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A REVIEW OF METHODS OF ESTIMATING MORTALITY RATES IN EXPLOITED FISH POPULATIONS, WITH SPECIAL REFERENCE TO SOURCES OF BIAS IN CATCH SAMPLING

by

R. J. H. Beverton (Fisheries Laboratory, Lowestoft)

and

S. J. Holt (Food and Agriculture Organisation of U.N., Rome)

1. Introduction

The use of catch samples for studying a fish population depends on the accuracy with which characteristics of the population can be deduced from those of the samples. Of the factors which can be investigated and measured in this way, that which usually presents the most difficulty is mortality, partly because mortality rates are derived quantities not simple properties that can be sampled directly. They have to be estimated with the help of theoretical models of the population based on certain assumptions; these assumptions have themselves to be tested by observation or experiment before the mortality estimates derived from them can be accepted as reliable. Moreover, variability and, especially, bias in sample data can affect the accuracy of mortality estimates in complex and sometimes unexpected ways. In general, the estimation of mortality parameters makes a greater demand on the sample data, with regard to both their extent and reliability, than does the analysis of any other factor, and it is probably true to say that if an adequate sampling system can be devised for estimating mortality rates it will almost certainly provide satisfactory measures of other parameters. It is for this reason that we restrict the scope of this paper to the problem of estimating mortality rates, and review the ways in which sample data of various kinds can be used for this purpose.

A knowledge only of the age-composition of a population enables us to find the total mortality rate, but separation of the two main components of total mortality - that due to fishing and that due to natural causes - is more difficult. It can be done by observing the changes in age-composition and abundance resulting from known changes in the intensity of fishing. In a fishery where the variation in intensity (either from one year to the next through changes in fishing effort or with age of fish as a result of differential gear selectivity) is too small to produce a measurable change in age-composition or is completely unknown, it is therefore impossible to separate the mortality components from catch sample data alone, however extensive and reliable the sampling may be. In these circumstances it is necessary to turn to other methods involving the use of results from experiments of various kinds. These include tagging experiments, computation of the ratio of catch to total population size (e.g. as estimated from egg-surveys), and assessment of the area 'swept' by the fishing gear during a year. These methods can provide estimates of the fishing mortality alone*, but if the total mortality is known from catch samples, natural mortality can be estimated by subtraction. Thus catch sampling is an essential part of any research aimed at obtaining estimates of both fishing and natural mortality rates, and in this paper the main emphasis will be on the use of information obtained in that way.

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*Tagging experiments can, in theory, be used to estimate natural mortality directly, but only in rather favourable circumstances (see section 6(a)).

Before proceeding, it may be helpful to recall the various factors that may cause error in mortality estimates, the majority of which - though not all - are also responsible for variability or bias in the catch samples themselves. These factors can be grouped as follows:-

(i) Those concerning properties of the fish population and habits of the fish; e.g. the effect of fluctuations in year-class strength on total abundance indices; tendencies for fish to segregate according to size or age; and dependence of the natural mortality rate on age, time, or population density

(ii) Those involving characteristics of the fishing effort, e.g. changes in total effort or its distribution relative to the fish population.

(iii) Those involving the characteristics of the commercial fishing gear and of the sampling device; e.g. gear selection (including release of small fish through the meshes and perhaps differential escapement of larger fish in other ways) and variation in sampling efficiency with fish density (e.g. through 'saturation' of the gear by large catches).

(iv) Those arising in the derivation of abundance indices from catch samples which do not cover the whole area occupied by the population.

(v) Errors in age-determination, in the case of methods based on age structure.

(vi) The basic statistical variation inherent in any sampling method. This is especially important where small samples are involved, as may be the case in research vessel sampling (as opposed to commercial catch sampling).

Every method of estimating mortality may involve errors from one or more of these sources, which have varying relative importance in particular fisheries. In discussing the various methods available for mortality estimation we shall be concerned primarily with sensitivity to bias from the first four of the above causes of error, the last two being more appropriate to a statistical treatment of the sampling system itself (see Gulland, No. 27).

2. Definition and theoretical treatment of mortality

In general, it is convenient to distinguish two main categories of mortality; that due to fishing, and that due to all other causes of death - the 'natural' mortality. In effect, three ways of representing these have been proposed at various times:-

(a) The annual expectation of death (e.g. Baranov, 1918; Ricker, 1948). This is the fraction of the fish present at the beginning of a year that will actually die during that year from a given cause. The fraction that will be caught has been called the rate of exploitation.

(b) The annual mortality rate (Thompson and Herrington, 1930; Ricker, 1940, 1944). This is the fraction of the fish present at the beginning of a year that would die during that year from a given cause if no other causes of death were operative.

(c) The instantaneous mortality coefficient (Baranov, 1918; Graham, 1935; Parrish and Jones, 1953; Beverton and Holt, in press; and others). This can be defined most simply as the relative rate of decrease at a given moment due to a specified cause, i.e. $dN/_{dt} \cdot 1/_{N}$, where N is the total number of fish.

The last of these is, in general, the most suitable method of representing mortality, partly because of its mathematical simplicity but more so because of the direct relation between an instantaneous coefficient and the cause of death. The instantaneous fishing mortality coefficient F, for example, is directly proportional to the fishing intensity generating it, provided the latter is measured in the appropriate units (see Beverton and Parrish, No.25). Moreover, this relation is independent of the magnitude of natural mortality; but that between fishing intensity and the rate of exploitation (a) is not independent in this way and, indeed, cannot be stated unless the value of the natural mortality rate is already known, while the annual fishing rate (b) has little meaning in reality if there is death from causes other than fishing. We shall show below that the proportional relationship existing between fishing intensity and the instantaneous fishing mortality coefficient F is of the greatest importance in analysing total mortality into its two components. The following theory uses instantaneous mortality coefficients throughout, but the inter-relations are set out in Appendix A and have also been discussed by Ricker (1948) and Widrig (1954).

3. Estimation of the total mortality coefficient (F + M) from catch samples, F and M constant

Let us consider a population of fish in which fishing mortality can be represented by an instantaneous coefficient F and natural mortality by an instantaneous coefficient M, both these being constant. From definition (c) above, it follows that the population is decreasing at an instantaneous rate dN/dt where

$$\frac{dN}{dt} = -(F + M)N$$

If the total number of fish at time t_o is N_o, this differential equation can be solved to give the number surviving at any later time t as

$$N_t = N_o e^{-(F + M)(t - t_o)} \quad \ldots\ldots\ldots\ldots \quad (1)$$

By taking natural logarithms of both sides we find

$$\log_e(N_t) = \left\{\log_e(N_o) + (F + M)t_o\right\} - (F + M)t \quad \ldots\ldots \quad (2)$$

The two variables in this equation, $\log_e(N_t)$ and t, are linearly related, the term in curly brackets being constant and the slope of the straight line being the numerical value of the total mortality coefficient (F + M). The true number N_t cannot, of course, be estimated directly by catch sampling, but exactly the same relationship holds if N_t is replaced by a proportional index of abundance, e.g. catch per unit effort. It should not be overlooked, however, that in deriving (2) it is assumed that both F and M are constants and, in particular, do not vary with factors such as age of fish or population density; hence it requires that fishing intensity is also constant. The assumption of constancy of F is particularly critical, since if F should vary with age of fish as a result of differential gear selectivity, the age-composition of the catch is no longer the same as that of the population (as it is when F is constant). This problem is mentioned further in section 5.

(a) Relative age or length compositions only

The simplest form of presentation of data is the age-frequency diagram, in which the relative number in each age-group is expressed as a percentage of the total number of fish in the sample. This was called by Baranov (1918) a catch curve, and some examples of the form such curves can have are discussed by Ricker (1948). In a catch curve, the fish comprising each age-group belong to different year-classes, so that to use it to estimate mortality the effect of fluctuations in year-class strength have to be eliminated as far as possible by combining catch curves for a number of years sufficient to average them out, although this procedure necessarily introduces a form of weighting which may not be the best and which is not reproducible from one set of data to another. Nevertheless, if fishing effort has been fairly stable over a period of years the average catch curve may be valuable in giving an estimate of at least the order of magnitude of the total mortality coefficient (F + M) from the slope of the descending straight line fitted to the natural logarithms of the age-frequencies. This linear property of log catch curves has been observed in a number of exploited fish populations (e.g. Jensen, 1939; Silliman, 1943).

Economy of sampling effort may be achieved by estimating the total mortality coefficient from certain 'integral' properties of relative age-compositions, of which a simple example is the average age of fish. To avoid complicating factors such as mesh selection that may influence the frequencies of the younger ages, the average age, $\bar{t}$, could be computed by starting from the youngest age, t', that is fully represented in the catch samples. The equation for computing (F + M) is then (see Appendix B for derivation)

$$(F + M) = \frac{1}{\bar{t} - t'} \quad .... \quad (3)$$

This principle of 'integral estimates' is of possibly wide application; for example, Tauti (1947) and Kurita (1948) have developed methods for estimating $(F + M)$ from a knowledge of the maximum age and the average age of fish in a sample of known size.

The use of length measurements combined with age-determination in the form of age-length keys is well-known as a means of increasing sampling efficiency (see e.g. Tanaka, 1953, for a recent review, and Gulland, No.27). However, length structure alone may be of value when regular age-determination is, for one reason or another, impracticable, provided some measure of the growth rate is obtainable by methods such as tank experiments, tagging, or measuring the change with time in the position of a mode in a length distribution due to a particularly strong year-class (e.g. Graham, 1934; Moore, 1951). Since the right-hand limb of a length-frequency diagram is generated by the combined effect of total mortality and growth, it follows that if the growth rate is known, $(F + M)$ can be estimated.

Edser (1908) was probably the first to notice that if the logarithms of a length frequency diagram for plaice were plotted, the right-hand limb was approximately a straight line. This is due to the fact that growth in length of plaice over a limited range of age is also approximately linear, so that over this range length can be taken as a direct index of age. Baranov (1918), by assuming a proportional increase of length with age, developed the theory for estimating total mortality from a length-frequency diagram, while Silliman (1945) extended this treatment to enable $(F + M)$ to be estimated from the average weight of fish in catch samples. Both these methods, however, are liable to give distorted estimates because the growth equations used give an adequate fit over a limited range of age only; for general use an adequate theoretical representation of growth over the full range of age likely to be encountered in samples is required. That which the authors have found most suitable is the growth equation developed by von Bertalanffy (1938), namely

$$l_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$$

where l_t is length at age t, and L_∞, K and t_0 are constants determined by fitting the equation to growth data, as described by Beverton and Holt (in press)*. If l' denotes the smallest length of fish that are fully represented in catch samples, and $\bar{l}$ the average length computed from l' upwards, the equation analogous to (3) for estimating $(F + M)$ is (see Appendix B for derivation)

$$(F + M) = \frac{K(L_\infty - \bar{l})}{\bar{l} - l'} \quad .... \quad (4)$$

The usefulness of this method depends partly on the pattern of growth among the age-groups in the catch, the best conditions being a rapid and continued increase of length with age over the important range, with the minimum of overlap between the length distributions of adjacent age-groups. These requirements are met to a sufficient extent in species such as North Sea plaice and cod; on the other hand, growth of North Sea herring above about four years of age is relatively slow. Here, the difference between $\bar{l}$ and l' (on which the accuracy of the estimate of $(F + M)$ is critically dependent) would be particularly small and sensitive to factors such as sampling variation and fluctuations in year-class strength or growth rate.

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*See Graham (1952) and Beverton (1953) for a brief account of the incorporation of this equation in theoretical population models and its fit to growth data of North Sea plaice.

(b) Age-composition and indices of abundance

If catch per unit effort data are available, and these give reliable estimates of abundance, the age-composition of the population can be expressed by indices of abundance of fish in each age-group. This makes it possible to compare the abundance of the same year-class in successive years of life, and an estimate of $(F + M)$ can be obtained by sampling in two or more successive years. From the point of view of sampling efficiency the best estimate of the abundance of an age-group is obtained by sampling continuously throughout a year (or fishing season); and we show in Appendix C that provided F and M are constant the mean annual estimate can be treated for mortality estimation in the same way as the instantaneous abundance N_t postulated in (2)[x]. For example, if an index of the annual mean abundance of a year-class when it is in age-group v is $\bar{N}_v$, and $\bar{N}_{v+1}$ when in age-group v + 1, we have from (2),

$$\bar{N}_{v+1} = \bar{N}_v \, e^{-(F + M)}$$

and hence

$$\log_e \left(\frac{\bar{N}_v}{\bar{N}_{v+1}} \right) = (F + M) \quad \ldots\ldots\ldots\ldots\ldots \quad (5)$$

If fishing effort has been reasonably stable over a period of years the abundance age-compositions for each year can be averaged to eliminate year-class fluctuations as described above for age-frequency data, but with the advantage that the weighting procedure involved can be examined statistically. Fig. 1 shows the average age-composition of North Sea plaice for the years 1929-38 plotted as natural logarithms of catch per 100 hours fishing; the right-hand limb is closely linear and its slope gives the estimate $(F + M) = 0.83$.

4. Separate estimation of F and M from catch samples: varying with time or age

In the preceding section we assumed both F and M to be constant; this enabled estimates of the total mortality coefficient $(F + M)$ to be obtained by sampling for age - or length - structure, but there was no way of analysing it further. To do this it is necessary, in the first instance, to assume M to be constant, as before; the principle is then to see how changes in fishing intensity are reflected in estimates of $(F + M)$. The more nearly proportional is the relation between intensity and total mortality the smaller M must be, and vice versa. It will be seen that there are therefore two essential requirements for obtaining separate estimates of F and M from catch samples:

(i) There must be changes in fishing intensity - either with time on the stock as a whole (e.g. as a result of changes in total fishing effort or its spatial distribution, see below) or with age of fish (e.g. as a result of gear selectivity) - large enough to produce measurable changes in estimates of $(F + M)$.

(ii) The different fishing efforts must be known and expressed in standardised units so that they are proportional to the values of F they generate (see section 2).

The required measure of amount of fishing has been called by Beverton and Holt (ibid) the 'effective overall fishing intensity' and denoted by the symbol $\bar{f}$; it is computed from a knowledge of the spatial distribution of the commercial catch and effort as described by Beverton and Parrish (No.25) and Gulland (No. 27). Since this intensity $\bar{f}$ is proportional to F we can write

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[x] Recent examples of the use of this method for North Sea plaice are to be found in Holt (1949), Beverton (1950) and Gulland (1952).

$$F = c\tilde{f} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (6)$$

where c is a constant.

The basic equation for separating F and M can now be derived by substituting for F from (6) in the total mortality coefficient, thus giving the equation

$$(F + M) = c\tilde{f} + M \quad \ldots\ldots\ldots\ldots\ldots \quad (7)$$

Hence $(F + M)$ is linearly related to $\tilde{f}$, the constant term being M. The procedure for estimating the two unknown parameters of (7), viz: c and M, and thus separating total mortality into its components, now depends on the circumstances responsible for the changes in F that have occurred.

(a) <u>Fishing effort stabilised at two different levels</u>

The essentials of this method were first developed by Silliman (1943) for the California sardine fishery. Here, the fishing intensity had been roughly stable for two periods each long enough for the corresponding total mortality coefficients to be estimated from catch samples as described in section 3(a). From analysis of commercial statistics it was found that the fishing effort in the second period was about four times that in the first. Denoting parameters for the first period by the suffix a and for the second by the suffix b, we have for the first period, from (7)

$$(F + M)_a = c\tilde{f}_a + M$$

and for the second

$$(F + M)_b = 4c\tilde{f}_a + M$$

Solving simultaneously gives

$$M = \tfrac{1}{3}\left\{4(F + M)_a - (F + M)_b\right\} \quad \ldots\ldots\ldots \quad (8)$$

and

$$c\tilde{f}_a = F_a = \tfrac{1}{3}\left\{(F + M)_b - (F + M)_a\right\} \quad \ldots\ldots \quad (9)$$

The estimates given by Silliman were $(F + M)_a = 0.518$ and $(F + M)_b = 1.612$, from which we find from (8) and (9), $M = 0.153$, $F_a = 0.365$ and $F_b = 1.459$.

(b) <u>Fishing effort varying with time</u>

This is the more general case in which the fishing effort on the stock as a whole varies from year to year during the period for which catch samples are available. As percentage age-compositions cannot be averaged over a period of years in these circumstances, it is essential to work with age-composition expressed in indices of abundance so that the average abundance of a year-class in successive years of life can be compared. However, the log ratio of the annual mean abundance in a pair of years does not now provide, in itself, an estimate of the total mortality coefficient in either year (compare (5)). Instead, if the mean abundance of a year-class in age-group v in year x is ${}_v\bar{N}_x$, and ${}_{v+1}\bar{N}_{x+1}$ in the following year x+1 (when it is in age-group v+1), (7) has to be written in the form

$$\log_e\left(\frac{{}_v\bar{N}_x}{{}_{v+1}\bar{N}_{x+1}}\right) + Q_{(10)} = c\tilde{f}_x + M \quad \ldots\ldots \quad (10)$$

where $Q_{(10)}$ is an additional term derived in full in Appendix D. The magnitude of $Q_{(10)}$ increases with the extent of the change in fishing intensity between each year of the pair, and it can be computed as described in that Appendix. The principle of the method remains the same, however. In this case, given indices of abundance for two or more pairs of years and the corresponding annual fishing intensities, an estimate of the total mortality coefficient can be computed for each pair of years which is linearly related to the fishing intensity in the first year of each pair. Thus, plotting the left-hand side of (10) against f_x should give a linear trend, the slope of the best fitting regression providing an estimate of c and its intercept on the y- axis an estimate of M.

The number of sea fisheries for which estimates of age-composition in indices of abundance have been published, and also in which fishing intensity is known and has varied sufficiently during the sampling period, is very limited. Thus although catch sample data of this kind for North Sea plaice and haddock during the inter-war period are available, the variation in fishing intensity - as far as can be judged from the limited effort statistics available - was so slight that its effect on the estimates of (F + M) cannot be distinguished from sampling variation. The method has, however, been applied successfully by the authors to Fry's (1949) data for the Lake trout fishery of L. Opeongo and to Rounsefell's (1949) data for the Frazer River salmon; in both these the fishing effort changed considerably. It will be noted that the larger the range of change in fishing intensity the lower need be the sampling accuracy of the abundance estimates to determine M within specified limits, and vice-versa. This use of catch sample data to obtain separate estimates of F and M therefore provides an objective criterion for sampling accuracy, and hence for the amount of sampling required in given circumstances.

(c) Fishing intensity varying with age of fish

In the foregoing we have supposed that changes in F are caused by changes with time in the total fishing effort However, the same principle can be used to separate F and M if F changes in a known way with age of fish as a result of differential gear selectivity, even though the total effort may be effectively constant. In this case the age composition of the catch is not the same as that of the population, so that to obtain true abundance indices the catch per unit effort of each age-group has to be corrected by the efficiency of the gear on fish of that age relative to one particular age-group taken as reference - for example, the youngest that is present representatively in the fishing area. If the fishing mortality coefficient on the youngest age-group v is denoted by F_v, then that on any other age-group v + r can be written as $S_{v+r}.F_v$, where S_{v+r} is the efficiency of gear on age-group v+r relative to age-group v. The same factor S_{v+r} is used to adjust the catch per unit effort of age-group v+r ($\bar{N}_{v+r}$), to the same units as the catch per unit effort of age-group v ($\bar{N}_v$). Thus for any pair of age-groups v+r and v+r+1, (7) becomes

$$\log_e \left(\frac{S_{v+r+1} \cdot \bar{\bar{N}}_{v+r}}{S_{v+r} \cdot \bar{\bar{N}}_{v+r+1}} \right) + Q_{(11)} = S_{v+r}.F_v + M \; \ldots\ldots \quad (11)$$

As in the case of (10), the log abundance ratio alone does not provide an estimate of the total mortality coefficient. The additional term $Q_{(11)}$ for (11) is given in full in App. D and solutions for F_v and M are obtained from a linear regression in a similar way, in this case by plotting the left hand side against S_{v+r}.

The main problem with this method is to obtain reliable estimates of the differential selection factors S_{v+r}, since on these depends the accuracy of the estimates of F_v and M, as do those of c and M in (10) on the estimated change in fishing intensity. Where selection is due to escape through meshes, the selection factors can be estimated from the ratios of the catch of each age-group per unit fishing time of the commercial gear to that of a small-meshed gear fishing on the same density of fish. In order to estimate F_v and M from (11) a minimum of three age-groups with differing selection factors are required; one of these could be the first that is completely beyond the mesh selection range, the other two lying partially or completely within it. If the mesh selection range is too narrow, or if entry to the catch is determined partially or wholly by recruitment of young fish to the fishing area (as in the British North Sea plaice fishery with the gear at present in use), the method cannot be used in this way. There is, however, the possibility that the catching power of the gear may differ among age-groups beyond the mesh selection range; if this can be measured it may be possible to use a number of age-groups and hence to obtain estimates of M for a wide range of age. Comparative fishing experiments can also be used to measure differential selectivity of this kind, but only if it is possible to work a different gear, on the same density of fish as the commercial gear, which can be relied on to have an equal fishing power on all the age-groups in question. The particular units in which the fishing effort of the calibrating gear is expressed need not, however, be the same as the commercial gear. Thus, suppose the catches per unit effort of age-groups v and v+r by the commercial gear are Y_v and Y_{v+r}, while those of the calibrating gear are Y'_v and Y'_{v+r}, the selection factor S_{v+r}, defining the ratio $\frac{F_{v+r}}{F_v}$ for the commercial gear, is given by the expression

$$S_{v+r} = \frac{Y_{v+r}/Y_v}{Y'_{v+r}/Y'_v} .$$

whether or not the efforts of the two gears are measured in the same units (see also Beverton and Parrish, No. 25). An alternative method is to use marking experiments as described in section 6(a), which avoids the difficulty of having to rely on one particular gear being truly non-selective.

The above treatment of differential selectivity of a single gear can readily be extended to the case in which a population is fished by more than one type of gear, some or all of which differ in their selective properties. A notable example of this is the Lofoten cod fishery in which three different gears - the long-line, the gill net and the purse seine - have been in simultaneous use during recent years. Rollefsen (1953) has shown that the age-compositions obtained from samples of catches by the three gears differ considerably throughout the age range; this must mean that the fishing mortality coefficient also changes with age. The extension of the above theory that is required when more than one type of gear is operating can be shown most simply by supposing that only two gears, designated as a and b, are involved.

Suppose gear a is taken as reference, and that the fishing mortality coefficient generated by it on the youngest age-group, v, is ${}_aF_v$. With the previous terminology, the value of F generated by gear a on any higher age-group v+r can be written as $S_{v+r} \, . \, {}_aF_v$, where S_{v+r} is the selection factor of gear a for age-group v+r relative to age-group v. The corresponding values of F generated by gear b on each age-group are obtained directly from the ratio of its annual catch of that age-group to that of gear a. Thus

$$\frac{{}_bF_{v+r}}{{}_aF_{v+r}} = \frac{{}_bY_{v+r}}{{}_aY_{v+r}}$$

The total fishing mortality coefficient generated by both gears in age-group v+r can therefore be computed in terms of that generated by gear a in age group v (i.e. ${}_aF_v$) by means of the expression

$$\begin{aligned} {}_aF_{v+r} + {}_bF_{v+r} &= {}_aF_v \left(S_{v+r} + \frac{{}_bY_{v+r}}{{}_aY_{v+r}} . \, S_{v+r} \right) \\ &= {}_aF_v \cdot P_{v+r} \end{aligned}$$

where, for brevity, the factor P_{v+r} replaces the expression in brackets. If indices of the mean annual abundance of a year-class in age-groups v+r and v+r+1 are obtained in terms of the catch per unit effort of gear a, then (11) becomes

$$\log_e \left(\frac{S_{v+r+1} \cdot \overline{N}_{v+r}}{S_{v+r} \cdot \overline{N}_{v+r+1}} \right)_a + Q_{(12)} \cdot = {}_aF_v \cdot P_{v+r} + M \ldots\ldots \quad (12)$$

(See App. D for additional term $Q_{(12)}$. Provided the age-selection factors for gear a and the ratios of the catch of each age-group by the two gears are known, the factors P_{v+r} can be computed and (12) contains only two unknown quantities, viz: ${}_aF_v$ and M, for which solutions can be obtained as before. The procedure for three or more gears operating together is a direct extension of this.

In the case of the Lofoten cod fishery Rollefsen states that there is probably no differential age-selection with the purse-seine; if such a gear is taken as the reference gear a, then the selection factors S_{v+r} in (12) are all unity. A more important criterion in choosing the reference gear, however, is that its catch per unit effort should give the most reliable index of abundance for computing the log-ratio term of (12), and the purse seine may not be the best for this purpose. Another feature of the Lofoten cod fishery, though one which might be present in any fishery based on spawning concentrations, is that fish enter the fishery by spawning-classes instead of year-classes, since all the individuals of a year-class do not mature at the same age (Rollefsen, 1935). In such a case it might be better to compute log-abundance ratios for a particular spawning-class in a pair of years, thus enabling all the data to be used, and to work throughout with spawning-classes instead of age-groups.

It may be noted, finally, that (11) and (12) can be extended to take account of known changes in fishing intensity with time, as well as differential gear selectivity, by writing $c_v\tilde{f}_x$ and ${}_ac_v.\hat{f}_x$ in place of F_v and ${}_aF_v$ respectively. The resulting estimates of c_v and ${}_ac_v$ then relate fishing intensity to fishing mortality for the age-group and gear in question.

(d) The special case of F = zero

A special case of the above theory arises when F is zero, the simplest of these being an unexploited stock when F is permanently zero and natural death is the only component of mortality. In this case the methods of section 3(a) for estimating total mortality give a direct estimate of M (e.g. Ricker, 1949). It may also be possible to estimate M in this way for young age-groups of an exploited stock that are below the retention range of the commercial gear, by research vessel sampling with a small-meshed gear.

Another possibility arises in a seasonal fishery where fishing is entirely restricted to a period less than a year's duration; in this case F is temporarily zero during the closed season. If age-groups enter the fishery in the same time pattern each year it may be possible to estimate the abundance of a year-class at the end of one season and again at the beginning of the next, giving a direct estimate of M during the closed season. Usually, however, seasonal fisheries are based on migratory species where age-groups may not enter with a sufficiently consistent time pattern each year to make this method reliable; for this reason and also to make best use of all the sample data, it may be better to estimate the average abundance of a year-class over the whole of each fishing season.

Finally, there is the possibility that F may be zero for a period of a whole year or more, a notable example in the North Sea being the cessation of fishing during the two world-wars. If indices of abundance are available for one or more year-classes present in catch samples both just before and just after the war period, their log-ratios give a direct estimate of the average value of M during that period. Application of this method to North Sea plaice (Beverton and Holt, ibid) has given an estimate of M of the order of 0.1. A less precise but more widely applicable use of war-time changes is that described by Beverton (No. 26) and mentioned here for comparative purposes. The case considered is that of a fishery initially in a steady-state which is terminated by a sudden cessation of fishing for a known period. It is shown that the ratio of total abundance when fishing first starts again to the average pre-war abundance, or the ratio of the mean length of fish in pre- and post-war catch samples, can be used to specify a range of pairs of values of F and M within which the values for the pre-war period must have been. This information is of some value in itself, especially if the ratio is large since the possible range of F and M is then more restricted; but if an estimate of (F + M) for the pre-war period is available, this, taken together with the war-time change, can give specific estimates of both F and M. In a provisional application to North Sea plaice it is shown that war-time changes in both abundance and mean length, combined with the pre-war estimate of (F + M) = 0.83 (see Fig. 1), confirm that M is small. The special advantage of this method is that it may enable a separation of F and M without having regular age-determination of catch samples or even - if the change in mean length is used - reliable indices of abundance. A final point: it may seem at first sight that Silliman's method for separating F and M using two steady periods (section 4(a)) does not require indices of abundance either. It is, however, essential to know the relation between fishing mortality and fishing effort - which means also that age-structure can be expressed in indices of abundance - and to know the relative change in fishing effort between the two periods. This information becomes unnecessary only when F is zero in one period.

5. The effect of unknown trends in F or M on estimates of mortality from catch samples

The estimation of total mortality described in section 3 (a) assumes that both F and M are constant, while the methods for separating these coefficients mentioned in 4(b) and 4(c) depend critically on there being known changes in F with time or age of fish, but it has still been necessary to assume that M is constant. Estimates of F and M are likely to be biassed if either have, in fact, a trend which is unsuspected, and these trends cannot always be measured, or even detected, from characteristics of the age-structure alone.

(a) Trends in F

The effect of a trend in F on the true age-structure of the population is of course the same whether the trend is due to changes in total effort with time or to differential age- selectivity of the fishing gear, but the age-composition as estimated by catch sampling may be different in the two cases. With unknown changes in total effort, commercial catch sampling would nevertheless give comparable estimates of abundance in terms of the catch per unit effort of each age-group - provided, of course, that the commercial gear is not differentially selective. But if the trend in F is due to differential selectivity of the commercial gear, estimates of the abundance of each age-group by commercial catch sampling will themselves be biassed and the age-composition of the catch will not be the same as that of the population.

Now, the simple theory of mortality, with F and M assumed constant, leads to the prediction that logarithms of the catch per unit effort of a year-class when plotted against age should lie on a straight line. If one or more of the youngest age-groups are manifestly not on the straight line that fits the remaining points well, it is probably safe to conclude that these age-groups are not sampled representatively. This is known from other evidence to be the case with the first three points of Fig. 1, for example, but the remainder are fitted very closely by a straight line. The question then arises whether this fact is, in itself, sufficient proof that F (and, for that matter, M) is effectively constant over this range, remembering that some scatter about the best fitting line is inevitable because of sampling variation and, probably, slight fluctuations in both parameters.

Fig. 2 shows some hypothetical age-compositions, in the form of indices of abundance of a year-class in five successive years of life, that result from certain postulated trends in F with age; these are calculated from the theoretical models set out in Appendix E. For each trend we show

(a) the age-composition of the population (●), as would be obtained by a non-selective sampling gear,

(b) the age-composition of the catch (0) obtained by the differentially selective gear that is responsible for the trend in F in the population.

A likely trend in F is a steady decrease with age caused by fish becoming progressively more able to avoid capture as they grow larger. Fig. 2(a) shows the log age-compositions of the population and catch, in arbitrary units of catch per unit effort, with F decreasing arithmetically from 1.0 to 0.2 in steps of 0.2 each year as indicated on the y-axis, M being constant at 0.1 throughout. The log age-composition of the population (●) is a definite curve, but that of the catch (0) is so close to the straight dotted line that in the absence of any other information it might seem reasonable to conclude that F and M were both constant (e.g. Jensen, 1939). However, the slope of this line is 1.2 which, with this interpretation, is the value that would be taken as an estimate of (F + M); in fact, since M is 0.1, this implies an apparently constant F (which we denote as $\bar{F}$) of 1.1 - higher than the actual F for any age-group. What this means is that if F were really constant at 1.1, the catch of each age-group would be almost identical to that actually obtained by the gear causing the decreasing F. Compared with a constant $\bar{F}$ of 1.1, the decreasing F allows a progressively greater survival with increasing age, but if the same gear is used for catch sampling it progressively under-estimates the abundance at each age by almost the same amount. In Fig. 2(a) these two opposing tendencies nearly cancel out, so that the catches that would be obtained with the constant $\bar{F}$ and the decreasing F are almost identical.

Figs. 2(b), (c) and (d) show three other examples of arithmetic decreases in F with age. In 2(b) the decrease (1.0 to 0.6) is less pronounced than in 2(a), in 2(c) it is decidedly severe (1.7 to 0.1), while 2(d) shows the same overall decrease as 2(c) but in irregular steps. In 2(c) and (d) the age-composition of the population shows fairly definite curvature, but the curvature might well not be regarded as significant in 2(b). None of the catch age-compositions show any well-defined curvature, but the extent to which the apparent constant $\bar{F}$'s differ from the actual trend will be seen from the values of $\bar{F}$ shown on the diagrams; in fact, the actual shape of a catch age-composition with an arithmetic decrease in F and a constant M is sigmoid, but this would be virtually impossible to detect in practice. It is only when the decrease in F is geometric (Fig. 2(e)), that the log age-composition of the catch might be suspected of curvature.

Figs. 2(f), (g) and (h) show examples of F increasing with age as indicated on the diagrams. In each case both the population and catch age-compositions have fairly well defined curvature; in 2(f) and (h), where the initial value of F is small, the catch curves have a mode that would be clearly detectable in practice. Finally, 2(i) shows the case of F first ascending and then descending with age, as might occur for example in drift-net fisheries. Here the population age-composition is virtually linear throughout, giving a value of $\bar{F}$ of 0.5, or just less than the highest actual value of F (0.6). The abundance of age-groups in the catch, however, increases while F is increasing but then descends linearly. A not unreasonable interpretation in this case would be that the first two points indicate incompletely recruited age-groups or are influenced by mesh selection and should therefore be rejected, but that F is constant for the last three age-groups. However, $\bar{F}$ estimated from the latter is 1.1, or nearly twice the highest actual value of F.

The conclusion from the examples shown in Fig. 2 is therefore that there is a considerable range of trends in F that could produce a catch age-composition, and some that could produce a population age-composition, indistinguishable in practice from that caused by a constant F having a value that might well be outside the actual range of the varying F. Particularly misleading are the age-compositions resulting from the use of a commercial gear that is progressively less efficient on fish of increasing age and which is also used to estimate the apparent abundance of each age-group. The consequences of using an estimate of an apparently constant $\bar{F}$ for assessing overfishing and predicting the effects of certain regulative measures may not, however, be as serious as might be thought. Provided the theoretical models used for these purposes are also based on the assumption that F is constant it seems that certain kinds of predictions, notably those of the effect of changes in total effort on steady yield, may not be seriously in error. The danger is, however, that attempts to break down an apparently constant total mortality coefficient when there is in fact an unknown trend in F may lead to a serious error in the estimate of M. The whole question is evidently one that needs further investigation. Meanwhile, the insensitivity of age-structure to certain major trends in F would seem to call for every effort to be made to measure as accurately as possible any differential selectivity of commercial and, especially, sampling gear, either by direct comparative fishing experiments or tagging methods as described in 6(a). It shows also the importance of a statistical analysis of the sampling system for establishing whether or not an observed age-composition could have a significant trend.

(b) Trends in M

Provided the commercial and sampling gears are non-selective or their differential selectivity is known, trends in M with age can be detected in age-structures; otherwise, of course, it is virtually impossible to distinguish between trends in F or M. For example, if F is constant, an M increasing with age will usually cause the log age-composition curve to be convex above, while the reverse is true for an M decreasing with age.

A more detailed analysis of trends in M is complicated by the fact that the pattern of change in M from one age to the next is seldom known a priori, as is the change in F with age if effort statistics or gear selectivities are known. Consequently, the terms that need to be added to the left hand sides of (10), (11) and (12) cannot be computed directly, since they depend on the magnitude of M in both years of the pair (see App. D). However, if M does not change rapidly with age and is small relative to F (as may well be the case in many heavily fished stocks), the additional term can be ignored and computing log-abundance ratios for successive pairs of age-groups could show a range of change of M with age.

More serious may be the consequences of a trend in M with either age or population density when applying the methods of section 4 for separating the components of total mortality. In the analysis of two stable periods (section 4(a)) the different levels of fishing effort will cause both the average age of fish and the population density to be different in the two periods. If M is correlated with either, it also will be different and this will lead to error in the estimates of F. Such trends are also likely to bias estimates obtained by the method of section 4(b), which utilises changes in effort with time, if the log-abundance ratios are computed from all the age-groups in the exploited phase of the population. In this case the points at high efforts will tend to be associated with lower densities and average ages than points at low efforts, causing a rotation of the regression line. This could be largely avoided by computing log-abundance ratios for each pair of age-groups separately and fitting a separate regression to each, thus minimising the effect of a trend in M with age; while splitting the data into groups of roughly equal population density and fitting a regression to each, would enable any variation of M with density to be assessed. However, if natural mortality is both large and variable, an analysis of the causes of death, enabling more realistic theoretical models to be set up, would be required for its proper estimation.

6. Methods of estimating F other than by catch sampling

The preceding discussion has shown the requirements that must be met to obtain a reliable estimate of the total mortality coefficient (F + M) by catch sampling and, further, to distinguish its components. There are, however, three other methods of estimating mortality in exploited fish populations, namely by tagging experiments, by estimating in absolute units the abundance of the population and the total annual catch and by considering the area 'swept' by the fishing gear in a given period.

(a) Tagging experiments

The idea here is that by setting up an experimental 'sub-population' of tagged fish it may be possible to obtain more detailed and accurate information than from catch samples of the whole population. However, compared with the untagged population, the properties and problems of analysis of a tagged population may differ in a number of respects which are relevant to mortality estimation.

Advantages

(i) A known number of tagged fish are liberated at a known time and place; that is, recruitment to the sub-population is controlled.

(ii) If tagged fish can be identified on recapture, either as individuals or as members of particular batches, the period at liberty is accurately known and age-determination is not required.

(iii) If the distribution of fishing effort is known sufficiently accurately it may be possible to select a liberation area in which the local fishing intensity changes much more rapidly than the total effort, thus enabling a separation of total mortality by methods analogous to those described in section 4.

Possible complications

(iv) The actual number of tagged fish from which subsequent recaptures are obtained may be very different from the number liberated, through heavy mortality - arising from the tagging operation - within a short time of release. In this event the number liberated is of little practical value for estimating F.

(v) There is unlikely to be complete detection and reporting of all recaptured fish; this has the same effect as (iv) in that the number liberated cannot be used in the estimation of F.

(vi) The operation of tagging or the presence of a tag may make a fish more or less liable to capture than an untagged fish. If the effect is temporary it is necessary to discard recaptures until the effect has disappeared, which again means that the number liberated is of no direct value. If the effect is permanent there is no way of adjusting the value of F for the tagged population to agree with that for the untagged population (except perhaps by special experiments..

(vii) Unless tagged fish can be distributed rapidly throughout the whole population in numbers proportional to the population density, the F obtained from recaptures will probably not be the true F in the population because the tagged fish are unlikely to be subject to the same effective fishing intensity. Usually, tagging has to be restricted to a limited area, in which case the estimate of F thus obtained has to be weighted by the distribution of commercial catch and effort to give the true F.

(viii) With a limited tagging area, dispersion of tagged fish from it appears as part of the 'natural mortality' unless a direct estimate of the dispersion rate can be made.

(ix) Tags may become detached from living fish. This also appears as a component of 'natural mortality', although it may be possible to estimate the rate of tag-loss by subsidiary experiments.

(x) Finally, the presence of a tag may itself be an additional cause of death among the tagged population, and there is no way of treating the data to distinguish this from the true natural mortality rate in the untagged population - except again, possibly, by taking account of tank experiments on viability.

The last three factors mean that the true natural mortality coefficient M must be replaced, for the tagged population, by a composite 'other-loss' coefficient X. Only if the effect of tagging on the survival of fish can be reliably established from long-term tank experiments, and dispersion from the tagging area and loss of tags from living fish can be estimated separately (see Beverton and Holt, in press), is it possible to use tagging data to estimate the true M for the whole population. To our knowledge, these requirements have never yet been met in any tagging experiments in a major sea fishery, although controlled marking experiments have been carried out in lakes (e.g. Shetter, 1952). On the other hand, it may be possible to obtain a reliable estimate of F by separating it from the total loss coefficient (F + X) in the tagged population using methods analogous to those mentioned previously. Thus the natural logarithm of the ratio of recaptures obtained in successive periods after liberation, provided the fishing effort is constant, gives a direct estimate of (F + X), while if factors (iv), (v) and (vi) are not involved, the number liberated can be used to obtain a separate estimate of F by methods such as those developed by Ricker (1948). If the fishing effort after liberation changes in a known way, F and X can be separated by an exactly analogous method to that mentioned in section 4(b), for which only indices of abundance of tagged fish are required The advantage here is that since the number liberated is not used, recaptures can be disregarded until a sufficient time has elapsed for any temporary effects of tagging to disappear. Moreover, as *ratios* of abundance are computed, the fact that not all recaptured fish may be detected or reported (factor (v) above) does not affect estimates of F or X obtained in this way, provided the percentage reported remains reasonably constant.

It must therefore be concluded that the calculation of F and M from tagging experiments makes as much and perhaps more demand on data than does its estimation from catch samples. There is, however, one other use of tagging data which is not affected by many of the complicating factors above, namely the estimation of the *relative* values of F for a series of age-groups, when these differ because of differential selectivity of the commercial gear. These relative values are found, in fact, to be in the proportion of the recaptures per unit number liberated of each age-group in a given period - the latter being as short as is sufficient to obtain a reasonable number of recaptures. The only requirements are that other factors should be the same for all sets of liberations and, preferably, that fish to be tagged should be caught by a non-selective gear (or, at least, a gear other than the commercial gear) to avoid the possibility of pre-selecting the most easily caught members of a size or age-group, should such inherent differences in 'catchability' exist. Even if it should be found that the commercial gear is not selective this at least would establish that estimates of F by catch sampling are reliable, while if differential selectivity can be measured in this way it may be possible to apply the methods of section 4(c) to obtain a full analysis of mortality from catch samples. We suggest that this combination of catch sampling and tagging experiments may prove to be a valuable technique.

(b) Estimation of the ratio of catch to total stock

It follows directly from the theory of mortality outlined in section 2 that F is given by the ratio of the total annual catch to the annual mean fishable stock. The details of the method depend primarily on how the total stock is estimated. In relatively small enclosed areas (e.g. lakes) tagging can be employed, using Petersen's method or various well known elaborations of it (e.g. Schaefer, 1951), but unless tagged and untagged fish behave similarly the estimate of total population size is influenced by many of the complicating factors listed above. Changes in sex-ratio through selective capture have been used to estimate the size of some populations of terrestrial animals (e.g. Petrides, 1949), and the method may be applicable to fish stocks. Probably the best method is from *egg-surveys*. If the seasonal egg-production can be estimated, then a knowledge of the fecundity of mature females of different sizes will give an estimate of the total stock weight of mature female fish. In this case the catch must be sampled for sex-ratio and maturity of females in order to compute the annual catch of mature females, but it is unnecessary to convert weight to numbers provided the egg-production of an individual fish is proportional to its weight. This is true of North Sea plaice, in which a rough estimate of F can be obtained by this method. Thus Simpson (1951) found the fecundity to be about 140 eggs per gm. and estimated the total egg-production in 1948 to be about 8×10^{12} (Simpson, 1952), this being based on the assumption that the spawning in the Southern Bight of the North Sea accounts for about half the total egg-production. The recent work of Bohl (1954) indicates that this assumption may not be much wrong. From these figures the total weight of mature female plaice in that year was about

$$\frac{8 \times 10^{12}}{140} = 5.7 \times 10^{10} \text{ gm.}$$

The European catch of plaice in 1948 was 8.4×10^{10} gm., and from the sex-composition and maturity data given by Thursby-Pelham (1939) it is probable that something between a quarter and half of this, by weight, consisted of mature females. Hence the ratio of catch to total population of mature females lies between the limits

$$\frac{2.1 \times 10^{10}}{5.7 \times 10^{10}} = 0.37, \quad \text{and} \quad \frac{4.2 \times 10^{10}}{5.7 \times 10^{10}} = 0.74$$

This is not inconsistent with the pre-war value of F of 0.7 estimated from age-composition data, remembering that the total fishing effort in 1948 may not have been quite as large as in the years immediately before the war, and that there is some indication that mature female plaice may be less liable to capture than mature males. With a comprehensive survey of egg-production and contemporary sampling of the European plaice catch for sex-ratio and maturity of females, it is reasonable to suppose that F could be estimated to within limits considerably narrower than the above.

There are, of course, certain difficulties with this method, although these are of quite a different kind to those encountered previously. They may include the identification of egg stages for the estimation of egg-production, the estimation of fecundity and the distinction between mature and immature fish in catch samples. On the other hand, the estimate of F obtained in this way is entirely independent of natural mortality, it does not require indices of abundance (i.e. catch per unit effort) or catch sampling for either age or length structure, and because it applies to a period of one year it is unaffected by fluctuations in year-class strength and fishing effort. It is important to note that if the commercial gear is differentially age-selective this method gives an estimate of F which is an average of the values for the age-groups in question weighted by the relative catch (in weight) of each age-group; thus it lies within the range of the actual trend in F (see section 5(a)). Where egg-surveys are practicable, estimating fishing mortality in this way at infrequent intervals, say every ten years or so, may provide a valuable independent check on the conventional catch sampling methods and perhaps deserves more attention than it has received hitherto.

(c) Estimation of the area 'swept' by the fishing gear

The basis of this method, which was first used by Baranov (1918), is that since F is a known function of the probability that a fish will be caught during a given period, it may be possible to estimate this directly by computing the area covered by the gear during a year. It may therefore be applicable to towed gears in which the area swept during a haul can be calculated from the dimensions of the gear and the distance towed, provided the whole of the fish population is within the range of the gear - both horizontally and vertically - while fishing is in progress. Suppose the area occupied by the fish population is A and, in the first instance, that fish are distributed uniformly over it. Suppose also that each unit haul of the gear sweeps an area a and catches the fraction p of all fish lying in its path. If there are initially a total of N_0 fish, then after n hauls have been made at random over the area the number of fish remaining, ignoring natural mortality, is

$$N_1 = N_o\left(1 - \frac{ap}{A}\right)^n$$

Put $\frac{an}{A} = k$; the number remaining is then

$$N_1 = N_o\left(1 - \frac{pk}{n}\right)^n \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (13)$$

Now if n is very large, e.g. is the total number of hauls made during a year by the fleet, (13) becomes

$$N_1 \simeq N_o e^{-pk}$$

Comparison with (18) of Appendix A shows that the quantity pk is identical to the fishing mortality coefficient F, so that we have

$$F = \frac{pan}{A} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (14)$$

This result remains valid when natural mortality is taken into account.

There are two main sources of error in estimating F in this way. One is that neither fish nor fishing are ever uniformly distributed over the whole area, the tendency being for fishing to be most intense where fish themselves are most concentrated. Thus the majority of hauls will take a larger fraction of the total population than if fish and fishing were uniformly distributed, and F will tend to be under-estimated by (14). This bias can be partially corrected if commercial statistics of catch and effort for sufficiently small sub-areas are available (e.g. statistical rectangles for demersal fish in the North Sea). The area swept per year in each sub-area could then be computed and F estimated from the weighted sum of these swept areas, the weighting coefficient for each sub-area being the ratio of the density in it to the average density over all sub-areas. This procedure is exactly analogous to the computation of the effective overall fishing intensity $\hat{f}$ (see Beverton and Parrish, No. 25). There remains, however, the difficulty that fish are unlikely to be uniformly distributed even within the smallest practicable sub-area and some may be on rough ground that is unfishable.

The other problem is that of estimating the value of p in (14) i.e. the proportion of fish in the area swept in each haul that are caught by the gear. By assuming complete retention, i.e. by putting p = 1, Baranov obtained an estimate of F of about 0.4 for North Sea plaice prior to the first world war. As far as can be judged from the limited effort statistics available for that period this figure is probably not far wrong, but as no allowance was made for the non-uniform distribution of fish and fishing it may be that this largely counteracted what would otherwise have been an over-estimate of F. The problem of estimating p may be solved for some gears and species by developments in underwater photography and television; in these circumstances and provided adequate commercial statistics of catch and effort are available, it should be possible to obtain a reasonably accurate estimate of F in this way.

7. Summary

(i) This paper reviews the methods at present available for estimating mortality rates in exploited fish populations. Mortality estimation is an essential part of any study of fishery dynamics and is considered here because it makes the greatest demand on the sampling programme; indeed, it may often be the deciding factor in planning that programme.

(ii) Mortality rates are derived quantities that cannot be observed directly but have to be deduced from sample data with the help of theoretical population models. Reasons are given for representing mortality by instantaneous coefficients, and the relation of these to other measures of

mortality are shown. Of particular importance is the fact that the instantaneous fishing mortality coefficient F is proportional to the fishing effort, provided the latter is computed in the appropriate way.

(iii) The estimation of mortality from age and length frequencies in catch samples is considered first. This information can be used only in the simple case when both F and M (the instantaneous natural mortality coefficient) are constant, and gives an estimate of the total mortality coefficient (F + M).

(iv) The separate estimation of F and M from catch samples requires the age-structure to be expressed in terms of an abundance index (i.e. catch of each age-group per unit effort). It is also necessary that F should have changed in a known way, either with time (as a result of known changes in fishing effort) or with age of fish (as a result of differential gear selectivity). Attention is drawn to the importance of periods when F is zero; either for part of the year, as in a seasonal fishery, or for several years, as happened in the North Sea during the war.

(v) The errors that may be introduced in mortality estimates if there are unsuspected trends in F are illustrated by hypothetical examples. Most serious are trends in F with age due to differential selectivity of the commercial fishing gear when the same gear is used for catch sampling and is thought to be non-selective. It is shown that in this case apparent age-compositions may well be obtained that are indistinguishable in practice from ones produced by a constant F, but which if interpreted in this way can give entirely erroneous estimates.

(vi) Three other methods of estimating mortality rates are discussed briefly from the point of view of their use in detecting or avoiding bias that may be present in catch samples. These methods involve analysis of tagging experiments, computation of the ratio of catch to total population, or estimation of the area swept by the gear. The last two give an estimate of F only, and this has to be subtracted from the estimate of (F + M) by catch sampling to give M. Tagging experiments can, in theory, be used by themselves to estimate both F and M, but the results are liable to bias from most of the factors influencing the catch sample methods and some additional ones peculiar to tagged fish. It is suggested that a useful technique may be to conduct tagging experiments simply to measure differential gear selectivity, which is much easier than estimating F or M in absolute units; this information applied to catch sample data may enable a separation of F and M to be made that would not otherwise be possible.

(vii) Some of the methods described are illustrated by application to the stock of plaice in the North Sea, and it is shown that they give reasonably consistent results. For the period 1930-39, F was about 0.7 and M about 0.1.

(viii) It is emphasized that, in the first instance at least, as many as possible of the different methods of estimating mortality should be used and the results compared, because of many sources of bias - some of which are undetectable - that may be present in any one method. It is suggested that a research programme to estimate fishing and natural mortality rates can be based primarily on catch sampling, supplemented with standardised statistics of commercial fishing effort and, if possible, with comparative fishing and tagging experiments to detect and measure differential gear selectivity. Egg-surveys to estimate the true abundance of the population may provide, at intervals, a valuable independent check on the mortality estimates obtained by routine catch sampling.

APPENDICES

Appendix A

Let the total number of fish at the beginning of a year be N_0. With constant instantaneous fishing and natural mortality coefficients F and M, the number present at any time t during the year is

$$N_t = N_0 e^{-(F+M)t} \qquad \ldots(15)$$

where t is measured from the beginning of the year. The number remaining at the end of the year is therefore

$$N_1 = N_0 e^{-(F+M)} \qquad \ldots(16)$$

Hence the annual total mortality rate and expectation of death is

$$\frac{N_0 - N_1}{N_0} = 1 - e^{-(F+M)}$$

and the annual survival rate is $e^{-(F+M)}$

The annual number caught is

$$Y_n = F\int_0^1 N_t \, . \, dt = \frac{FN_0}{F+M}\left(1 - e^{-(F+M)}\right) \qquad \ldots(17)$$

Hence the annual expectation of capture (≡ rate of exploitation) is

$$\frac{Y_n}{N_0} = \frac{F}{F+M}\left(1 - e^{-(F+M)}\right)$$

Similarly, the annual expectation of natural death is

$$\frac{M}{F+M}\left(1 - e^{-(F+M)}\right)$$

The annual fishing rate has been defined as the fraction of the fish present at the beginning of a year that would be caught during the year if no other causes of death were operative. In this case, instead of (16) we have

$$N_1 = N_0 e^{-F} \qquad \ldots(18)$$

so that the annual fishing rate is

$$\frac{N_0 - N_1}{N_0} = 1 - e^{-F}$$

Similarly, the annual natural mortality rate is $1 - e^{-M}$

Instantaneous coefficients and expectations of death relating to specific causes can be simply added together to give the total value for all causes of death; this is not the case with the annual fishing and natural mortality rates.

Appendix B

Expressions for the mean age and length of fish in the catch above age t' and corresponding length ℓ', can be derived by considering a year-class after it has entered this phase of the population. Its numbers at any age $t \geqslant t'$ are defined by (15), so that the number caught throughout the period from $t = t'$ to $t = \infty$ is

$$Y_n = F\int_{t'}^{\infty} N_t \, . \, dt$$

The total age of all fish caught is

$$F\int_{t'}^{\infty} t.\,N_t\,.\,dt$$

Hence the mean age of fish in the total catch from the year-class between ages t' and ∞ is

$$\bar{t} = \frac{F\int_{t'}^{\infty} t\,.\,N_t\,.\,dt}{F\int_{t'}^{\infty} N_t\,.\,dt} \qquad \ldots(19)$$

substituting for N_t from (15) and integrating, gives

$$\bar{t} = t' + \frac{1}{F+M}$$

For a population in a steady state this is also the average age of fish above age t' in the annual catch.

An expression for the mean length of fish in the catch can be derived in a similar way. Thus, instead of (19) we have

$$\bar{\ell} = \frac{F\int_{t'}^{\infty} N_t\,.\,\ell_t\,.\,dt}{F\int_{t'}^{\infty} N_t\,.\,dt}$$

Substituting for ℓ_t from the von Bertalanffy growth equation

$$\ell_t = L_\infty \left(1-e^{-K(t-t_o)}\right) \qquad \ldots(20)$$

and for N_t from (15) and integrating gives

$$\bar{\ell} = L_\infty \left(1 - \frac{F+M}{F+M+K}\,e^{-K(t'-t_o)}\right) \qquad \ldots(21)$$

However, from (20) the length of fish at age t' is

$$\ell' = (L_\infty \left(1-e^{-K(t'-t_o)}\right)$$

from which

$$e^{-K(t'-t_o)} = \frac{L_\infty - \ell'}{L_\infty}$$

Substituting in (21) and rearranging gives

$$F+M = \frac{K\left(L_\infty - \bar{\ell}\right)}{\bar{\ell} - \ell'}$$

<u>Appendix C</u>

For a population defined by (15), the mean number present during the first year is

$$\bar{N}_1 = \frac{\int_0^1 N_t.dt}{\int_0^1 dt}$$

Since the denominator is unity we have

$$\bar{N}_1 = \frac{N_0}{F+M}\left(1-e^{-(F+M)}\right) \qquad \ldots(22)$$

At the end of the first year the survivors will number

$$N_1 = N_0 e^{-(F+M)}$$

Their annual mean abundance during the following year is, similarly,

$$\bar{N}_2 = \frac{N_0 e^{-(F+M)}}{F+M}\left(1-e^{-(F+M)}\right) \qquad \ldots(23)$$

Hence

$$\log_e\left(\frac{\bar{N}_1}{\bar{N}_2}\right) = (F+M)$$

so that provided F and M are constant through both years the annual mean abundances give a true estimate of the total mortality coefficient $(F+M)$

Appendix D

Suppose a year-class enters age-group v at the beginning of year x, when its numbers are $_vN_x$. Its mean abundance during year x, when the fishing intensity is $\tilde{f}_x$ is given from (22) by the expression

$$_v\bar{N}_x = \frac{_vN_x}{c\tilde{f}_x + M}\left(1-e^{-(c\tilde{f}_x+M)}\right) \qquad \ldots(24)$$

Similarly, its mean abundance in the following year $x+1$, when the fishing intensity is $\tilde{f}_{x+1}$, from (23), is

$$_{v+1}\bar{N}_{x+1} = \frac{_vN_x e^{-(c\tilde{f}_x+M)}}{c\tilde{f}_{x+1}+M}\left(1-e^{-(c\tilde{f}_{x+1}+M)}\right) \qquad \ldots(25)$$

Dividing (24) by (25) and taking natural logarithms gives

$$\log_e\left(\frac{_v\bar{N}_x}{_{v+1}\bar{N}_{x+1}}\right) + \log_e\left\{\frac{(c\tilde{f}_x+M)\left(1-e^{-(c\tilde{f}_{x+1}+M)}\right)}{(c\tilde{f}_{x+1}+M)\left(1-e^{-(c\tilde{f}_x+M)}\right)}\right\} = c\tilde{f}_x + M \qquad \ldots(26)$$

The second logarithmic term of the left hand side is the term $\varphi(10)$ of (10), referred to in section 4(b). Solutions for c and M are obtained by successive approximation. Thus if the term $\varphi(10)$ is ignored we have

$$\log_e\left(\frac{_v\bar{N}_x}{_{v+1}\bar{N}_{x+1}}\right) \simeq c\tilde{f}_x + M$$

and plotting the log ratio of abundance in pairs of years against the fishing intensity in the first year of each pair, $\tilde{f}_x$, gives first estimates of c (slope) and M (intercept). These are then used to compute approximate values of $\varphi(10)$ for each pair of years, which can then be added to the corresponding log-abundance ratios and the whole of the left hand side of (26) replotted against $\tilde{f}_x$. This gives more exact estimates of C and M, the process being repeated until there is no appreciable difference in successive estimates of these parameters. Examples of the application of this method are given by Beverton and Holt (in press).

Additional terms for (11) and (12), in which F varies with age as a result of differential gear selectivity, can be deduced and used in an exactly similar way. For (11) the correction term is

$$Q_{(11)} = \log_e \left\{ \frac{(S_{v+r}\cdot F_v + M)\ (1-e^{-(S_{v+r+1}\cdot F_v + M)})}{(S_{v+r+1}\cdot F_v + M)\ (1-e^{-(S_{v+r}\cdot F_v + M)})} \right\}$$

and for (12) it is

$$Q_{(12)} = \log_e \left\{ \frac{(P_{v+r}\cdot {}_aF_v + M)\ (1-e^{-(P_{v+r+1}\cdot {}_aF_v + M)})}{(P_{v+r+1}\cdot {}_aF_v + M)\ (1-e^{-(P_{v+r}\cdot {}_aF_v + M)})} \right\}$$

Appendix E

Consider a year-class entering age-group v and numbering N_v fish, that is then fished by a differentially selective gear. If the fishing mortality coefficient while in age-group v is F_v, then the catch of the year-class while in that age-group is given from (17) as

$${}_vY_n = \frac{F_v\ N_v}{F_v + M}\left(1-e^{-(F_v+M)}\right)$$

and that from the same year-class when in any subsequent age-group $v+r$ is

$${}_{v+r}Y_n = \frac{F_{v+r}\cdot N_v\, e^{-\sum_{p=v}^{v+r-1}(F_p+M)}}{F_{v+r}+M}\left(1-e^{-(F_{v+r}+M)}\right) \qquad \text{...(27)}$$

The true annual mean abundance of the year-class when in age-group $v+r$ i.e. as estimated by the catch per unit effort of non-selective gear, is

$$\bar{N}_{v+r} = \frac{{}_{v+r}Y_n}{F_{v+r}} \qquad \text{...(28)}$$

If, however, the catch per unit effort of the differentially selective gear is used to estimate abundance, but the gear is thought to be non-selective, the catch of each age-group will be divided by the same unit of effort whereas, in fact, an adjusted effort should have been used according to the change in F with age (see (28)). Thus the age-composition of the catch is not the same as that of the population. In Fig. 2 the population age-structures (●) have been calculated from (28) and those of the catch (O) from (27).

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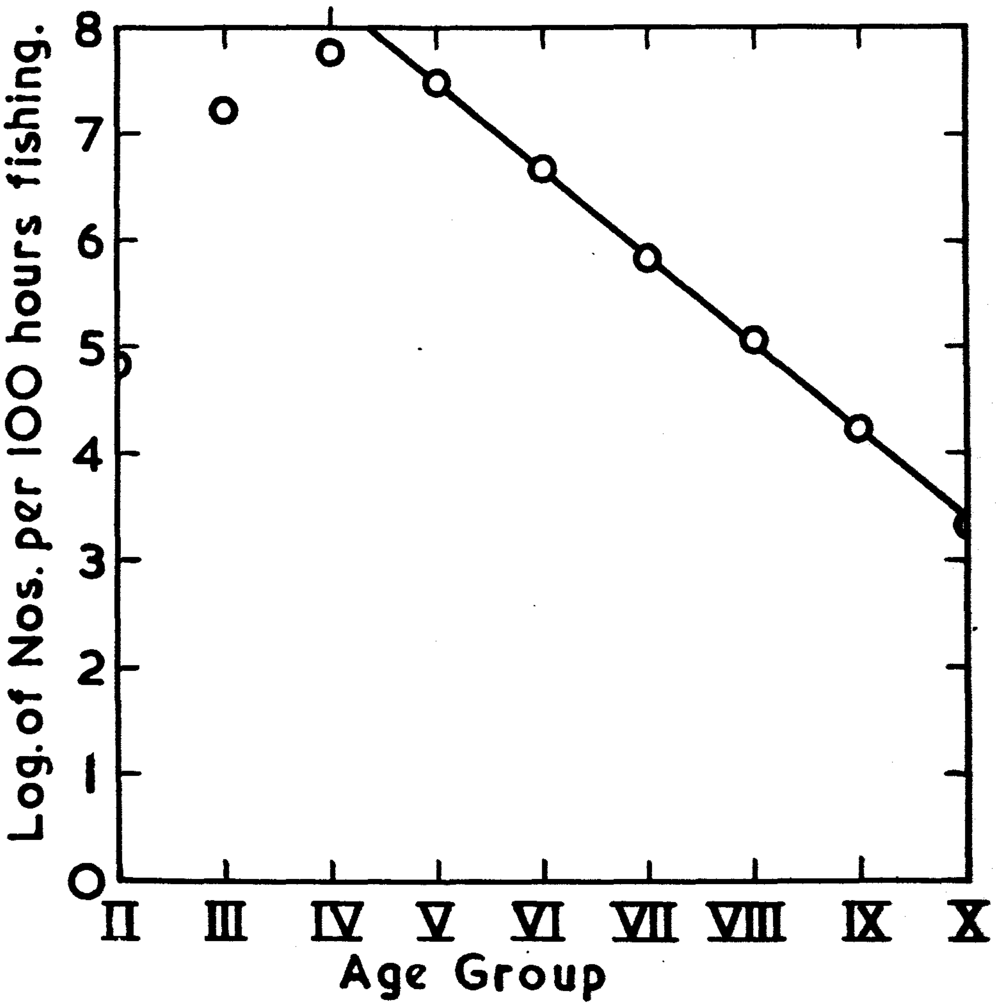

Fig. 1 Plaice age-composition. Natural logarithms of the average number of each age-group caught per 100 hours fishing by 1st class steam trawlers, 1929-38. The slope of the line gives an estimate of the total mortality coefficient of (F+M) = 0·83.

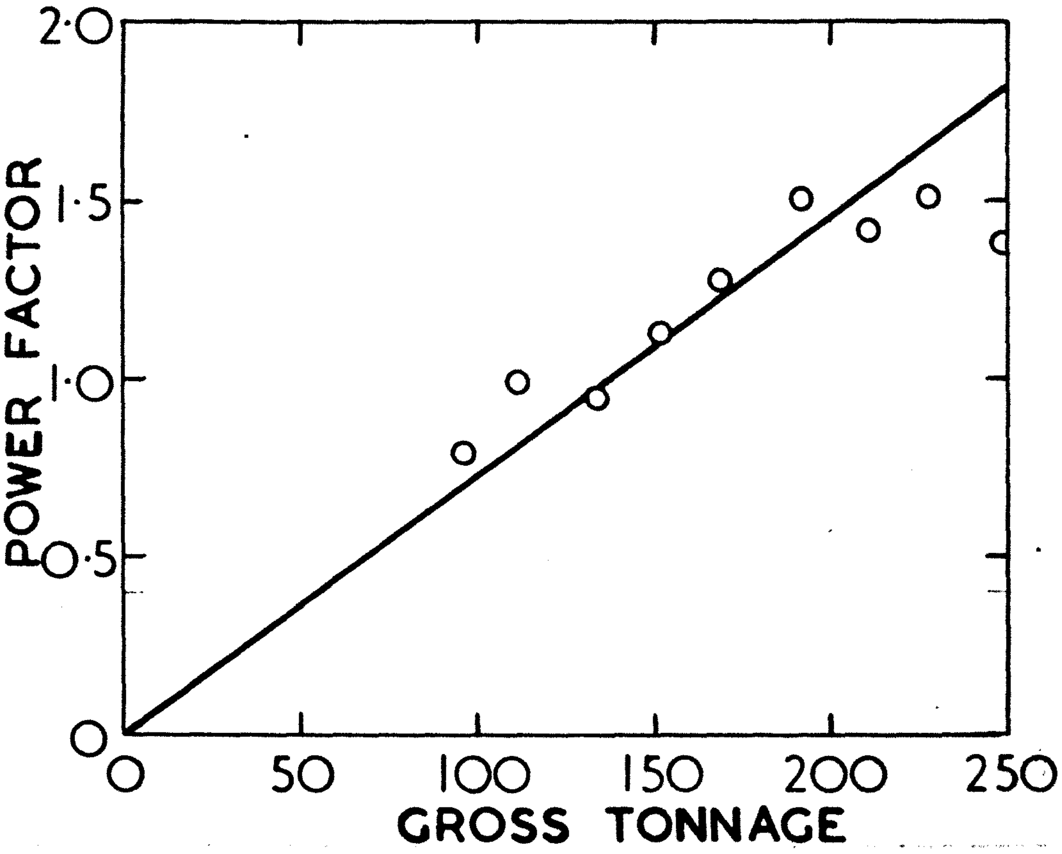

Fig. 1. Relationship between relative fishing power and gross tonnage for steam trawlers.

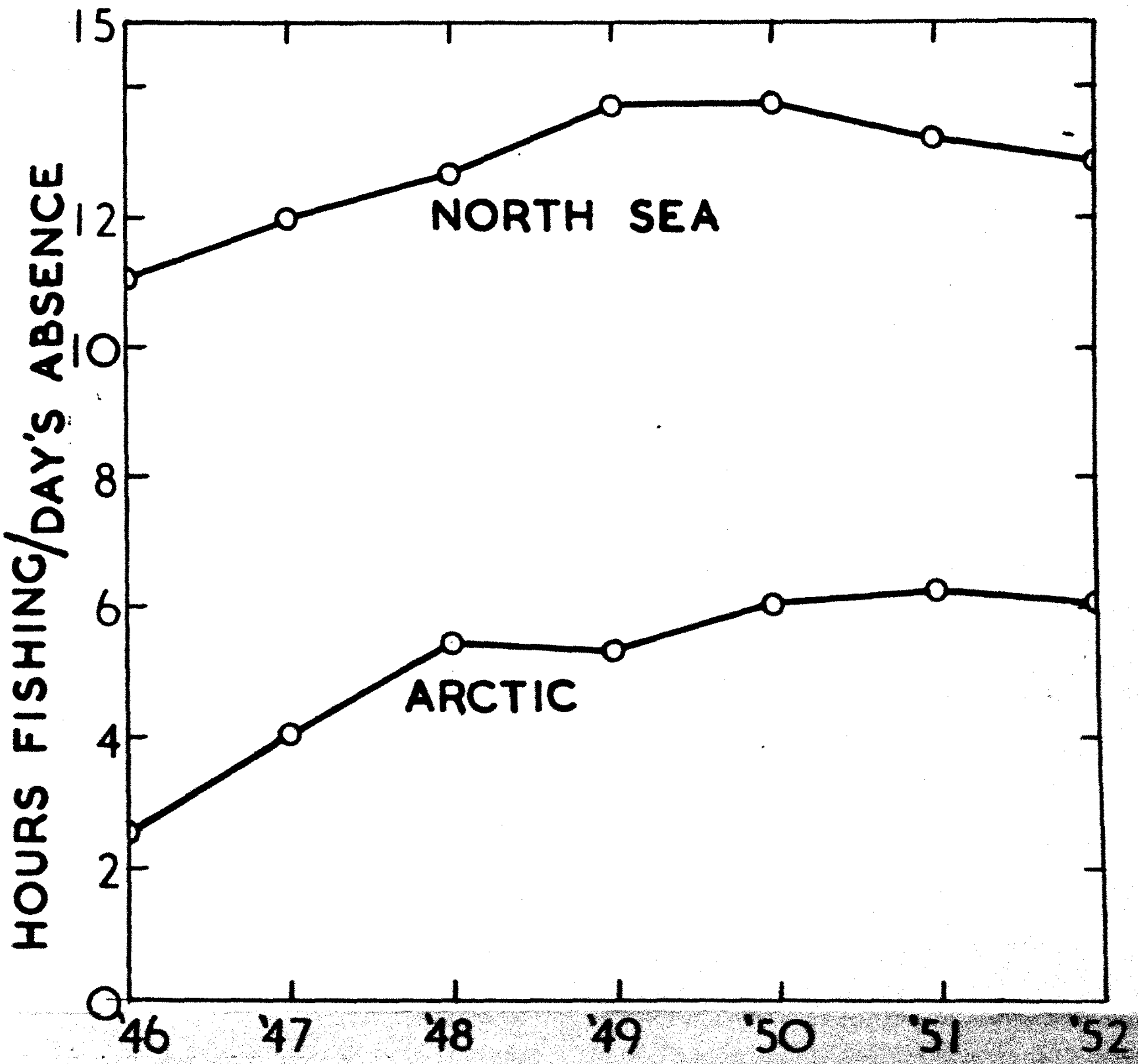

Fig. 2. Trends in hours fishing per days absence, 1946-1952.

Some Suggested Standard Units of Fishing Power and Effort

Type of vessel	Fishing power unit	Fishing effort unit	Additional factors to allow for:-
Steam trawler	gross-ton	ton-hour (or multiple)	Gear differences and future gear modifications. Differences in fishing power between major classes or nationalities of vessels other than are accounted for by tonnage and gear. Differences in fishing power on major species or groups of species.
Motor trawler	gross-ton) B.H.P.)	M.T. ton-hour) B.H.P.-hour) (or multiple)	Above factors for steam trawlers, plus: conversion of motor trawler ton to S.T. ton (1.4?), or B.H.P. to S.T. ton (2?).
Seiner	1-seiner (tonnage?)	seiner-hour (seiner-ton-hour?)	Above factors for steam trawlers, plus: conversion of seiner-hour to S.T. ton-hour (260?).
Drifter	net (of standard length)	net-haul) net-hour)	Conversion of unit of drifter effort to S.T. ton-hour as reference (?).
Ring-netter) Purse-seiner)	length of net (?)	length of net x no. of shots (?)) searching distance x no. of shots (?))	Conversion to appropriate reference unit of effort (e.g. drifter or S.T. unit (?)).
Long-liner	no. of hooks (or multiple)	hook-hour) hook-shot) (or multiple)	Conversion factors to reference unit of effort, if relevant.

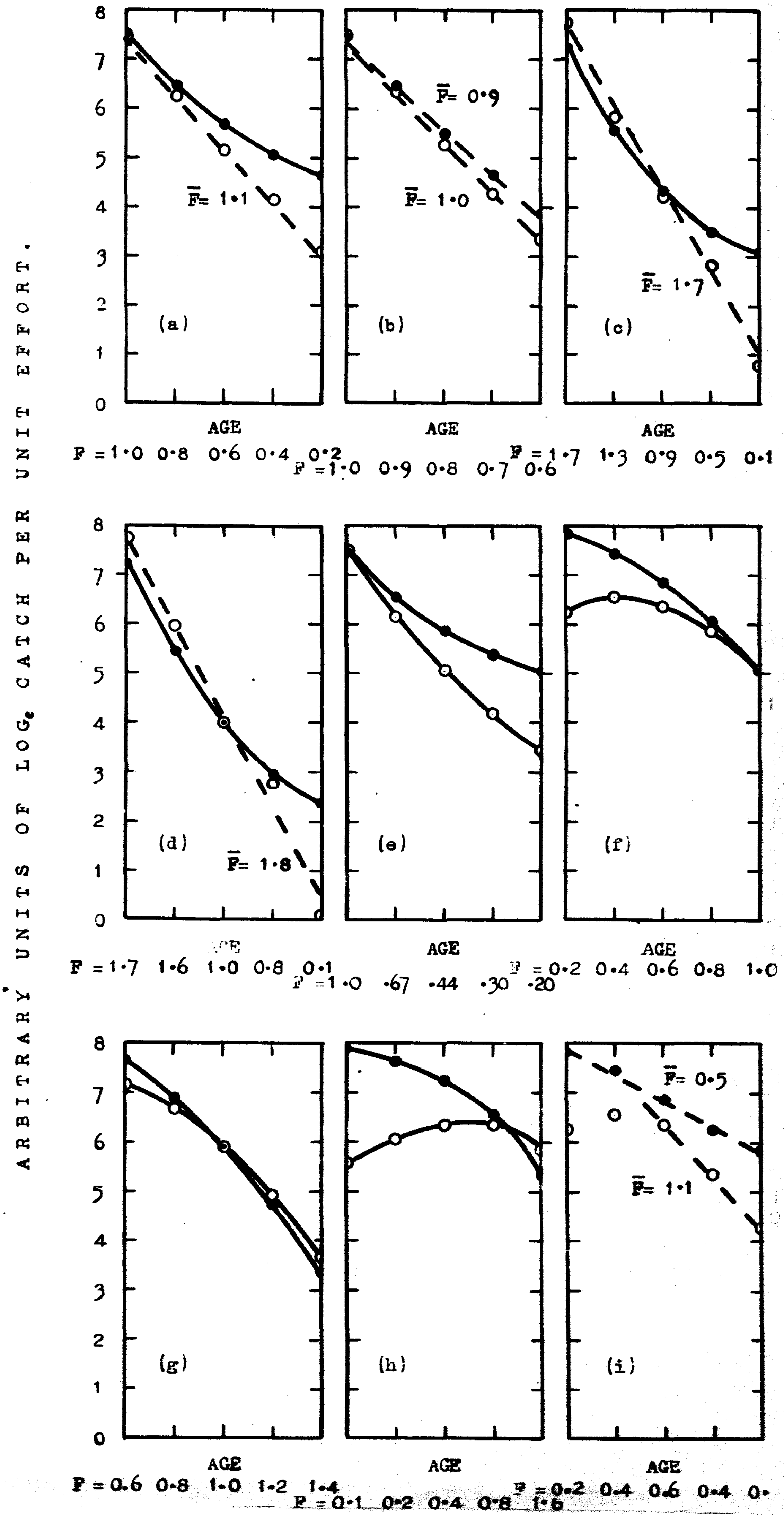

Fig. 2 Examples of population (●) and catch (○) age compositions resulting from certain postulated trends in F with age.