

Estimation of the Abundance of a Fish Stock from Egg and Larval Surveys

by

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Introduction

The concept that the abundance of fish could be estimated from the numbers of their spawning products was first put forward by Hensen towards the end of the last century. The aim of the Nordsee Expedition of 1895 was to assess the total stock of fish in the North Sea from quantitative plankton surveys sampling their eggs. This brilliant idea failed largely because it was far in advance of its time in that the basic data necessary for such a project were not at that time sufficiently well known. With a few notable exceptions the method - providing as it does the only practicable way of estimating the absolute abundance of adult numbers of a fish stock - has tended to be neglected in the present century more than the importance of its aims warrants.

The basic concept is a comparatively simple one. If one can estimate the total production of eggs or larvae of a stock, P , throughout a spawning season, and determine the mean fecundity, F , of a mature female and the proportion of females in the mature stock K then the total abundance of the mature stock

$$M = \frac{PK}{F}$$

If the total exploited stock is required rather than the mature component this can be subsequently obtained from a knowledge of the proportions of mature and immature fish in commercial catches. Alternatively, since in all fish so far investigated fecundity is proportional to weight, the stock can also be obtained directly in what for many purposes is a more convenient form as the total weight of the mature stock by using the fecundity per unit weight relationship in place of the straight fecundity.

The fecundity of many species of fish in the ICES area is now adequately known (Raitt 1933, Simpson 1951, Baxter 1959), the sex ratio can be obtained from market sampling (on the assumption that the sex ratio in the catch is the same as that of the stock) so only the estimation of egg production raises serious problems.

Before this can be attempted certain basic features of the spawning biology of the stock in question must be adequately known. The first essential is a real knowledge of the identification of the spawning products so that there is no possibility of confusion with another species with closely similar eggs or larvae. The rather elementary state of knowledge of fish egg identification at the time of Hensen's expedition was one reason for its failure. The other biological data required are a knowledge of the extent of the spawning area and the period of time over which spawning takes place, to give a firm basis on which to plan an adequate sampling programme, and a knowledge of the rate of development over the range of temperatures encountered on the spawning grounds during the spawning season, such as that given for plaice and cod by Apstein (1909).

The techniques of estimating seasonal production of eggs (or larvae) can best be considered in two parts, those dealing with fish with planktonic eggs - the majority of species of commercial importance - and those with benthic eggs of which only the herring has so far been investigated in this way.

Species with Planktonic Eggs or Larvae

For a species with planktonic eggs or larvae the problem is one of obtaining estimates of egg production during the spawning season by a series of samples (cruises) giving an adequate representation of time changes in production and within cruises, by sampling over the area of distribution sufficiently often to give an adequate representation of changes in egg density over the spawning area. The problem is

therefore more amenable to solution, with a reasonable allocation of resources, when the spawning area is small and the spawning season is short. Unfortunately, the majority of species of commercial interest in the ICES area have a wide spread of spawning areas and a spawning season extending over at least three months. However, for most of these egg production at the beginning and end of the season is comparatively small in relation to that at the height of the season, and need only be roughly estimated without seriously affecting the estimate for the season as a whole. Similarly egg density at the fringes of the spawning area normally adds little to the estimated total for the area as a whole.

Considering first the estimation of cruise totals, this is done by sampling a grid of stations covering the known spawning area. Normally such a grid has stations regularly placed at fixed distances apart. This considerably simplifies subsequent computation but for maximum efficiency of estimation there is much to be said for having a flexible sampling system, which allows greater intensity of sampling in areas of highest density where the variability in space is normally greatest, and more widely spaced stations at the fringes of the distributions which add comparatively little to the total numbers, and where variability over short distances is likely to be small. It is of course necessary to sample efficiently the total range of depth within which the eggs or larvae are distributed. This can be done either by a vertically hauled or an obliquely towed gear. The Hensen vertical net has traditionally been the favoured instrument for such quantitative investigations of planktonic organisms, but largely because of the increasing realisation of the variability of distribution over quite short distances the current tendency is to favour towed oblique instruments which to some extent integrate such local patchiness. In either case care should be taken that all depth strata are representatively sampled and, since a measure of the volume of water filtered by the gear is required, an instrument which gives this is desirable. The number of the egg stage being considered in the samples can then be converted for comparative purposes to the number per standard volume of water per unit of depth fished. If, for example, a standard of 10 cubic metres of water per metre of depth is taken as a standard the numbers are then in effect the number below 10 square metres of sea surface. For subsequent integration of cruise totals over time it is also necessary to correct these figures for the number of days' accumulation of eggs which they represent. This will depend on (a) the stage of development which is chosen as the index of egg production and (b) the time taken to develop to that stage at the temperature prevailing at the time of the cruise. The stage chosen should be one which can be easily and accurately separated from all subsequent stages and one for which the time from spawning to attainment over the relevant temperature range is known, but these conditions having been met it should be as short as possible to reduce to the minimum the bias in the estimate due to mortality during that stage.

One now has for each cruise an observation from each station of the number of eggs spawned per day below a square metre of surface. It must now be assumed that each of these observations represents not only the point in space at which they were taken but over a surrounding area such that the sum of these areas for all stations is equal to the area within which the spawning product is distributed. The simplest way of doing this is to take the mean of these station values and multiply by the number of standard areas in the total distribution. This gives an unbiased estimate if the distribution of stations is a random one. If, however, use is made of a knowledge of egg distribution to increase sampling intensity in areas of high egg concentration such a system of weighting all observations equally will give an estimate biased upwards. Alternatively each station observation can be weighted by the area of a polygon surrounding it constructed by drawing the perpendicular bisectors of the straight lines joining each station to adjacent ones. This gives a result identical to linear interpolation between stations. A third method of arriving at a cruise total is by drawing isometric lines and measuring the area contained within each contour level. This technique owes much to the work of Buchanan-Wollaston (1923, 1926) who developed a graphical method of determining the precise position of egg contours between the plotted station values, thus eliminating the personal factor normally involved in contour drawing. This was the procedure used by Simpson (1959) for Southern Bight plaice and by Parrish and Saviile (1962) for herring in the northern North Sea. Sette and Ahlstrom (1948) used all three techniques in their estimation of the eggs of the Pacific sardine and attained results which differed only insignificantly in relation to the other sources of error.

Having obtained a series of cruise totals, representing the numbers of eggs spawned per day during the period of each cruise over the spawning area, the next procedure is to integrate these over time to give a total egg production during the complete spawning season. The problem here is essentially the same as that of

integrating station values over space to give cruise totals and each cruise total has to be considered as representing egg production, not only over the time period of that cruise but over an adjacent period of time such that the total equals the whole of the spawning period. Sette and Ahlstrom (1948) solved this by weighting each cruise total by the duration of the cruise plus half the time interval between that cruise and the adjacent ones on either side. An alternative solution is that used by Simpson (1959) where cruise totals are plotted as ordinates against the mid-date of the cruises and the area under the resulting curve of seasonal spawning intensity is measured to give the seasonal total production. A third way of meeting this problem is to make some assumption about the form of the seasonal curve of spawning intensity. This can be particularly useful where cruise spacing is so wide as to invalidate the assumption of linearity between cruises. Saville (1956) for Faroe haddock assumed a normal curve of spawning intensity and discussed the relevance of this form to other published data on spawning intensity. With this form of curve one can, from a knowledge of the timing of the beginning and end of the spawning season calculate from tables of the normal deviate the proportion of the seasonal egg production which would be spawned within any time period and so raise any cruise total to a seasonal total.

The major steps involved in arriving at the total egg production can be represented mathematically as follows:-

Let c_{ij} be the number of eggs below standard area at the i th station on the j th cruise within the development stage being assessed,

d = time in days at the prevailing temperature taken to develop through the stage being assessed.

Then number of eggs produced per day at the i th station on the j th cruise below a standard area =

$$\frac{c_{ij}}{d}$$

If w_{ij} is the number of standard areas represented by the i th station on the j th cruise, then the number produced per day in the spawning area on the j th cruise =

$$\sum \frac{w_{ij} c_{ij}}{d}$$

If t = time in days represented by the j th cruise the number of eggs produced over the period represented by the j th cruise is

$$\sum \frac{w_{ij} c_{ij} t}{d} = C_j$$

and the total egg production over the season is = $\sum C_j$.

Alternatively where the distribution of stations is a random one if A = number of standard areas contained in the spawning area and n = number of stations sampled

$$C_j = \frac{At \sum c_{ij}}{dn}$$

and as before egg production over the season = $\sum C_j$.

Species with Benthic Eggs

Perhaps more attention has been devoted to the use of egg censuses as a measure of spawning population size in herring than in any other species of fish. Because herring eggs are attached to the substratum the estimation of their abundance raises rather different problems from those in fish with free floating eggs. Most work in this field has been done on the Pacific herring where the eggs laid between tidal levels, although much of it has been of a comparative rather than of an absolute abundance. As the spawning of this species takes place largely between tide levels an index of egg abundance can be obtained by visual inspection. For the Canadian Pacific herring this is done as a routine each season by fishery inspectors who give an estimate of the extent, width and density of spawn along the area of coast line for which they are responsible. This is subsequently converted to miles of "standard spawn" by weighting the length of spawn deposition by factors varying from 1 to 5 allocated according to the estimation of spawn density (Stevenson & Outram, 1953). The number of herring required to produce a standard mile of spawn (x) has been assessed indirectly by the same authors by plotting population size, calculated by allocating arbitrary values to x , against x for different years, and

from a knowledge of the probable relative sizes of the population in different years fixing limits within which x must lie. The value obtained in this way was 0.09×10^8 whilst an independent estimate by Hourston (1953) gave a value of 0.08×10^8 . From such data Stevenson and Outram calculated population sizes for British Columbia herring populations over several years. Exploitation rates calculated from these differed considerably from those from tag returns in individual years but the mean value over a five year period by the two methods was in close agreement. As far as is known only two attempts have been made to assess the population abundance of stocks of Atlantic herring from egg numbers. The pioneering effort in this field was that of Runnström (1941) on the herring spawning off the coast of Norway in spring. Runnström used a Petersen grab with an opening of 0.1 m^2 as his sampling instrument. A grid of about 400 stations was sampled, covering a spawning area whose extent was estimated at 425 km^2 . The volume of eggs per grab haul was measured and the station value was weighted by the area it represented taken to be the rectangle with sides half the distance between adjacent stations. By summation of these station values a total volume for the whole spawning area was calculated. The fecundity of a spawning female was also expressed in terms of the volume of eggs spawned and so by division the number of spawning females obtained. Runnström calculated, from the catch by bottom gill nets in the district where the major spawning took place, a fishing mortality for this stock of 26% which is in reasonable agreement with Lea's (1930) estimate of total mortality of 20%. However, there seems no justification for taking the catch by a single method of fishing as being the only catch contributing to fishing mortality, nor, as the present view of Norwegian herring workers is that "large" and "spring" herring are a single stock (Østvedt, 1961) of taking the catch from only the spring spawning districts. If one takes the mean catch for the total Norwegian fishery over the years for which Runnström gives the mean abundance of spawners it amounts to rather more than his estimate of the size of the spawning stock so there seems little doubt that his estimate of egg abundance is a serious under-estimate. The most probable source of under-estimation in his data would seem to arise from the fact that only one sample was taken at each station during the course of the spawning season. It thus seems probable that many stations were sampled before the full extent of spawning had taken place there whilst at others a considerable amount of hatching might have taken place before samples were taken.

The only other reported attempt to estimate the abundance of a spawning stock in Atlantic herring was that by Parrish *et al.* (1959) for the spring-spawning Clyde stock. Their method differed from that of Runnström in one major respect. Instead of taking spot samples over a wide area a patch of spawn was first located by dredge. This was then surveyed in considerable detail by taking closely spaced samples on transects across it with a grab so that its limits were accurately delineated and the mean abundance of eggs within it was accurately measured. In this way what was probably a very accurate estimate of egg abundance within this single patch was obtained. Unfortunately the method was very time-consuming with the result that with the resources available similar estimates could not be made of other possible sites of spawn deposition within the spawning area. On the basis of the distribution of ripe fish in space and time and on the distribution of recently hatched larvae a rather arbitrary decision was made that 4-5 patches of similar size were present within the area during the spawning season.

Assessments based on Larval Stages

Stock abundance estimates based on larval data are in general less satisfactory than those based on eggs because of the enhanced mortality factor. Estimates of mortality in the egg stage, during hatching, and in the early larval stages are unfortunately very few but it is generally accepted that the hatching period and the period of yolk-sac absorption are likely to be the ones of particularly heavy mortality. Thus in estimating a larval stage one may be in fact computing only a small, and unknown, fraction of the initial egg production which alone is a function of spawning stock size. Without a measure of mortality between recently spawned eggs and the larval stage, larval data cannot therefore be used as an index of the absolute size of the spawning stock; such data can however still be of value in that one can be sure that any estimate of stock based on it will be an under-estimate and so can be used for setting an upper limit to the possible size of the fishing mortality coefficient.

In a stock with benthic eggs and a very extensive spawning area estimation of egg abundance by grab surveys may be impracticable. This is the situation for the herring spawning in the northern North Sea in summer and for this stock an independent estimate of the upper level of the possible range of values of fishing mortality could be extremely useful. Parrish and Saville (1962) followed this line of reasoning in attempting to estimate the fishing mortality of Bank spawners in the

North Sea from abundance estimates of herring larvae. The basic procedures in utilising a planktonic larval stage for this purpose are identical with those for planktonic eggs. The only additional factors which must be taken into account in utilising the data are the enhanced mortality between the initial production and the stage used as an index of population size and any tendency on the part of a more active stage to evade the sampling gear. Both of these act in the same direction in causing under-estimation of stock size and so of over-estimating F.

Reliability of Egg and Larvae Assessments

The problem of assessing the reliability of stock estimates from such data has been given serious consideration only in the case of estimates based on planktonic stages although the basic problem is very similar in the two cases. The major sources of variability in assessments of total production of planktonic eggs are (1) errors associated with actually taking the samples, (2) errors involved in integrating samples representing points in space over space to give estimates of abundance over the total area of distribution and (3) errors introduced by similarly integrating cruise totals over time to give estimates of the total production over the spawning period. Another source of error which must be considered is that due to mortality within the stage taken as an index of population size. This differs from the others in that it always results in an underestimate of the true value i.e. it is a bias rather than a random error.

A good deal of work has been done on the variability of a single haul taken with various types of plankton gear. Estimates of error due to this source for hauls with a Hensen net range from 25% of the mean (Saville 1956) to 64% of the mean (Cushing 1953). For oblique and horizontal hauls the corresponding range in the published literature is 31-93% (Windsor & Clarke 1940). These are standard deviations expressed as percentages of the mean for a single haul. The application of the variance of a single observation to the estimation of error due to that source on a season's estimate has been discussed by Sette & Ahlstrom (1948). Using Silliman's (1946) estimate of a standard deviation of 0.176 of the logarithm of the number for a single haul, they calculated a coefficient of variation of 5-10% in their seasons' estimates due to this source.

In the majority of cases, however, this error must be relatively small in comparison with that introduced by taking a sample over a small area as being representative of the much larger area represented by the square of the distance between station positions. A combined estimate of the variance due to this and to the variability of replicate samples at the same point in space and time is a more useful value in estimating the reliability of egg estimates. Taft (1960) attempted to do this for the data on sardine egg counts given by Sette & Ahlstrom. From an examination of the means and variances of the station values within cruises he concluded that the distribution of eggs within the survey area was a non-random one which renders inappropriate the estimation of variances by mean square differences from the mean. The distribution of egg counts did give a satisfactory fit to a negative binomial distribution for which a transformation of the type

$$y_{ij} = \log_{10} (C_{ij} + \frac{1}{2}K)$$

gives an approximately normal distribution, where C_{ij} is the count of eggs at the i th station on the j th cruise and K is the contagion coefficient of the fitted binomial distribution of the station values on the j th cruise. The variable y_{ij} then has a variance = $0.1886 \psi'(K)$, where $\psi'(K)$ is the trigamma function of K . From this analysis Taft got factors, ranging from 1.4 to 2.5, by which the cruise estimates must be multiplied or divided to give the 95% confidence limits. A negative binomial distribution would appear to have a wider relevance to this type of data. Some of the data given by Saville (1956) on haddock eggs at Faroe were examined from this point of view. Three out of the four cruises tested gave a significant fit to a negative binomial and for these the 95% confidence limits were calculated on this basis. These gave for the 1950 season, for example, confidence limits of $16 \times 10^{11} - 63 \times 10^{11}$ compared with estimates of $13 \times 10^{11} - 51 \times 10^{11}$ on the assumption of a random distribution of eggs. The differences between the limits calculated on these two assumptions seem to be relatively small.

A more serious objection to this procedure is that although it may give a more valid estimate of the reliability of cruise estimates it cannot give anything other than a qualitative value of the reliability of seasonal estimates. Taft found that the values of K for different cruises within a season were not homogeneous and so the data could not be pooled to give a common value of K . As the distribution of the sum of a set of counts from different negative binomials is unknown the reliability of seasonal estimates cannot be treated quantitatively on

this basis. Cushing (1957) took a rather different approach to the problem of estimating the reliability of his estimates of pilchard eggs in the Chamel. He divided the surveyed area into rectangles, each of which contained 3-5 stations. His estimate was then based on the mean number of eggs in each rectangle weighted by the area of the rectangle. From an analysis of variance of the egg counts on a log.transformation, with a between and within rectangle classification, he obtained an estimate of the variance of the mean number of eggs within rectangles from which the estimated error of each cruise total and, by summation, of the seasonal total was obtained. It should be noted, however, that these estimates, although giving a summation of the errors involved in integrating station values over space to give cruise totals make no allowance for errors involved in taking cruise estimates as being representative of a much wider period of time; in other words it assumes sampling of a population which is stable in time over inter-cruise periods.

The errors involved in spawning assessments due to variations in spawning intensity in time have nowhere been adequately assessed because of the large resources which would be necessary to do repeated sampling, over short time intervals of the entire spawning area. Taft (1960), for the Pacific sardine, did repeated sampling at daily intervals over a period of five days of 25 stations spaced 4 miles apart. The analysis of these data gave at least an indication of the scale of the variability of egg counts over short time intervals. The ratio of the highest day's total to the lowest differed by a factor of 30. An analysis of variance of the resulting data gave a coefficient of variation for days of 4.8. Over this time period and station spacing the variability in time was almost as large as that over space. This would seem to entail that a seasonal estimate of egg production arrived at by combining cruise totals would be no more accurate than any of the individual cruise estimates and might well be considerably less accurate.

In summary such estimates as are available for the confidence limits of egg production assessments suggest that these are of the order of one half and double the estimated number (Cushing 1957, Taft 1960, Saville 1956) with the proviso that in all cases the error due to time variations has either not been accounted for or inadequately estimated.

In spite of the variability to which such estimates of egg production are subject their use in estimating total stock size in the few cases where they have been applied in this way gives results which are not incompatible with other data. Beverton & Holt (1956), using Simpson's data (1952) for the production of plaice eggs within the North Sea, got estimates of the fishing mortality for North Sea plaice lying between 0.37 and 0.74 which were in reasonable agreement with the pre-war value of F of 0.7 estimated for this stock from age composition data. The data for haddock egg production at Faroe given by Saville (1956) can be used in a similar way. Using the age compositions of the stock in the period February to April in the years 1950, 1951 and 1952 given by Jones & Main (1951, 1952, 1953), and applying to these the haddock fecundity-length relationship of Raitt (1933) one can compute the mean fecundity of the spawning stock at Faroe in each of these years. These divided into the egg production of the Faroe region in these three years give estimates of the numbers of mature females. Taking a 50-50 sex ratio this gives the sizes of the total spawning stock shown in Table 1. The annual landings of haddock in these three years from Faroe were taken from the "Bulletin Statistique". From the data given by Jones & Main the number of mature individuals contained in these total landings were computed. The instantaneous rates of fishing mortality on this stock in the three years was then computed from the formula

$$F = \frac{C Z}{n R(1-e^{-Z})}$$

where F is the instantaneous rate of fishing mortality, C_n is the catch in numbers of fish, Z is the instantaneous rate of total mortality and R is the total stock in numbers.

Table 1

Year	Mean Fecundity	Egg production	Total Spawning Stock (E)	Annual catch ('000 kgs)	Annual catch of mature fish (C_n)	F
1950	1.40×10^6	58×10^{11}	8.30×10^6	11.983	6.211×10^3	1.34
1951	0.46×10^6	70×10^{11}	30.58×10^6	14.409	10.828×10^3	0.49
1952	0.47×10^6	67×10^{11}	28.58×10^6	14.271	12.238×10^3	0.58

Jones and Main (1954) give annual monthly rates for Faroe haddock of 73% in 1950 and 49% in 1951 and 1952. These are equivalent to instantaneous rates of total mortality of 1.31 and 0.68 respectively. These taken in conjunction with the fishing mortality rates given in Table 1 would mean rates of natural mortality of 0.09-0.19 which is close to the figures calculated for other stocks of demersal fish from other types of data. More striking, the F's calculated from the egg production data show the same marked change between 1950 and 1951 as was found by Jones & Main from age composition data. It would appear therefore that in spite of the variability inherent in the method population abundances can be estimated from egg production data which at least give useful confirmation of parameters from other sources.

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