitefish of Lake Wabamun (Miller 1949) and for lake trout of Lake Opeongo (Fry 1949). Thus, reductions in fish stocks caused by exploitation have commonly been proven to be reversible.

APPLICABILITY OF FISHERY EXPLOITATION PRINCIPLES TO POWER PLANT IMPACTS

Cushing (1975, p. 138–139) points out that "Many populations of wild animals are exploited but the commercial fish stocks are numerous . . . No other wild populations have been so well documented for such long periods of time." This imposing body of accumulated experience with fish populations has provided the basis for the development of successful management principles in fishery science. However, are these principles and the experience from which they are derived, based as they are on fishery exploitation of the (usually) mature age groups of a stock, applicable to the situation in which some fraction of the earliest life stages (eggs, larvae, and juveniles) is cropped by entrainment and impingement? Can the contention that "The agent of

mortality — predatory fish, commercial or sport fisherman, or power plant — is an indifferent matter from the standpoint of population response" be sustained? The questions are important ones. If answered affirmatively, any empirical evidence for compensation in a particular stock, in combination with one of the generally proven compensation models based upon the entire foundation of fishery-management science (e.g., Ricker or Beverton-Holt stock-recruitment function), can be used to provide estimates of power plant impact. This taking into account of compensation would greatly increase the degree of realism associated with assessing the effects of power-plant-induced mortality on fish populations.

It turns out that the question whether it is different (possibly worse) to kill young fish than to kill older fish was answered more than 20 years ago by Ricker (1954, p. 607):

Exploitation that takes fish at an age when natural mortality is still compensatory means, for practical purposes, a fishery for young during the first year or two of their life — the earlier the better. The removal of such young is at least partly balanced by increased survival and/or growth of the remainder; in fact, the effects of removals at this stage are equivalent to reduction of the spawning stock which produced the brood in question. If the reproduction curve for the population is of any of the types 3–8, such reduction will at first increase net production of recruits, which will produce more eggs and permit a larger catch of young in future years. This ascending spiral of abundance may continue until the level of stock is reached which produces maximum recruits.

Ricker goes on to say "... it is clear that any general prejudice against exploiting young fish is unsound." Ricker's analysis of the situation has not been challenged. Insofar as population response is concerned, no different principles are involved. Killing some fish during the egg, larval, and juvenile stages (which is what power plants do) is no worse than killing the parents that would have produced these young (which is what fisheries do). The entire foundation of fishery management experience and principles, therefore, can be applied with confidence to problems of power plant impact. It can be reasoned that fish populations can readily sustain "exploitation" by power plants at levels comparable to those experienced in commercial and sport fisheries. In a well-managed fishery, an annual exploitation rate of 50% or more for some species might well be a goal eagerly sought by fishery managers and fishermen rather than a threat to be guarded against. Even for species with rather low compensatory capacity, an exploitation rate of approximately 30% and reduction of the stock to about 46% of its pre-exploitation abundance would be necessary to achieve the very conventional goal of maximum sustained yield (Ricker 1958, p. 268).

As has been pointed out, the workability of such management plans, based on current fishery concepts and models, has been directly proven by

empirical data such as that summarized in Table 2. A 50% exploitation rate in a fishery, however, is not likely to be comparable to a 50% exploitation rate caused by a power plant. Once a particular year class of fish becomes vulnerable to a fishery, it is likely to be exploited during each remaining year of its life, although the rate may vary with age. For example, assuming recruitment to the fishery at age 4, a 50% exploitation rate could well mean that half the members of age class 4 are captured, half of the survivors of age class 4 are captured at age 5, and so on for older age classes.

Compared with this annually repeated fishery mortality, a 50% exploitation rate caused by a power plant, which would affect each year class only once during its lifetime (during the first year when the young are entrained or impinged), would represent a very much smaller mortality. What relative impacts, measured in terms of stock reductions, the two mortalities would be translated into depends on the characteristics of the fishery. Clearly, the power plant mortality, falling as it does on the very young, precedes the age of first reproduction. The fishery mortality, on the other hand, could begin several years after the fish first reproduce, and some part of the population's reproductive potential would then be protected from reduction. However, most fish reach a size desirable in sport or commercial fisheries by the age at which they make significant reproductive contributions. Therefore, the common case will be for a given exploitation rate caused by a fishery, and hence repeatedly imposed in successive years on each year class of fish, to translate into a greater impact than would the same exploitation rate caused by a power plant, and hence imposed only once on each year class.

In most real-world situations, power plant impact would be added to a pre-existing fishery exploitation rate rather than applied to an unexploited stock. Even in this case, however, the addition of an exploitation rate greater than 25% to a pre-existing fishery exploitation rate of 25% would not endanger the stock of many species.

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