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Fisheries Dynamics and the Concept of Maximum Equilibrium Catch

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Development of the concept of maximum equilibrium catch

Although fishing is one of man's oldest occupations, and many of the sea fisheries are very ancient, they were generally, until modern times, of rather low intensity. Consequently the "overfishing" problem did not arise. With the application of power to fishing vessels (first steam and later internal combustion engines) beginning in the latter part of the last century, the amount of fishing and the total catch from the sea fisheries rapidly increased. The catch did not generally increase as rapidly as the fishing effort, however, and in such heavily fished areas as the North Sea questions soon became acute as to the effects of heavy fishing on the fish stocks and as to possible damage to future harvests of too intensive a fishery. Obtaining quantitative answers to such questions became the business of a large number of researchers. A good many of us are so engaged at the present time.

The first question, of course, is whether the amount of a given kind of fish which man is able to take from the sea is sufficient to have any noticeable effect at all on the supply. This matter was discussed very early by McIntosh (1889), Garstang (1900), and others. It was a controversial matter then, and continued so for some years. The subsequent history of the fisheries for the North Sea demersal species, the Pacific halibut, the haddock of Iceland and of the Northwest Atlantic, and of numerous other fisheries, leaves little doubt on this score. There is yet a good deal of controversy among students of these matters as to the relative importance of fishing, as opposed to other causes of changes of population abundance and catch, on particular fish stocks. However, nearly all researchers are convinced that a modern commercial fishery can, and sometimes does, have a pronounced effect on the fish populations being exploited, and that it can become so intense as to reduce the population to a degree that the harvest may also be diminished. There are still those, however, who will not agree to the latter point. Huntsman (1953), for example, states that "The high reproductive rate that obtains in most fishes . . . permits man to remove very large proportions of populations of fish in suitable environments without affecting future generations of the fish. It gives also the likelihood that fishing will never be so intense as to decrease the take of fish in the long run, except where practically the whole stock can be removed." And again, "There seems to be no good basis for restricting fishing in order to increase the long term yield." Dr. Huntsman appears to believe that the very obvious changes which have taken place in the yields of a number of our great fisheries, and which are well documented by sound statistical data over many years, are merely results of natural fluctuations in population numbers, and that the very clear relationship of these changes to changes in the intensity of fishing is purely coincidental. Since the same pattern of changes in catch and in catch per unit of fishing effort has been observed to follow increased intensity of fishing in a good many fisheries, as shown for example by Russell (1939, 1942), this would seem to beg too much of coincidence. Most convincing of all, perhaps, is the very notable effects on some North Sea and Atlantic fish stocks of the respites from fishing which occurred during the two world wars, and which have been discussed in scientific symposia under the auspices of the International Council for the Exploration of the Sea, the last having been held in 1947.

The sequence of events when a stock of fish is subjected to a fishery of increasing intensity is well known. In the early period of the fishery, when the annual catch is small, the average catch per unit of effort is high, corresponding to a high abundance of the fish population. With increasing intensity the annual catch increases, though not in proportion to the increased intensity of fishing; meanwhile the abundance decreases. Eventually, if the fish are sufficiently valuable to make fishing economically possible at quite low population levels, as the intensity is still further increased, the total catch falls off as well. Finally, when the abundance has fallen to a point where the fishery is not attractive to more fishermen, the intensity ceases to increase, and may even decrease, so that the amount of fishing and the catch tend to remain at a more or less constant level. This level is determined, of course, not by the total catch but by the catch per unit of effort and the value of a unit of catch.

This sequence of events seems capable of a rather simple interpretation in terms of the dynamics of the fish stock. Initially, when there is no fishing, the natural losses from the stock are, on the average, just equal to the increments to the stock due to reproduction and growth. With the removal of a part of the stock by fishing, it is reduced to a lower abundance, but at this lower abundance its rate of replacement is larger, so that the removals from fishing are at least partially offset by the ability of the fish at lower population levels to reproduce, survive and grow better. The amount which the population can produce by the annual excess growth and reproduction over losses due to natural causes we may term the natural rate of increase for the given level of population. If, at any level of population, only that amount is caught each year which is capable of being produced each year by this natural rate of increase, the population, and the catch, would remain stabilized on the average. The catch which can, on the average, be obtained at a given level of population, without resulting in any net change in the size of the population, may be termed the equilibrium catch, because it is the catch which is in equilibrium with the productivity of the population at the given level.

Now, as the fishery becomes increasingly intense and continues to remove each year a catch in excess of the equilibrium catch, the population falls continuously. The natural rate of increase and the corresponding equilibrium catch, however, rise for a time as the population falls. There is eventually reached a population level at which the equilibrium catch is maximal. Further increase in fishing intensity drives the population down to levels where the natural rate of increase, and the corresponding equilibrium catch, is less than the maximum. This is the writer's concept of what is meant by "overfishing."

It should be pointed out, as has been indicated by Thompson (1952), that the intensity of fishing which will be applied, not only to the population as a whole, but to each separate component, depends on the density of the stock, which is detected by the fishermen as the catch per unit of effort expended. In attempting to maximize their profits fishermen will constantly attempt to fish the greatest concentrations of fish, so that the stock and each of its components in an unregulated fishery is reduced to that level at which further increase in effort proves to be no longer profitable. Thus, the population level at which the fishery will tend to stabilize itself bears no necessary relation to the level of maximum equilibrium catch, but may be above or below it, depending on the unit value of the catch. If the unit value of the catch is sufficiently low, the fishery will cease to increase in intensity before the level of maximum equilibrium catch is obtained, and overfishing is, in this case, not economically possible. For a good many of the sea fisheries, however, it has been shown by experience that the unit value of the catch is large enough so that the intensity can and does increase to a degree that reduces the equilibrium catch below the maximum.

Objectives of research on fisheries dynamics

It is conceived here that among the primary practical objectives of research on the dynamics of commercial fish populations and the fisheries on them are:

1) To determine for a commercial fish stock whether the existing population level is above or below that corresponding to the maximum equilibrium catch.
2) To provide estimates of the population level, and corresponding fishing intensity, which will provide the maximum equilibrium catch.

In attaining these objectives, fisheries researchers are, of course, faced with a number of difficulties arising from the complexities of the biology and ecology of fish populations. Most outstanding, perhaps, is that the concepts of the population-dependent natural rate of increase and the corresponding equilibrium catch can be applied only to average values of a number of years, since, due to the great variability of environmental and biological factors affecting recruitment, growth, and mortality, the actual increments to the population vary a good deal from year to year. In application, this variation from the mean values must be discounted. In a good many fisheries, particularly those using trawls or gill nets, the gear is selective by size of fish, so that not only the magnitude of the stock but its size composition is to be considered, since, by regulation of mesh sizes, the intensity of fishing on different sizes of fish may be controlled. Again, as has been pointed out by Dunlop and Bell (1952), a stock of sea fish may consist of a number of components, semi-discrete in their seasonal behavior patterns, upon which the intensity of fishing may bear unevenly. Although these and other problems make difficult the most refined estimates, the application of some rather simple theory, developed during the last few decades, has made possible considerable progress toward the objectives stated above. It is, at least, possible to calculate sufficiently good approximations for the improvement of the catch of many sea fisheries by control of fishing effort or catch.

General formulation of the problem of estimating equilibrium catch

In order to treat quantitatively the problem of estimating equilibrium catch and maximum equilibrium catch, it is necessary to erect some mathematical model. Except for the work of Baranov in 1918, which did not come to the attention of most students until the 1930's, one of the first formulations of the problem was given by Russell (1931), who formulated the matter in sufficiently general terms to serve as an excellent basis for discussing contemporary as well as more recent development. Russell stated the matter essentially as follows:

If P_1 represents the weight of the catchable stock at the beginning of a year, and P_2 represents the weight of the catchable stock at the end of that year

$$P_2 = P_1 + A + G - M - C \quad \ldots\ldots\ldots\ldots \quad (1)$$

Where:

A is the amount by which the stock of fish of catchable sizes is increased in weight by recruitment of new individuals during the year

G is the increase in weight of the stock by growth during the year

M is the loss in weight of the stock by natural deaths during the year

C is the weight of the annual catch

If we put this in a slightly different form

$$P_2 - P_1 = A + G - M - C \quad \ldots\ldots\ldots\ldots \quad (2)$$

it may be seen that this states the obvious fact that the change in the weight of the stock is equal to the additions to the stock by recruitment and growth, less the subtractions by natural mortality and fishing. Obviously, when C is greater than $A + G - M$ the stock decreases, when C is less than $A + G - M$ the stock increases, and when C is exactly equal to $A + G - M$ the net change is zero.

The sum of the three terms $(A + G - M)$ is, of course, what we have referred to earlier as the natural rate of increase, and the catch when $C = A + G - M$ is the equilibrium catch.

The problem, then, reduces to the estimation of the value of $(A + G - M)$ for different values of P. Since, as Russell pointed out, the several terms are inter-connected biologically, the value of this sum will vary with P, and there will, in general, be some maximum value, which we wish to determine.

Attempts to apply the equation (2) — or an equivalent formulation — to fisheries dynamics have been of two kinds. One approach, which has received the greatest attention in recent years, is by way of estimating the individual terms for recruitment, growth, and mortality and combining them to estimate the equilibrium catch. The other approach is to consider the sum of these terms (the natural rate of increase) as a function of P having a specified form, and to determine the parameters from the available numerical data.

Approach by combination of elemental rates

The earliest work known to the author is that of Baranov (1918). This pioneer writer assumed that the number of fish recruited annually to the population is constant for all sizes of population. He assumed that growth is age-specific but independent of size of population; his assumption here was that the length of the fish is directly proportional to their age, and that the weight of a fish is proportional to the cube of its length. He assumed that the percentage rate of natural mortality is constant. He assumed that the instantaneous rate of fishing mortality is proportional to the fishing intensity (number of units of fishing effort). Under these assumptions he computed the equilibrium catch for a population of fish, having a specified rate of increase of length with time, for various values of natural mortality rate and fishing intensity.

Thompson and Bell (1934) computed the equilibrium catch for various rates of fishing mortality, under the assumptions that recruitment is constant, percentage rate of growth is constant, and percentage rate of natural mortality is constant. They also computed changes in population and yield which would be expected in the halibut fishery, assuming recruitment constant, percentage rate of natural mortality constant, growth to be age-specific (using average age-weight data from samples of the stock), but constant at each age for all sizes of population, and instantaneous fishing mortality rate to be proportional to number of units of gear fished. With these simplified assumptions they found the calculated changes in abundance and catch corresponded rather well with the actual changes over the period of years examined.

Ricker (1944), in reviewing this type of calculation, points out that the assumptions that certain of the rates involved remain constant when the fishing effort — and consequently the size of the population — changes do not correspond to reality, so that such calculations cannot be valid over a very large range of population sizes. In point of fact the rates of recruitment, growth, and natural mortality may all be expected to be dependent on population density.

Parrish and Jones (1953) have computed the equilibrium catch assuming recruitment constant, percentage rate of natural mortality constant, and growth rate to be age-specific, following a particular mathematical form due to Bertalanffy, but constant at each age for different population densities, and the instantaneous fishing mortality rate to be proportional to the amount of gear fished. They have computed curves of equilibrium catch versus rate of fishing for two different values of natural mortality rate. They state, however, "Of course, these curves are not valid over their whole range, since with increase in stock density, there will possibly be some decrease in growth rate and increase in natural mortality rate, so that the ordinates to the left of the curve (lower fishing intensity) are probably over-estimates." Since recruitment must fall off, also, at very low levels of population, the values computed for very high fishing rates are doubtless also over-estimates.

Beverton (1953) has made similar calculations, based on the same assumptions and similar methodology, to those of Parrish and Jones. He has also made calculations of the variations in equilibrium yield for a trawl fishery, where the effect of variation in age at recruitment, due to regulation of size of mesh of net, is taken into account.

This type of approach seems adequate to indicate when a fishery has been overfished, and to indicate the direction regulations need to take. Quoting Beverton (1953) " . . . the model can establish the main dynamic properties of a fishery and can indicate the first steps which are required to regulate it, but for making accurate predictions of the regulation required and of its probable effects it is necessary to take other factors into account. Of particular importance here is the variations of the parameters of population density. . . . Introducing phenomena of this kind makes the model more realistic and gives it the properties of 'self-compensation' which are characteristic of natural populations. . . ."

The introduction of variations of the elemental rates with population density into such a model presents a good many complexities, and the writer knows of no stock of sea fishes for which enough is known about these relationships to make possible any precise calculations.

Approach from law of population growth

An alternative approach to the problem is possible, as indicated earlier, if we consider the *sum* of the terms A + G — M in Russell's equation, which we call the natural rate of increase, to be a function of the size of the stock of fish of catchable size. Considered from this aspect, Russell's equation takes the form

$$P_2 - P_1 = \overline{f(P)} - C \quad \ldots\ldots\ldots\ldots \quad (3)$$

where $\overline{f(P)}$ represents the annual natural rate of increase corresponding to the mean stock during the year. If we can specify the form of $\overline{f(P)}$, it may be possible to compute its parameters from catch statistics and other data, and so estimate the equilibrium catch for various magnitudes of stock, or intensities of fishing.

The earliest consideration of this approach to fisheries data was made, quite independently of Russell, by Hjort, Jahn and Ottestad (1933). These authors employed the "auto-catalytic" or "sigmoid" growth law of populations to show that the natural rate of increase — which is, of course, equal to the equilibrium catch — has a maximum value at some intermediate level of population.

Bückmann (1938) and Graham (1939) have also discussed the theory of this approach in a general way. Graham (1935) has applied this approach in a rough way to the estimation of the equilibrium catch of the demersal fish stocks of the North Sea. He has assumed that "the 'logarithmic' rate of natural increase of the stock at a given moment is directly proportional to the difference between the weight of the stock at that moment and the maximum weight the area will support." In our notation, he assumes, essentially,

$$\overline{f(P)} = K_1\overline{P}(L - \overline{P})$$

where K_1 and L are constants. He applied this to the data of the North Sea demersal fish stocks by estimating the essential constants in this equation from consideration of the increase in stock which resulted from the decrease in fishing intensity during the first World War, plus certain tagging data employed to estimate the natural rate of increase at one level of population. This method of computation was, admittedly, somewhat approximate.

Graham (1953), in a review paper, has stated that the difficulty in employing this approach is that "in order to fit these curves to data, it is necessary to have knowledge of the yield and population density under several steady states of fishing." It seems possible, however, that the equation may be fitted to data even where the fishing rate is constantly changing. The writer has, therefore, studied the problem of applying this approach, (Schaefer 1954). Results are briefly reviewed here; for details the reader is referred to the original paper.

Returning to equation (3) and writing ΔP for the change in population during the year, we have

$$\Delta P = \overline{f(P)} - C \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (4)$$

If we may assume, as is usually done in fisheries dynamics, that the catch per unit of fishing effort is proportional to the mean population encountered by the fishery during the year, and that the instantaneous rate of fishing mortality is proportional to the intensity of fishing (number of units of fishing effort), we obtain

$$\Delta P = \overline{f(P)} - K_2F_t\bar{P} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (5)$$

where F_t is the total number of units of effort during the year, $\bar{P}$ is the mean population, and K_2 is a constant.

K_2F_t is, of course, the instantaneous fishing mortality rate, so that K_2 may be evaluated from data of marking experiments, or by other means.*

Since $K_2\bar{P} = U$, where U is the catch per unit of effort, which is available from the usual catch statistical data, we can, knowing K_2, estimate $\bar{P}$ for each year of a series for which suitable catch statistics are available. From the series of values of $\bar{P}$ we can estimate the population at the beginning and end of each year, approximately, by interpolation, and thus estimate ΔP. Given estimates of ΔP and the catch, we can estimate $\overline{f(P)}$ for each year of the series.

When we plot the estimates of $\overline{f(P)}$ against $\bar{P}$, the points would fall on a curve if there were no other influences than the population growth law relating these two variables. Actually, due to effects of variable environmental factors, measurement errors, and other unaccounted-for sources of variation, the points will scatter about an average curve. By observing the trend of $\overline{f(P)}$ against $\bar{P}$, however, we may ascertain how the equilibrium catch varies, on the average, with population size.

This may be illustrated by the data of the Pacific sardine fishery. The constant K_2 was evaluated from data of tagging experiments. In Figure 1 is shown the values of $\overline{f(P)}$ estimated for the years 1933 through 1950, plotted against U (which is proportional to $\bar{P}$). It may be seen that although there is a good deal of scatter, the trend of the relationship is clearly evident.

Similarly, for Pacific halibut of the southern grounds (Area 2), we have estimated the constant K_2 from tagging data. Using this and the record of catch and catch per unit of effort, we have made estimates of equilibrium catch for each year from 1916 through 1946. In Figure 2 are plotted these values of estimated annual equilibrium catch, $\overline{f(P)}$, against the corresponding values of $\bar{P}$ (and U). The means of these values of $\overline{f(P)}$ for each ten units of U have also been plotted (the centers of the crosses). It may be seen that $\overline{f(P)}$ increases with stock size up to a catch per unit of about 80 pounds per

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* Thompson (1950) has estimated this constant for the Pacific halibut by considering the changes in catch and stock over a period of years when the stock declined and then returned to near its original condition. His method of calculation involves, however, the assumption that $\overline{f(P)}$ is constant over the period. This assumption obviously is not acceptable over more than a very small range of stock sizes.

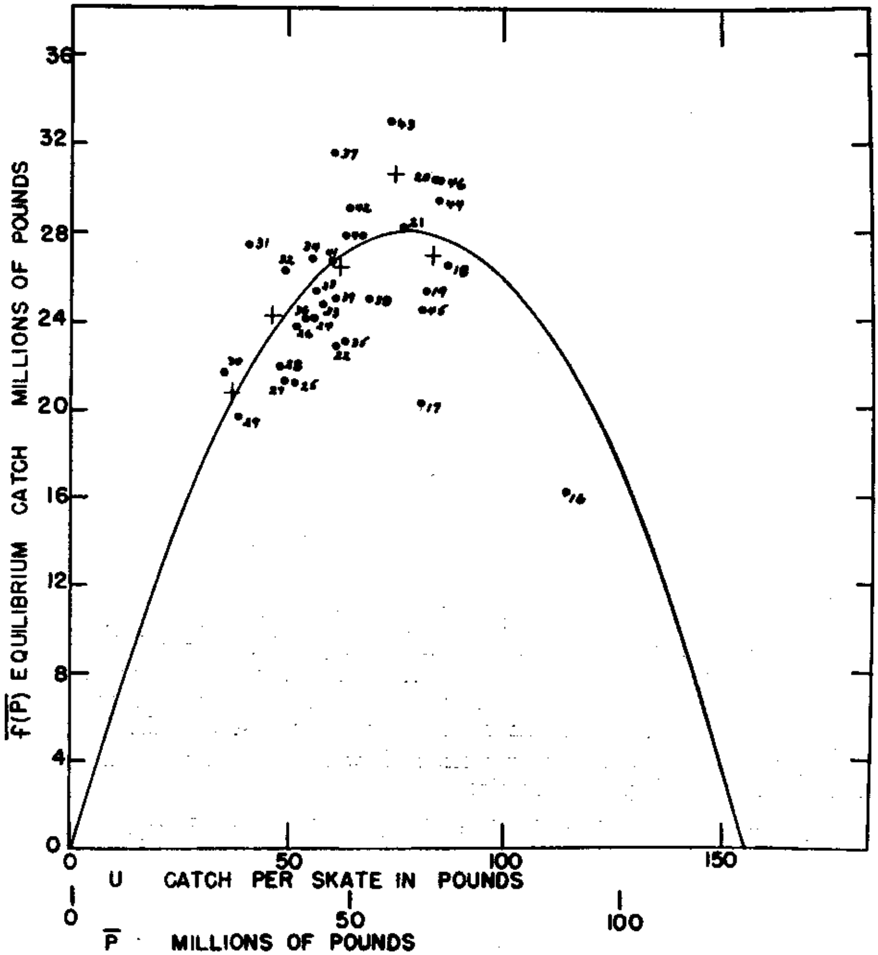

FIGURE 1—Relationship between population and estimated equilibrium catch, Pacific sardine. (Numbers indicate calendar years to which points correspond.)

skate, at least, corresponding to a mean population of some 62,000,000 pounds.

If we further specify the form of the relationship between $\overline{f(P)}$ and $\overline{P}$, or U, which is the same thing, we may fit a curve of the specified form to the points on these graphs. There seems to be reason to believe that the Verhulst-Pearl logistic adequately describes the growth of marine fish populations. This law

$$\overline{f(P)} = K_1\overline{P}\,(L - \overline{P}) \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (6)$$

is the same employed by Graham (1935) as a basis for his analysis of the North Sea demersal fish stocks.

Specifying a curve of this form, we have fitted a curve to the sardine data, under a criterion of least squares, as illustrated in Figure 1. From this curve we would estimate that the maximum equilibrium catch is about 600,000 tons per year at a mean population level corresponding to a catch per unit of effort of 692 tons per boat month.

Similarly, for the Area 2 halibut data, fitting a curve of this form to the data of Figure 2, we obtain a curve with a maximum at a mean population level corresponding to a catch per skate of 78 pounds. At this population level the estimated equilibrium catch is 28.2 million pounds per year.

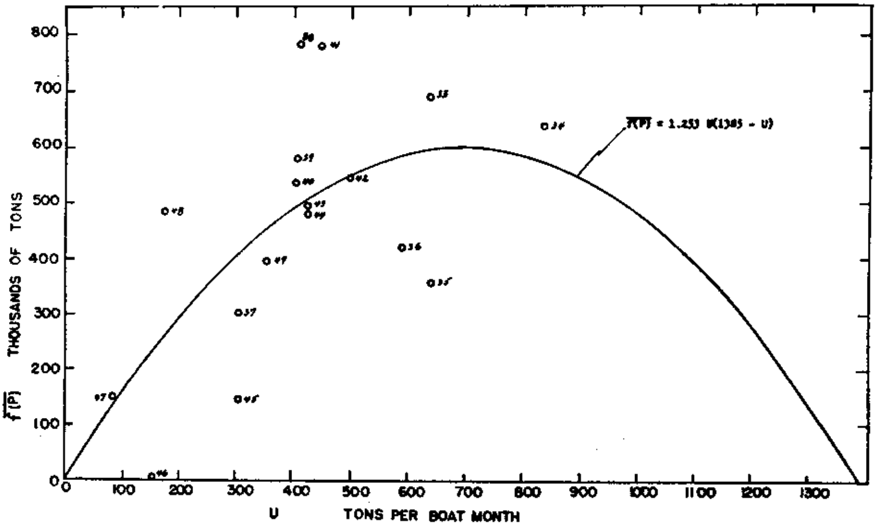

FIGURE 2—Relationship between population and estimated equilibrium catch, Pacific halibut south of Cape Spencer (Area 2). (Numbers indicate calendar years to which points correspond.)

Combining equations (5) and (6) we may arrive at a form of the logistic equation which is perhaps somewhat superior for illustrating both the dynamics of a fishery and its history. We obtain

$$\Delta P = K_1\overline{P}(L - \overline{P}) - K_2F_t\overline{P} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (7)$$

and, substituting $K_2\overline{P} = U$

$$\Delta P = \frac{K_1}{K_2^2}\, U\, (L_U - U) - F_tU \quad . \; . \; . \; . \; . \; . \; . \; . \; . \quad (8)$$

where $L_U = K_2L$, L, of course, is the upper limit of the stock which can exist under average conditions and L_U is the corresponding catch per unit of effort.

In a state of equilibrium, $\Delta\overline{P} = 0$, we have

$$F_t = \frac{K_1}{K_2^2}\,(L_U - U) \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (9)$$

which defines the relation between intensity and stock when the catch and natural rate of increase are in equilibrium. We may call this the *line of equilibrium conditions.*

If, now, we plot the line of equilibrium conditions, and on the same graph plot the fishing intensity and catch per unit of effort (F_t, U) for each year, we have a graphic illustration of the effect of fishing on the stock, and the historical course of changes in fishing intensity, stock, and catch, in relation to the equilibrium catch. Such a diagram is shown in Figure 3 for the Pacific halibut of the southern grounds, the constants for the line of equilibrium conditions having been estimated as described above.

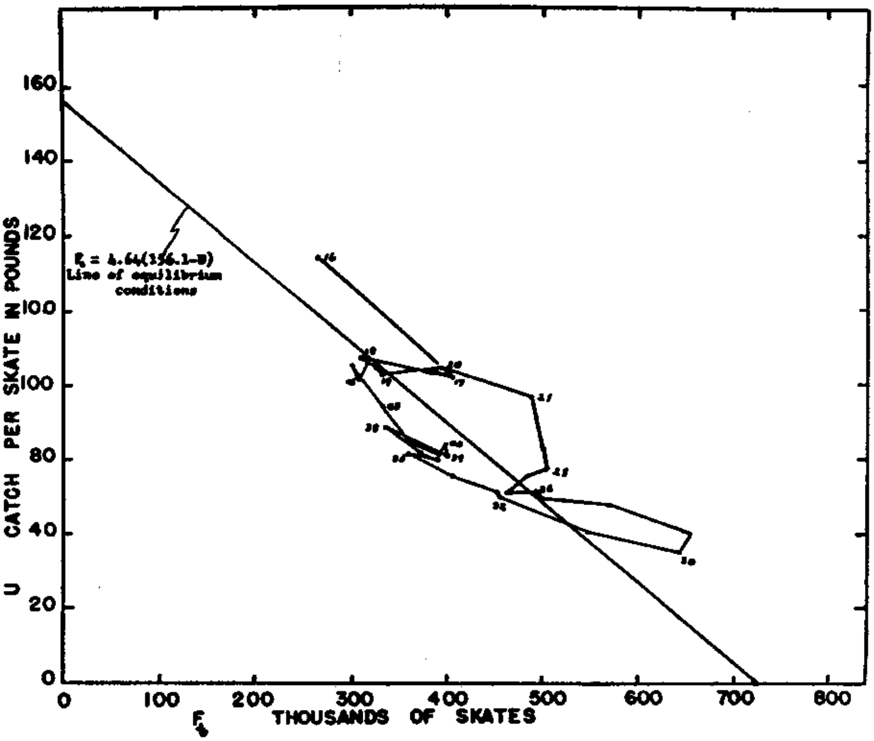

FIGURE 3—Relationship between intensity of fishing and mean population, Pacific halibut south of Cape Spencer (Area 2), 1916 to 1947.

In such a diagram as this, if (7) adequately describes the effect of stock size on natural rate of increase, and effect of fishing on the stock, we will expect that when (F_t, U) falls above the line of equilibrium conditions (the catch being greater than the equilibrium catch for the given size of stock) the population and the catch per unit of effort will decrease. Conversely, when (F_t, U) falls below the line of equilibrium conditions, the stock and catch per unit effort will increase.

We may see that the course of events in the halibut fishery was just what would be expected from the theory. From 1916 until 1930, the points fall generally above the line of equilibrium conditions, and the stock is rather steadily decreasing. Regulation of the fishery — which curtailed the fishing intensity — commenced in 1931. From 1932 to 1947, during which the stock was being built up, the values of (F_t, U) fall below the line of equilibrium conditions, approaching it closely in the latter years when the fishery was becoming stabilized under regulation.

This approach — from the laws of population growth—to the estimation of equilibrium catch at different stock sizes, and of the maximum equilibrium catch, seems to be one of the more promising recent developments. in the field of fishery dynamics. It offers a means of estimating the status of a fishery, and indicating the direction, if any, which management needs to take to improve the sustainable catch. It makes possible such estimates without information on age composition, rates of growth, and rates of natural mortality, which are difficult to obtain in sufficient detail for many fisheries. As applied in the foregoing examples, this approach requires data of tagging experiments for estimating one of the essential constants. Alternative procedures which will not require tagging data seem, however, to be possible of development and application. Investigations of this matter have been commenced with encouraging preliminary results. It is hoped to be able to present a practical procedure in the near future. This, of course, is a matter of particularly great importance for the tuna fisheries, in the study of which the writer is primarily engaged, since there we have no tagging data of consequence, and only faint hope of obtaining in the near future an adequate measurement of exploitation rate by such means.

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Changing Concepts In Fishery Research On the Great Lakes

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It must seem illogical to approach the subject of accomplishments of fishery biology on the Great Lakes by detailing certain weaknesses of earlier researchers and points of view. Yet the paradox may not be as grievous as would appear. Surely we may count it an accomplishment to have become aware of defects both in our way of doing and of thinking and to have made a start toward the development of new lines of attack which we feel will make our future efforts more productive.

Before undertaking the painful specification of past shortcomings, let us digress momentarily to give a minimal background on the Great Lakes and their fisheries.[1] The five lakes have a combined surface area of 95,000 square miles—61,000 within U. S. boundaries and 34,000 under Canadian jurisdiction. The U. S. waters of the Great Lakes are shared among eight states, each of which has full jurisdiction over the fisheries within its boundaries. Thus we have altogether nine fishery codes.

Ecological conditions vary widely both between and within lakes — often in contiguous waters. We know, for example, that within the relatively limited confines of an area as small as Green Bay — only 118 miles long and at most 23 miles wide — the life histories of certain shallow-water species differ greatly between the northern and southern ends. It is these highly variable shallow waters that are most productive. This same Green Bay, for example, has contributed 60 to 70 per cent of Lake Michigan's total production in recent years. Only the deeper waters of the three upper lakes and Lake Ontario offer anything even approaching the degree of uniformity and stability of habitat encountered in the open sea.

Commercial production of fish in the Great Lakes is relatively small — characteristically 70 to 80 million pounds in U. S. waters in recent decades — but is economically important. As an illustration, the dollar value of Great Lakes production equalled that of the Pacific sardine when that fishery was at its height. The lakes are without large fishing ports; the catches are

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[1] For accounts of the Great Lakes fisheries at various periods see: Milner (1874); Smith and Snell (1891); Rathbun and Wakeham (1897); Koelz (1926). Gallagher and Van Oosten (1943) gave considerable historical information on the fisheries, offered detailed discussions of problems of regulation, and published all available records of production through 1940. Van Oosten (1938) wrote a historical sketch with special references to State of Michigan waters.