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Abundance and Fishing Success

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Introduction

Knowledge of changes in exploited natural fish populations depends on interpretation of records of fishing success. When put in a form which permits numerical estimation, this interpretation specifies a mathematical or statistical model which defines the dependence of fishing success on abundance and distribution of fish, on fishing techniques and on other contributing factors. In this way the interpretation adopted in a study assumes key importance. It determines the types of data collected, the methods of analysis used, and ultimately, the kinds of conclusions that can be drawn.

Studies of fish abundance known to us have adopted a simple model for a base, more perhaps for its mathematical convenience than for its relevance to the nature of the fisheries studied. This has limited the conclusions about population events which could be drawn from the data, a limitation which has become more evident with increasing demands for knowledge of the details of responses of populations to environmental and fishing factors. Not only has it apparently failed to yield accurate information on past abundance changes in important fisheries, but it makes no explicit provision for measuring the effects of applications of the rapidly advancing technology of fishing on catch.

Because of the central role which fishing models play in our data collections and the inferences we draw from them, it is important to be clear on the interpretation and assumptions underlying them, and to recognize the extent to which they limit or contribute to our understanding. A review of the conditions underlying use of present models leads us to suggest here an alternative interpretation of fisheries, giving rise to a rather different mathematical model. The definitions and relationships it specifies are dictated by the need for a fuller and more fundamental description of the interactions among fish abundance and distribution, fishing operations, and the resulting catch. As might be anticipated, the new model requires data in a somewhat different form than that in which most fisheries statistics are now routinely collected.

I. The Classic Catch Equation

In elementary terms the catch of fish per unit gear operation (C/f) may be considered as some fraction (c) of those fish initially present (S) in the area "swept"by the gear. That is:

$$C/f = cS \qquad (1)$$

In the case where unit operations of the gear do not overlap the fraction c is the probability that a fish in the swept area will be caught by a unit gear operation, or the gear (fishing) efficiency. This concept has been the common point of departure for theories of fishing. The next step has been to determine how the combined catches from a number of localities and over a period of time are related to the whole population under exploitation. This is done by extending equation (1) to the whole population and putting, for f units of effort

$$(C/f)_t = qN_t \qquad (2)$$

where N_t is the population size in numbers at time t, and q, termed the catchability coefficient, is the fraction of the total population caught by one unit of operation. Repeated applications of effort reduce the stock, and considered over a period of time, t, equation (2) must be replaced by

$$\overline{(C/f)}_t = q\overline{N}_t \qquad (3)$$

where $\overline{(C/f)}_t$ and $\overline{N}_t$ are averages over the period t. As first noted by Ricker (194o, 1944), when the population is subject to uniform fishing and natural mortality rates, $\overline{N}_t$ is given by

$$\overline{N}_t = N_o(1-e^{-Z_t})/Z_t$$

where N_o is the population size at time t = o, and Z_t is the total instantaneous mortality rate during time t expressed in terms of the component fishing and natural (instantaneous) mortality rates. That is $Z_t = qf_t + Mt$.

In equations (2) and (3) the analogue of the first simple model of "sweeping" fish from a given area has been preserved. However, since we are considering the whole population, a knowledge of gear efficiency, c, is no longer sufficient to define the relation between abundance and catch. Of the area "A" occupied by the total population, only the area "a" is swept by a unit of gear. Hence the catchability coefficient is defined as

$$q = ca/A$$

From this it is clear that the catchability coefficient is inversely proportional to the area over which the total population is distributed. This is rarely, if ever, known with any assurance, so that in practice, the procedure is often adopted of specifying an area A over which it is assumed that some closed part of the total population is more or less uniformly distributed. Within this defined area we may then attempt to define the average density at time t as

$$D_t = N_t/A$$

and to measure it by use of the catch equation in the form

$$(C/f)_t = q'D_t \qquad (4)$$

In this more frequently used form, the catchability coefficient, q', is defined as the elemental efficiency of the gear times the area it sweeps in the specified area A, hence is the fraction by which application of a unit of effort reduces the average density. The value of q' will still, of course, be sensitive to deviations from the assumption that the population is occupying the whole of the defined area A.

In his original work Baranov (1918) termed q (actually q') the real elemental intensity of fishing, and derived it as the product of fishing efficiency and the geometric intensity of fishing in the population area. The more general term, catchability coefficient, is preferred here since instead of deriving it from component parts as above, we may simply define it as the fraction of the population captured by the operation of a unit of effort, or even more simply as the probability of capturing a fish. The catch equation in this form goes back to Baranov (1918) and independently to Ricker (194o, 1944). A similar equation was derived by Nicholson and Bailey (1935) to describe the number of contacts a predator makes with its prey. It has been used essentially unchanged by all subsequent workers.

Assumptions underlying the catch equations

Catch equations (3) and (4) have been widely used for the interpretation of fisheries data. Given that it is possible to define a closed population of average size $\bar{N}_t$, DeLury (1947) points out that this amounts to assuming that:

1. The units of effort, f, as defined, operate independently,
2. Catchability, q, is constant.

Ways in which these conditions may be fulfilled have been discussed in detail by various authors.

The Baranov Model

The fishery model originally proposed by Baranov was assigned two important properties to fulfil the conditions. First, the population was uniformly distributed over the population area and the fish were considered to be immobile. Second, the area of operation of each unit of gear was independent of the area fished by other units, and of its own previous areas of operation.

That is, the process of fishing was linked to that of random sampling from a homogeneous population. In practice, Baranov recognized that there will of course be variations in the population density on the area. However, if these be random then estimation of the average density and catchability coefficient from commercial catch records for any time period t becomes a straightforward statistical sampling problem.

The Ricker Model

Ricker (194o, 1944) also developed a random sampling type of fishing model, but recognized that this could be achieved with less static underlying conditions than those envisaged by Baranov. Thus the intuitive base for his model was a very mobile population which, if locally depleted, would quickly reinvade the fished area. The condition for uniform exploitation and independence of application of effort units would thus be attained even with stationary gear, so long as the gear units were not dense enough to blanket each other or to impede fish redistributions. He further pointed out that if mobile fleet units were widely dispersed over the area occupied by a moderately mobile population, average catchability obtained from observations of a non-uniformly distributed population would, in the long run, tend to be very nearly the same as that on a uniformly distributed stock.

As noted earlier, Ricker's formulation also took into account the fact that decreases in population size from one period to another were related to natural mortality as well as fishing mortality, whereas Baranov had considered only the latter. This extension has been an important feature of later developments in population abundance studies.

The Nicholson and Bailey Model

A model similar to those applied to fisheries was independently developed by Nicholson and Bailey (1935) with reference to general predator-prey relationships. Their discussions are distinguished by the introduction of the concept of searching. They argued, however, that even where individual predators search systematically, the combined searching efforts by a number of predators will be effectively random as long as they operate independently. This condition is perhaps always fulfilled for the special case they considered of singly occurring parasites (predators) which make only one successful "contact", provided that the activity of the host is unaffected or it is killed outright by the contact. Bailey, Nicholson and Williams (1962) approach a more realistic treatment of the problem by allowing a variable "area of discovery" of hosts by parasites (analogous to fishing efficiency "c" of equation (1)). However, theor more recent model still visualizes the success of searching as proportional simply to the product of area of discovery and average population densities of hosts and parasites. In common with the fishery models, it appears to be insensitive to distribution changes at given population densities.

II. Evidence for Heterogeneity in Distributions

The problem of fitting the catch equation when there is a non-uniform distribution of either the fish or the fishing was appreciated by Baranov (1918), who recognized that it may have had important implications for the interpretation of sampling in Hjort's classical studies of the Norwegian herring fishery. Samples apparently came from separate schools and rarely displayed the full population length-composition. Since the size segregation inevitably involved year-classes which were of rather different strengths, Baranov noted that average catch per unit effort would not represent overall population density if fishermen could effectively concentrate their operations on the schools which were larger because they contained the members of the strong year-classes.

Gulland (1955) has examined the problem of representative sampling for density in the light of his analysis of North Sea haddock and plaice data. He assigned the catch and effort data to the smallest practicable area and time units and calculated the density index for each. For particular periods he then compared the average subarea density index with the overall density index. Since both came from the same population, their ratios should be 1 if the population was uniform throughout. The fact that the weighted subarea density index was about 1/3 larger is thus a measure of the extent to which fishermen were successful in concentrating their effort in subareas where average catch per unit was high, and avoiding those where it was low. Fluctuations in the density index from season to season were indicative of how this was influenced by seasonal movements and concentrations of fish, and the changing preference for fishing particular species at different times of the year.

Similar results were reported by Calkins (1961) as part of a continuing study of the catch statistics for east Pacific tuna populations. Using Gulland's density index he obtained weighted measures of annual catch per unit effort on 6o x 6o mile subareas which were $1\frac{1}{2}$ to 4 times (mean 1.9) the unweighted or overall density index. The ratios of the two indices fluctuated irregularly from season to season. Comparisons among different periods are complicated by the fact that the number of subareas was allowed to vary, a calculation procedure which may have been responsible for an appreciable fraction of the ratio fluctuation. However, the fact that correlation coefficientsbetween the two indices of density were low is likely indicative of changing degrees of concentration of the fishing and heterogeneity in distribution of the fish. Similar conclusions were drawn by Doi (196o) in his study of fish populations in the Strait of Bungo.

Studies of this sort do not, of course, give direct information on the true population density or its distribution. They do, however, confirm the general knowledge that the patterns of distribution of fish and the fishing effort are not uniform throughout the population areas. They also indicate the extent to which attempts to calculate average density may be affected by this heterogeneity. It appears that unless considerable care is taken to account for changes in distribution, measures of relative abundance may be much in error.

Factors contributing to heterogeneity in density indices

The above results leave little doubt that fishing success is markedly influenced by the fisherman's prior knowledge of fishing areas, of patterns of fish distribution, and possibly also the fishing success in various areas at the time he sets out on a fishing trip. However, the skill and selectivity exercised during his operation do not stop at relating his activity to statistical areas of the size used by Gulland, Calkins or Doi, the smallest of which appears to have been of the order of the 3,6oo-square-mile subareas used by Calkins. This fact is well documented in the case of tunas (Orange, Schaeffer and Larmier, 1957), and in fact it appears that most fish occur in schools, small aggregations or concentrations, and it is the fisherman's intention to relate his fishing activities to these local areas of high density. Some indication that he is successful is reflected in general by the high variances and skewed frequency distributions of the catch per unit effort.

Evidence of the nature of local variation in catch has been reported by Maéda (1960) in an extensive study of catch data for tunas of the central Pacific. He found evidence for contagious distributions of the several species taken by Japanese commercial longlines, indicating that there are significant variations in concentration of fish relative to the area effectively "swept" by the commercial gear. Several salmon species showed evidence of "weakly contagious schools" while some benthic species showed strongly contagious distributions. Taylor's (1953) analysis of Georges Bank research vessel data suggests that demersal species in that area are also contagiously distributed. It is not known to what extent these variations may influence catch. However, the evidence of Ochiai and Asano (1955) that the size of a fish school may affect the individual's reactions to capturing gear, especially at low densities, suggests that they are not necessarily related in simple fashion to the fisherman's ability to detect and fish them.

Effects of heterogeneity on measures of abundance change and its relation to fishing effort

From the studies reviewed above, it appears that local heterogeneity in fish distributions, the searching activities of fishermen, and their interactions, may have a significant effect on fishing success. Considering the possibly complex nature of these effects, it is not surprising that actual catch data when analyzed by use of the classic catch equation frequently show inexplicable variations. For example, Beverton and Holt (1957, o.239) were unable to use North Sea catch and effort data for haddock, plaice and other species in regressions of their index of total mortality on effort, to measure average catchability or natural mortality. Their mortality index is essentially the ratio of successive annual average catches per unit effort. They ascribed the high variability about the regression to a combination of "sampling error" and changes in natural mortality rate. Similarly, Taylor (1958) failed to find a significant regression between the same kind of mortality index and estimated effort for the Georges Bank haddock fishery over a 30-year period. Yet, in both cases, total fishing effort during the period of study appears to have changed more than twofold. Paloheimo (1961) points out that evaluation of their results is made somewhat difficult by the fact that their method of calculating mortalities was perhaps unnecessarily sensitive to the types of error found in catch data. But, in any case, area-to-area and season-to-season variations in the distribution of fish and fishing seem likely to lead to difficulties of the sort encountered by these authors. This is supported by an analysis of Japanese sardine data by Yamanaka (1961) in which he demonstrated the effects on the estimation of mortality rates of various types of "availability" change related to movements and concentrations of fish in the areas fished. In view of Calkin's results, variations of a similar sort may be partly responsible for the poor fits of average catch per unit effort and effort data found by Schaeffer (1957) in his approach to the study of changes in tuna abundance, and similar effects were evident in the data for other species as well (Schaeffer, 1954).

In the case of short-term variability in density indices, hence, catchability, Gulland (1961, 1962) implies that the simple relations expected from the basic catch equation might be more readily apparent if the data were to be averaged over rather long periods of time, periods related to the average length of time during which a year-class is exposed to fishing. Here the interpretation of data becomes complicated by climatic trends and technological changes. However, meaningful information on these latter factors is sometimes available as a basis for corrections. In Gulland's examples the data for plaice (Gulland, 1961) and hake (Gulland, 1962) yield considerably better agreement with theory than do data for cod and haddock, the other species studied. Interestingly enough, it is these former species which are frequently captured as so-called "incidental" or "by-catch" when fishermen are directing their principal efforts towards the capture of species such as cod and haddock; that is, fishing for them may more often approach a random sampling process than it does for cod and haddock. However, there is no evidence in the studies reported by Gulland that the difference was actually associated with the fishermen's motives or ability to take advantage of fish concentrations.

Despite the improvement in the fit of catch and effort data which appears to result from averaging over long periods of time, the scatter of points about the expected average relation is still so great as to make choices of an underlying production model border on the subjective (Dickie, 1962). It might be concluded then that treatments of this sort have not effectively circumvented the problems of catch variations related to distributions of the fish and fishing. Such a conclusion suggests that there is a need to collect and interprete fishery data in a functional relation which recognizes the types of underlying variation.

III. Formulation of a Searching Model

From the above review we have concluded that difficulties encountered in attempts to use the classic catch equation result from the failure to describe fisheries by the underlying random sampling procedure it implies. That is, fish are distributed in schools or aggregations and fishermen search for them. There is ample evidence for the aggregation or schooling behaviour of fishes, and in some cases at least, evidence that these aggregations have a significant relation to the area swept by the gear. There is also ample evidence in some pelagic fisheries, such as the tuna fisheries, that searching is an important component of the fishing operation. In recent years, developments of electronic detection devices have vastly increased the radius of detection of both pelagic fish schools and of other fishing vessels. They have also opened the possibility of direct searching for concentrations of demersal species, and otter-trawl fishermen have been quick to adopt them. However, even in the case where direct searching is not possible, fishermen may still be said to search. For example, a good catch often increases the chances of successive good ones because a fisherman will remain in the locality. On the other hand, a poor catch likely means that he will move, again increasing his chances of success. It might therefore be concluded that fishing, even in the past, might reasonably be expected to depart from the random model, and that any mathematical analogy which purports to describe the nature of fishing operations in any detail must attempt to take into account both the schooling behaviour and the searching activity as well as their interactions.

Constructing such a model requires knowledge of fish distributions and fleet operations in a detail that is seldom readily available. In the following account we have therefore attempted only a theoretical construction at a rather general level, making simplifying assumptions about the sizes, shapes and distributions of schools, and of the operation of the boats. The results are used to deduce the possible effects that changes in schooling and distribution may have on catch, relative to changes in actual abundance. From the results, we conclude that there is good reason to study fisheries from this point of view.

The searching model as treated here is one aspect of the more general predator-prey relationship. A mathematical formulation of this problem is presented elsewhere (Paloheimo, in press) and the reader is referred to it for mathematical details. Ivlev (1955) has explored this relationship in experiments on the feeding of fishes and concluded that changes in food distribution may affect the rate of food consumption in much the same way as do changes in food abundance. His results have been further discussed by Rashevsky (1959).

Distribution of fish

For the purposes of the model we consider the distributions of fish in schools as two- rather than three-dimensional. This two-dimensional distribution may be taken as a projection of the actual three-dimensional distribution of fish onto a plane. In the case of gear operating on the bottom, say a trawl, the distribution would be a projection on the plane (bottom) of all fish within say the 2- or 3-fathom bottom stratum. In the case of midwater fishing the projection would be essentially from top to bottom. Any apparent difficulty arising from the projected schools overlapping on the plane while in fact they are at different depths can be circumvented by assuming that fishing vessels can exploit only one school at a time.

We then assume that schools on the plane may be represented more or less by disks. For simplicity, we further assume that within the school boundaries the distribution of fish is uniform although this assumption is not very important to the conclusions drawn. For purposes of exposition, we will also consider that the school centres are randomly distributed. The size (radius) of schools can be variable; however, it can be shown that to calculate the mean catch we may use the mean school radius.

The school centres being randomly distributed, there is, of course, a chance that two centres are close enough so that the schools overlap. In nature this probably would mean that the two schools would merge and hence it might be thought that this problem could be overcome in the mathematical formulation by letting the school radius vary and assuming that the schools are distinct. However, it is very difficult to generate theoretical distributions of non-overlapping disks except for the case of fixed radius. Hence we have assumed that the school centre density is low so that the probability of overlap is small and can be ignored, or that if the schools are dense, their radii are the same.

School density and density of fish within schools

We denote the density of schools (i.e., school centres) in the fishing area by λ. This means that in an area A there are λ A schools on an average, or, more precisely, m schools with a probability $[(\lambda A)^m/m!]\ e^{-\lambda A}$. Furthermore, let there be on an average n fish per school. If each fish occupies a fixed space, which for convenience we denote by $b\pi$, then for a two-dimensional school the radius would be

$$r = \sqrt{bn} \qquad (5)$$

If, instead, we assume that as the numbers of fish per school increase the school increases both in depth and width, then the school radius will vary with the $\sqrt[3]{bn}$, i.e.,

$$r = \sqrt[3]{bn} \qquad (6)$$

Since the density of schools is λ and the average number of fish per school was assumed to be n, the average density of fish in the whole area is λ n. This we denote by D, i.e.,

$$\lambda n = D \qquad (7)$$

By keeping the overall density D constant we may study the effect of schooling on fishing success irrespective of changes in density. The effect of variable school radius due to changes in density of fish within schools may be studied by letting b vary in (5) or (6).

Searching for fish schools by fishermen

A fishing area is thus considered in our analogy as a plane on which we have randomly located disks representing schools of fish. A fishing vessel is searching the area with a speed (cruising speed of the vessel) which is assumed to be constant and for convenience is scaled to be the same as the time unit. Hence we may speak of the searching time interchangeably with the searching speed. When the vessel or the projection of its path on the plane crosses the school boundary it detects the school with a fixed probability. In practice the probability of detecting the school may well depend on the size of the school or the density of fish within it, but for simplicity we assume here that the probability of detection is constant.

If the radius of perception of the fishing vessel is appreciable compared with the radius of schools, this may easily be taken into account. In calculation of the searching time, it is in fact equivalent to increasing the school radius by the radius of perception. Hence, we may assume that either the radius of perception of the radii of schools is zero without any loss of generality. The actual school radius r must, of course, still be used in estimation of the fishing time (cf. equation (8) below).

Assumptions related to fishing a school

A fishing vessel, such as an otter trawl, when fishing will make a series of transects through the school. Besides removing fish from the school, fishing can have other effects on it, such as dispersing the fish. The effect of fishing on a school may also be dependent on the size and density of the school. Little is actually known of reactions of fish to fishing, and we must again substitute a postulate for our ignorance. In effect, we will assume that a fishing vessel catches a constant proportion, g, of a school sighted. There is, of course, also a possibility that the school is so big that the size of the gear or the vessel's capacity to carry fish is limiting. For a discussion of the effect of limited storage on the fishing success, we refer to Paloheimo (in press).

The time spent actually fishing as opposed to the time spent searching for schools is assumed to be proportional to the (two-dimensional) area covered by the school. Denoting the fishing time by $\tilde{\tau}$ we thus put $\tilde{\tau} \sim r^2$ or

$$\tilde{\tau} = ar^2 \qquad (8)$$

where r is given by (5) or (6). In practice the fishing time is often a discrete variable; for example, in the case of Canadian trawlers in the NW Atlantic, fishing time is usually a multiple of the standard two-hour dragging time. In addition to the above simplifications we exclude from this study any consideration of time spent on the trip to the grounds or idle time on the grounds.

Catch equation

Restricting our considerations to a short enough period of time so that the distribution of fish does not change appreciably on account of fishing, an expression for mean catch may be based on the model described above. We recall first that the mean number of schools in area A was given by λ A, hence the size of the area which contains on an average one school is $1/\lambda$. If the radius of schools is r, then from the point of view of searching we have a situation where schools may be represented by their centre points, if at the same time we consider the radius of detection of school centres to be r. As pointed out by Nicholson and Bailey (1935), this means that in time t' the vessel has searched an area 2rt'. If we now enquire about the time taken to locate one school, then on the average this is obtained by equating 2rt' with $1/\lambda$ where the latter was the area in which on the average one school can be found. Hence from $2rt' = 1/\lambda$ we get $t' = 1/2\lambda r$ as the mean searching time for one school. The total time required to locate one school and exploit it is then $(1/2\lambda r) + \tau$. In time t the number of schools found and exploited is thus given by

$$\frac{t}{\frac{1}{2\lambda r} + \tau} = \frac{2\lambda rt}{1+2\lambda r\tau}$$

or since we assumed that each school consists of n fish and gn of them are caught, the catch C(t) in time t is given by

$$C(t) = \frac{gn\ 2\lambda rt}{1+2\lambda r\tau} \qquad (9)$$

Substituting D for the overall density of fish (i.e., $D = \lambda n$, equation (7)), we get

$$C(t) = \frac{g2Drt}{1+2Dr\tau/n} \qquad (10)$$

If the probability of detecting a school is P, where $P < 1$, then in both equations (9) and (10) λ or D must be multiplied by P.

Although not explicitly stated, the above derivation and formulae assume that the travelling distance between the successive schools is fairly large compared with the school radius. When this is not true, the equations become a good deal more complicated (cf. Paloheimo, in press).

The variance of the catch C(t) given in (9) can be shown to be

$$\mathrm{Var}\ C(t) = \frac{2\lambda r + 8\lambda^2 r^2\tau + 8\lambda^3 r^3\ \mathrm{Var}\,\tau}{(1+2\lambda r\tau)^3}(gn)^2 t \qquad (11)$$

Note that as the fishing time tends to zero, the mean catch tends to $(2\lambda r)gnt$ and the variance to $(2\lambda r)\ (gn)^2 t$. Here the first factors are the same for both the mean and variance, corresponding to searching for randomly located points with no delay time. If the schools are not all the same size but vary, we must add two more components to (11), namely

$$\frac{2\lambda r\ \mathrm{Var}\,(gn)}{1+2\lambda r\tau} \qquad (12)$$

expressing the contribution of variation in numbers of fish in schools to the variance of the catch, and

$$\frac{(2\lambda r)\ 2gn\ \mathrm{cov}\,(gn,\tau)t}{(1+2\lambda r\tau)^2} \qquad (13)$$

related to the covariance between the fishing time and the numbers of fish in schools.

Effects of schooling on catch

The effect of schooling on the catch may be studied by use of equation (1o). We note first of all that if the actual fishing time τ is small compared with the searching time $1/2\ \lambda\ r$, the catch is proportional to g2Drt, i.e., at a constant density D it increases linearly with the radius of schools. To obtain an expression for the catch when the fishing time is appreciable we must make assumptions about the density of fish within schools and about the fishing time.

If in equation (1o) we put $\tau = ar^2$ (equation (8)) we get

$$C(t) = \frac{g2Drt}{1+2Dr^3\ a/n} \qquad (14)$$

and if in addition we put $r^2 = bn$ (equation (6)) we have

$$C(t) = \frac{g2Drt}{1+2Drab} \qquad (15)$$

The catches per unit time are plotted against the radius of fish schools in Figures 1 and 2. The curves in Figure 1 represent equation (14) for different constant levels of a/n and D. Figure 2 represents equation (15) for different levels of the product ab. Figure 1 thus shows the effect of changes in r on catch when numbers of fish per school are constant, or what is the same thing, when the density of fish within schools varies inversely with the square of radius r. Figure 2 shows the effect of changes in either r or D on catch when the density of fish within schools is kept constant.

We observe from Figure 1 (attached) that, at a given level of D, if the density of fish within schools decreases, the catch first increases to a maximum and then decreases as the schools spread over larger and larger areas, i.e., as r increases. This means that at first an increase in the school radius makes the schools more readily detected by the fishing vessels, but as the school density decreases this advantage is nullified by the increased fishing time required to catch the proportion, g, of the school. If, however, the density of fish within schools does not change, Figure 2 shows that the catches continue to increase, tending to an asymtote as the size of schools increases. There is no decrease in catches since the fishing time per fish caught does not change.

In Figure 1 a comparison between solid and broken lines reveals how in equation (14) a change in overall density affects catch. It shows that the same catch per unit time may be obtained at very different density (abundance) levels, depending on the interaction of schooling behaviour with density. In equation (15) a change in r is exactly equivalent to a change in D. Without any additional calculations Figure 2 may therefore be taken to illustrate the effects of a change in overall density of fish when both school radii and density of fish within the school remain the same. These results from both equations emphasize the fact that it may be impossible to distinguish between effects of abundance or distribution changes when only data on catch per unit of time are available. We further note that in either case the catch per unit of time on the fishing ground is not necessarily linearly related to the density or abundance of fish even if the distribution does not change.

In equations (14) and (15), it was assumed that fishing time per school is proportional to r^2. In addition equation (15) specifies that the number of fish per school increases as the square of the radius, or that the schools of fish are more or less two-dimensional. No such restriction was made in equation (14); in fact in calculating examples in Figure 1 numbers per school were kept constant. If, however, the schools increase in depth as well as in area, a somewhat different equation corresponding to (15) is obtained. In this case, we have $r = \sqrt[3]{bn}$ (equation(7)) and hence from (14)

$$C(t) = \frac{g\ 2Drt}{1+2\ Dab} \qquad (16)$$

The expected catch now increases linearly with the school radius, theoretically _ad infinitum_, even when the density is kept constant. There is, of course, a practical limit to this increase, imposed by the physical limitations to the size and depth of individual schools, by the holding capacity of the gear, and the vessel itself. Where these limitations do not apply, the schooling behaviour can have a much greater effect on the immediate catch than does the actual abundance of fish.

Fleet vs individual vessel operations

The preceding derivation is more pertinent to description of fishing by independently operating fishing vessels than to the operations of a co-operating fleet. The transition from an individual fishing vessel of known efficiency to that of a co-operating fleet operation is laden with difficulties. For a satisfactory solution we would need to know the operation of the fishing fleet as opposed to the random searching by one vessel. In a general account or analysis like this, one can scarcely say more than that it is important to be aware of the possible effects that co-operation between the vessels of a fleet may have on the individual catches. We may, however, indicate how information on fleet activities can be used within the framework of this presentation.

Suppose for example that there are k vessels in the fleet and that fish are so distributed that schools are large enough to be fished profitably by all vessels in the fleet. Suppose further that as soon as one of the vessels detects a school, it communicates this information to all other vessels which cease their searching and steam to the location where the school was found. Ignoring the real possibility that more than one vessel detects a school large enough to be profitably exploited, in which case only part of the fleet steams to the new location, we may define τ' equal to the average travelling time for the other k-1 vessels. The average fishing time, previously denoted by τ, now has two components. In the first place the school is fished by the vessel which detected it for the time τ'; in the second place by each of the k vessels for additional time, say τ''. Since obviously $\tau = \tau' + k\tau''$, additional time τ'' is given by $\tau - \tau'/k$. With these modifications catch equation (10) becomes

$$C(t) = \frac{kg2Drt}{1+((k-1)2Dr\,\tau'/n) + 2rD\,\tau/n} \qquad (17)$$

We note from (17) that the average catch, when the travelling time τ' is negligible, is simply k times the catch made by an individual vessel. By taking into account the additional travelling time by (k-1) vessels, during which no searching takes place, it would be concluded that the actual catch per vessel decreases as a result of co-operation. However, this conclusion is valid only within the limited confines of our assumptions. The conclusion that co-operation does not pay no longer holds if for example the schools are so big that one vessel is incapable of exploiting a school without making a trip to port during which time it may lose track of the school; if there are great variations in the sizes of school; or if the fleet faces strong competition for schools from other fleets of fishing vessels.

In the case of gears such as hook and line or gill nets, which are not generally fished with the aid of electronic detecting devices, the effect of "co-operation" among the fleet may be more important. The performance of a single vessel may be greatly increased by the auxiliary information on the distribution of fish provided by the skipper's awareness of the performance of other vessels. Because of it, although unable to carry out active search, the skipper of a single vessel may still know roughly where to fish and still be able to limit his fishing to generally productive areas. Thus the catchability coefficient, q, generated by such fisheries would change with changes in the distributions of fish, although not as drastically as in the case of actively searching fisheries which can make direct use of the local heterogeneity.

IV. Comparison with the Classical Catch Equation

In our searching model the catch is given in terms of the total operational time, including both the searching and fishing time. Current practice, however, is to ignore the searching time and calculate the catch per fishing time or other suitable measure of the amount of fishing. In the searching model the actual fishing time was denoted by τ. This is equivalent to effort, denoted earlier by f, when the latter is measured in terms of hours fished (dragged, etc.). For a school of n fish, of which the fraction g is caught, the catch per time fished is then

$$C/f = gn/\tau \qquad (18)$$

To compare this with the classical catch equation (4), that is $(C/f) = q'D$ (where for convenience we omit the subscript t), we must relate the fishing time per school (i.e., τ) to the area of the school and to the density of fish within it. For two-dimensional schools $\tau = ar^2$ (equation (8)) and $r^2 = bn$ (equation (5)), we thus have from equation (18)

$$C/f = \frac{gn}{abn} = \frac{g}{ab} = \left(\frac{g}{abD}\right) D \qquad (19)$$

or that

$$q' = \frac{g}{abD}$$

Similarly, for the three-dimensional school

$$C/f = \frac{g\sqrt[3]{n}}{ab^{2/3}} = \left(\frac{g\sqrt[3]{n}}{ab^{2/3}D}\right) D \qquad (20)$$

or that

$$q' = \frac{g\sqrt[3]{n}}{ab^{2/3}D}$$

The catch per unit of effort in equation (19) is equal to g/ab and hence is apparently independent of the overall density or abundance of fish. Thus for searching fisheries C/f is related only to the distribution of fish within schools; in this case it is proportional to the within-school density, i.e., to $1/b$. This implies (cf. (19)) in effect that the catchability coefficient q' is inversely proportional to the overall density of fish and is not, as is commonly believed, independent of it. It is only in the rather special circumstances when changes in overall density are exactly counterbalanced by changes in the distribution of fish that q' may be considered constant. From equation (19) these circumstances are met only when the density of fish within schools $1/b$ varies in proportion with the overall density, D, i.e.

$$1/b = n/r^2 \sim D = \lambda n$$

In terms of the catch per unit of effort concept, we are thus led to the conclusion that a change in abundance affects the C/f index only so far as the abundance change is reflected in the within-school density of fish. The catch per unit of effort will not be affected by a change in abundance if this shows up as an increase in numbers of schools or in their radii.

In the case of the three-dimensional schools we find that, other things being constant, q' is still inversely proportional to the density. That is, if q' is to be constant, the distribution of fish mush change with the density in such a way that $\sqrt[3]{n}/b^{2/3} \sim D$. Since $bn = r^3$ and since

$$\frac{\sqrt[3]{n}}{b^{2/3}} = \frac{n}{r^2} \sim D$$

were are led to the conclusion that for q' to be constant or for C/f to reflect changes in the abundance, the distribution of fish must change so that the within-school density of fish, when projected on the bottom plane, changes in proportion to the overall density. This conclusion is similar to the one reached for two-dimensional schools.

An explanation for the insensitivity of the catch per effort index to the changes in the abundance of fish may be sought in the fact that in searching fisheries only schools or localities where fish are present are fished. That is, a change in abundance of fish may affect the searching time rather than be reflected in the C/f index.

As was pointed out earlier, time spent fishing is a variable fraction of the total operational time of the fishing vessel. Hence we may be well advised to calculate the catch in terms "per unit operational time" rather than "per unit of effort". This conversion may be accomplished by multiplying (18) by the fraction that the fishing time is of the total. Since the average searching time is $1/2\lambda r$ and the total operational time per school of fish is $(1/2\lambda r) + \tau$, the fraction of time spent actually fishing is

$$\frac{\tau}{(1/2\lambda r) + \tau} = \frac{2\lambda r\tau}{1+2\lambda r\tau}$$

Multiplying (18) by this fraction we arrive at the expression

$$C/t = \frac{g2Dr}{1+2\lambda r \Upsilon} \qquad (10')$$

where instead of fishing f we now use t to signify that the catch is expressed on the basis of total operational time. Equation (1o') is equivalent to our catch equation (1o).

From (1o') or (1o) we get expressions for $C(t)/t$ corresponding to equations (14), (15) and (16). Thus, e.g., when $\Upsilon = ar^2$ and $r^2 = bn$, we get from (15)

$$C(t)/t = \frac{g2r}{1+2Drab} D$$

To compare this result with the classical catch equation (4), the catchability coefficient q' must be equated with 2gr/1+2Drab. From this it is apparent that the catchability coefficient in our equations is no longer as dependent on the overall density D as in (19), but this "improvement" has been bought at the expense of making it dependent on r, the mean school radius. We therefore concluded that the catchability coefficient, whether derived from C/f or C/t is heavily dependent on the school sizes and numbers of fish. In fact, changes in λ, n, or r independent of changes in D may have marked effects on fishing success.

The transition from $(C/f)_t = q'D_t$ or $(C/f)_t = qN_t$ to an average relationship such as (3), averaged over a period of time when there is a marked decrease in the population, is currently accomplished by assuming that q' is constant. Since we have shown that q' is very sensitive to any changes in the distribution of fish, or for that matter in the abundance of fish, such transition assumes that the removal of fish or passage of time alters the basic distribution of fish in a very specific way. The record of past attempts to use the catch equation illustrates the futility of such assumptions. Widening the catch per effort concept, such as attempted here, opens up a possibility of making allowance for observed changes in the fish distribution in integrating for an average relationship. However, lacking specific information on the interaction between the abundance and distribution, we have refrained from further such elaborations.

V. Discussion

Our explicit treatment of the variables affecting catch calls attention to the complexity of the mechanisms underlying the success of the fishing operation. Since we have little quantitative information on the various phases of the operation, we are reduced to making subjective judgments of the reality of a general model. The model suggested here is certainly a simplification. It is perhaps an oversimplification bordering on the crude. Yet, in spite of the limitations which one might anticipate in practice, we believe that the exercise of developing and studying it may have practical value. In the first place it allows us to make inferences about the usefulness of various kinds of data in the scientific measurement of the effects of fisheries on stock abundance. In the second place, it permits us to judge the practical importance of searching, or fishing strategy in general, on the immediate and long-term fishing success.

In connection with the measurement of the effects of fishing, one of the most important inferences from the formulation studied here concerns the potentially important effects of the heterogeneity in fish distribution. The magnitude of this effect was illustrated in Figures 1 and 2. The figures, or even more clearly, the corresponding equations (14), (15) or (16) and later on, equations (19) and (2o) imply that, while average catch per operational time or per unit effort may reflect changes in average abundance levels, they may equally reflect changes in fish distributions. It is, of course, possible to obtain information on the heterogeneity by studying simultaneously with the average C/t or C/f index the variance of the individual observations used to calculate the average. Unfortunately, however, as was pointed out earlier by Neyman (1949) the variance is rather insensitive to relative changes in D (the density), and in r (the radius of schools). Hence, we conclude that indices of average catch per unit effort must be accompanied by independent information on the fish distributions before we can use them to study abundance changes and diagnose changes in them relative to changes in the fishery.

For the purposes of practical fisheries management, a knowledge of the influence of heterogeneity in distributions has relevance in different ways. In the first place, the fisherman is interested in knowing what kinds and amounts of fish can be caught with a given type and amount of fishing effort. Fish schools or aggregations tend to be characterized by particular associations of species or sizes. The searching efforts will be selectively directed towards some schools, and will attempt to avoid others on which the relative economic returns are less. The possibilities for doing this are in themselves an important area of fisheries studies. Where selectivity can be exercised effectively, the result in terms of the classical catch equation is to vary the catchability coefficient, q, depending on age, species and relative abundance. Thus, while it is possible to make general statements about long-term total yields relative to total mortalities, application of the result to any particular fishery is of doubtful value. Given the interactions between distributions and searching, the relevant considerations are the interaction of economic yield and fishing practices in a particular case. The formulation suggested here has the possible advantage of indicating explicitly some of the underlying factors contributing to variations in fishing success, hence a basis for studying them from the point of view of modern fishing techniques.

VI. Data Requirements

Present data collections may in some cases supply the information needed for detailed study of the nature of the fishery. For example, an appreciation of at least the type of statistical distribution of the fish may be obtained from a study of the frequency distribution of catches in successive unit operations of the gear. Where length of set and the manner of making it are little affected by the size of the catch, such data may be used to describe the distribution directly. But, in practice, this is likely to be difficult since commercial data, even from standard length sets, will still reflect the unknown selectivity exercised by the fisherman in determining at what levels of density, for what species and size composition, or under what other conditions it is economical for him to fish. It seems certain that in the long run, commercial data will have to be supplemented by direct measures of school sizes and distribution, such as may be obtained from echo-sounder and sampling surveys by research vessels. A comparison with results of commercial fishing may then provide a measure of the effectiveness of the selectivity of the fishing operation.

The searching and fishing activity of fishing vessels can best be described by having access to detailed log-book records. Ideally, these would give not only the catches per unit operations of gear, but also the time and position of each individual operation. Such records could be used to study the time spent at each locality and its relation to the catches and species obtained. They could also give an index of the actual time spent searching, as opposed to that spent fishing.

It is unlikely that the interaction between schooling behaviour of fish and the operation of commercial gear can be immediately studied by analysis of fishing records, as may be possible for the distributions of fish of searching activity of fishermen. Certainly, we know of no readily available sources of data or records which could be called upon to aid this study. At the moment, it appears that information on this point could only be obtained through specially designed fishing experiments involving co-operation between commercial and research vessels; the latter following changes in the fish distribution which might be related to fishing activity.

It may appear from subsequent study that the various factors dealt with in this paper make such different contributions to fishing success that, on a long-term basis, information on all of them is an unnecessary luxury. However, in view of the variability revealed by past attempts at fishery analyses, and the resulting uncertainty about the underlying factors, some attempts to identify the relative importance of all the significant contributors seem unavoidable. Judging from the foregoing study it would be rash to suggest that any of them can be dismissed lightly. It will be only through a detailed analysis of particular fisheries that we can decide what data are required on a routine basis.

VII. Abstract

Attempts to apply the classical catch equation to fisheries data for the purpose of measuring relative abundance or density changes have frequently been frustrated by unexplained variability in the average catch per unit effort figures used as density indices. A review of recent studies indicates that this variability reflects the fact that the underlying random sampling procedure implied by the equation does not provide a sufficient description of fisheries. There appears a need for re-formulation and study of catch data in terms which explicitly recognize the heterogeneity in fish distributions and directed fishing operations.

A simple theoretical model of this type is examined. In it, fish are assumed to occur in schools which are distributed at random on a population area. Fishermen, with a given radius of perception, search for these schools, detecting them with given probability, and upon successful detection, fish out a certain proportion. Taking into account both the searching and fishing time, expressions are derived for the resultant catch per unit time. It is found to depend as much on size of schools and densities of fish within them as on the overall density or abundance.

Current practice ignores the searching time component of the fishing operation. A detailed examination in terms of our simple searching model indicates that the resulting catch per unit effort index, that is, catch per actual fishing time, is related simply to within-school density. Other things being constant, this implies that there is an inverse relationship between the catchability coefficient and overall density or abundance. Such a conclusion is in direct conflict with classical theory, but may provide an explanation for the failure of past catch per unit effort studies to yield significant measures of, for example, mortality rates.

It is concluded that, where there is heterogeneity in fish distributions, catch per unit effort, whether expressed in terms of total operational (i.e., searching and fishing) or only fishing time, cannot provide a measure of abundance change unless additional information on the distribution of fish and the operations of fishing vessels is available. Explicit formulation of fishing operations in the manner suggested here has the advantage not only of allowing us to make inferences about the usefulness of various kinds of data in measuring abundance, but of judging the practical importance of searching or fishing strategy in general on the immediate and long-term fishing success.

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Figure 1. The effect of schooling behaviour on catch of fish when overall density of fish is constant and density within schools decreases as school radii increase (equation (14)). Curves are drawn for different constant values of fishing time per unit area (more specifically a/n) at two levels of overall density (D).

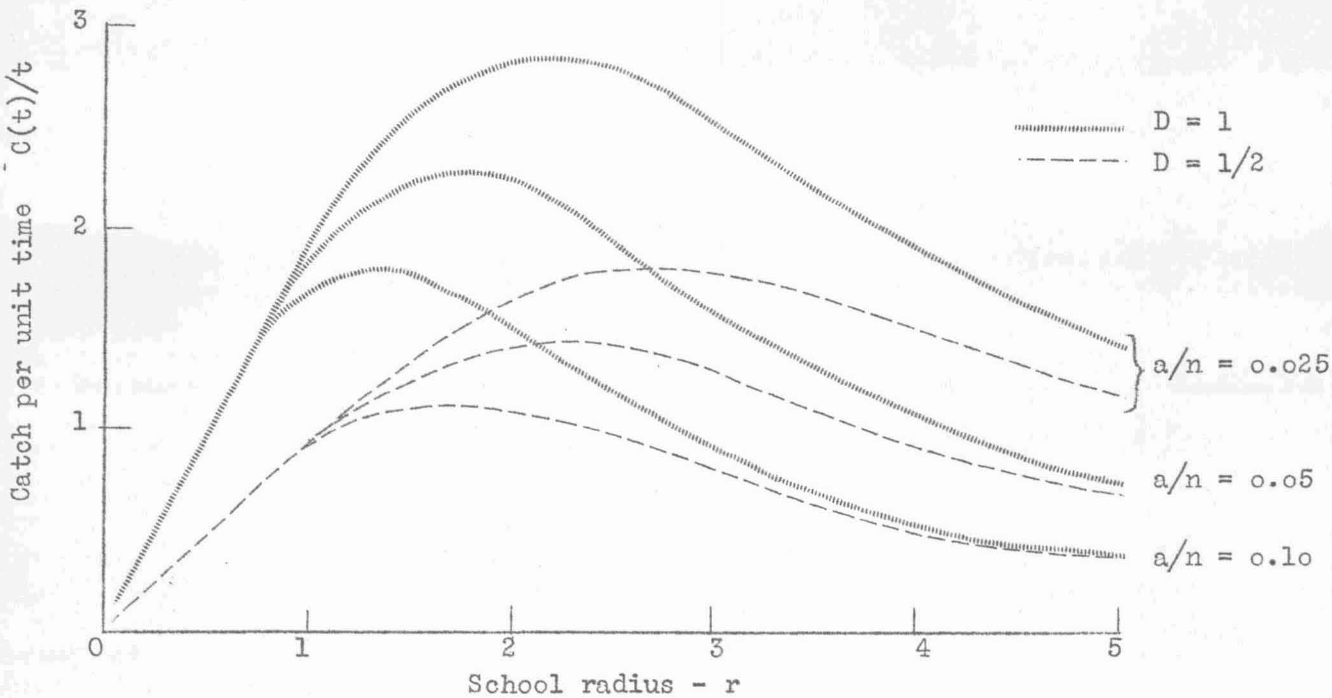

Figure 2. The effect of schooling behaviour on catch of fish when either mean school radius or overall density varies. Density of fish within schools is constant (equation (15)). Curves are drawn for different constant values of the product ab, i.e., fishing time per unit area times density within schools.