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Some Considerations in Estimating Populations of Planktonic Fish Eggs

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Introduction

Attempts to estimate the annual production of planktonic fish eggs began with the work of Hensen and Apstein (1897). Hensen chose the planktonic egg of the plaice as the most suitable organism for quantitative investigation. He developed the concept that the number of eggs spawned by the average female plaice and the number of eggs in the sea area could provide the basis for an estimate of the number of spawning adults on the bottom of that sea area. Hensen's treatment of the problem was dependent upon a set of assumptions, among which were:- (1) capture of all eggs in a known volume of water, (2) uniform distribution of the organisms over an extensive sea area, and (3) proper identification of the catch.

The second assumption drew sharp criticism and has often been distorted beyond any possible intention of Hensen. Johan Hjort (in Murray & Hjort, 1912) considered the implications of the assumptions and concluded, "As regards Norwegian waters it is therefore, as far as I can see, at present impossible to realise Hensen's idea of counting the fishes of the sea, or to cope with the problem of calculating the stock arising from the developed larvae". Hjort pointed out that knowledge of the area of distribution of the eggs, the influence of currents on the eggs, and the spawning time of the fish was necessary before a useful estimate of the number of eggs could be made.

Since the time Hjort wrote there have been extensive investigations of planktonic fish eggs in an attempt to estimate the number of eggs from a specified population or in a given sea area. The number of investigations of planktonic fish eggs directed at estimating annual abundance seems to demonstrate either a belief that the objections of Hjort, and other difficulties, can be met satisfactorily or that the magnitude and difficulty of the problems involved have not been comprehended.

The potential value of planktonic fish egg investigations has been widely recognized. Beverton & Holt (1954), in discussing the estimation of total fish populations, asserted that, "Probably the best method is from egg surveys" (italics by authors). Simpson (in Graham, 1956) stated: "While it is not easy to obtain an estimate of the numbers of fish comprising any particular stock by sampling the adults, it is sometimes practicable to determine the total number of eggs laid by that stock in a season and, with the aid of data on the mean number of eggs laid by an individual female, to calculate the number of individuals taking part in the spawning". However, the only census for a marine fish known to Simpson in 1956 was that of Buchanan-Wollaston (1923) for the plaice, an estimate based on 9 and 5 days in two sampling periods.

Methods of Estimating Annual Egg Abundance

Several methods have been described for estimating the annual abundance of planktonic fish eggs, using the techniques which accounted, in some way, for the variations of abundance in time and space. The methods developed by Buchanan-Wollaston (1915, 1923, 1926) included constructing contour lines of equal egg abundance on charts of distributions and integrating the areas within the contour lines. His approach provided a reproducible method of depicting observed distributions and estimating egg abundance. The major objection to his approach is that there is no procedure for measuring the variability of the estimate of annual egg abundance; the significance of differences between years is unknown. Simpson (1959a, 1959b) followed the methods of Buchanan-Wollaston (1923, 1926) to estimate the annual egg production of the plaice in the North Sea for 9 years and in the Irish Sea for 1 year. Van Cleve & Seymour (1953) used the method of drawing contour lines suggested by Buchanan-Wollaston (1923) to obtain an index of the annual abundance of halibut eggs on the Cape St. James Bank for 11 years. They felt that ideally, ".... a particular locality or a series of localities could be found which, if sampled adequately, would yield the same results as are obtained from the entire universe".

Sette (1943) developed the concept that the distribution of haddock eggs conformed to a normal frequency surface. However, he based his estimate of the annual egg abundance on the average catch of seven cruises. Again, there was no procedure for measuring the variability of the estimate of annual egg abundance. Sette abandoned this approach in his later work; the author knows of no other application of his method.

Sette & Ahlstrom (1948) tried several methods of estimating the annual abundance of the eggs of the Pacific pilchard. They found little difference between three methods:- (1) weighing egg abundance proportionally to the areas of polygons constructed around the sampling locations; (2) a simplified procedure using averages; and (3) isometric (contour) lines. Their procedure used linear integration of the data from each cruise over space and a second linear integration of all of the cruises over time. They acknowledged that variability was to be expected from the distribution of eggs in time and space, but used the variability associated with a single sample, estimated from paired hauls, to determine the variability of their estimates of annual egg abundance. The neglected variability associated with time and space made their estimate of the total variability too low by an unknown amount. Saville (1956) used these methods to estimate the annual egg abundance of the haddock at Faroe for 4 years.

Taft (1956) extended the treatment of the data examined by Sette & Ahlstrom (1948). He calculated confidence limits for the estimated egg abundance for a cruise; those limits suggested considerably greater variability in annual egg abundance than had been assumed in the earlier work. Taft did not develop confidence limits for the estimated mean of annual egg abundance. He assumed no variability at locations during the time between observations, but recognized that such variability would probably make the annual estimate less precise.

Most of the published investigations lasted only one or two years. All of the estimates relied on observations during short periods in different years or were based on one or few samples at each location in any spawning season. The significance of the differences in abundance between years, lacking adequate estimates of error, was a subjective judgment by the investigator. It is not clear that any estimate of annual egg abundance has been used to make important decisions about the stocks of spawning fishes.

Puget Sound Studies

The earlier investigators who estimated the annual egg abundance of fish populations were aware of the distributions in space and time, but failed to develop methods of measuring those sources of variability. Implicit and explicit assumptions, some quite unrealistic, introduced unknown errors into those estimates. The exclusion of some sources of variability led to repeated underestimation of the probable errors accompanying the estimates.

Studies were made in Puget Sound on an egg population which was a complex of three species of pleuronectid flatfishes. The diameter of the planktonic eggs ranged from o.94 to 1.oo mm, which distinguished those eggs from other eggs in the samples. The eggs were similar in their spherical shape, lack of oil globules, small perivitelline space, and unsculptured shell, but when cromatophores had formed on the embryos the three species were readily separated. It seemed of interest to concentrate on estimating the variability in space and time of the abundance of eggs. Other important aspects of the overall problem, such as species composition, age distributions, and mortality rates, were not studied intensively. The first step was to estimate the variability encountered, making as few assumptions as possible about distributions in time and space.

The techniques of analysis of variance were appropriate for the problem. Analysis of variance is useful in (1) testing hypotheses, (2) estimating population parameters, (3) estimating the variance of main effects, and (4) measuring the comparative efficiency of experimental designs (Snedecor, 1956). The emphasis of the program was on gathering data for such treatment.

The estimates of experimental error were used to set contour intervals about observations on charts of egg distributions (Cushing, 1953). The contour intervals, although based on a subjective choice of probability level, provided a criterion for deciding whether the variations in distribution were meaningful.

The technique was used for a variety of experiments in the Puget Sound studies. The progression of contour levels with time or distance seems useful for making decisions for future sampling programmes.

Analysis of Variance

Winsor (Winsor & Walford, 1936; Winsor & Clarke, 194o) introduced the analysis of variance technique to the treatment of plankton data. The use of the technique has also been reported by Barnes (1949a, 1949b, 1951), Motoda & Anraku (1955), Silliman (1946), and Tester (1951, 1955), among others. Nine sets of data from the Puget Sound studies, varying in time-space complexity, were treated by analysis of variance techniques.

A survey sampling 12 stations for one year was used to estimate annual egg abundance. Duplicate samples at stations and replicated cruises provided a basis for estimating the relative magnitudes of those sources of variability. The observations of eggs per standard volume of sea water were subjected to a logarithmic transformation to meet the implicit assumptions of analysis of variance. A random model was used, as the main interest was to estimate the components of variance rather than population means. The random model gave an inefficient estimate of annual egg abundance, but was appropriate until observations of distributions in time and space provided a basis for establishing fixed factors in a mixed model. The components of variance revealed that the major source of variability was cruises (time), with stations (location) less important, and duplications (paired hauls) least important. The number of cruises necessary to reduce the confidence interval about the estimated annual egg abundance to a specified length was computed at three probability levels (Figure 1).

The discouragingly wide confidence limits indicated that a large expenditure for cruises would be required to obtain an adequate estimate of annual egg abundance. A survey of 1oo cruises would have resulted in confidence limits of 75 and 133 % of the estimated annual egg abundance at the o.1o probability level. Therefore, there was a temptation to establish some sort of index of annual egg abundance, invoking untested assumptions. However, other results of the program suggested some of the difficulties inherent in such an index of abundance.

Abundance with Time

The seasonal pattern of egg abundance was of great importance because time was the major source of variability. A curve of egg abundance with time could be integrated to obtain annual egg abundance. Knowledge about the shape of the curve could also provide a basis for reducing the length of the confidence interval, as well as some background for evaluating earlier methods of estimating annual egg abundance.

In the Puget Sound studies an index of egg abundance for cruises was based on the average catch at three central stations. The seasonal increase and decrease of abundance were almost rectilinear on a logarithmic scale, although the data were too few to determine the shape of the curve with precision (Figure 2). While the confidence intervals about each cruise index were long, the annual range of egg abundance was many times greater. A parabola, $Y = 157.92 + 23.49 X - o.12 X^2$, where Y = egg abundance and X = days beginning 9 XII, was fitted to the data to illustrate an attempt to reduce the variability by an assumption about the shape of the curve of egg abundance with time. The parabola proved to be a poor fit for the data; two straight lines would have reduced the variability further.

The shape of the curve of egg abundance with time generally has been accepted to be unimodal and several authors have taken it to be a normal curve. The belief that egg abundance continously increases to a maximum and then continously decreases could not be refuted by the paucity of observations at sea. Nordgaard (1914) determined the seasonal curve of abundance of eggs for a population of plaice for five seasons. He maintained the fish in a pond and periodically removed the eggs from a filter over the outlet. The peak of abundance fell at a different time each year and the number of eggs in the week of maximum abundance varied about sevenfold. The curves rose to a sharp peak in four seasons, but there was no peak in the fifth season; the curves were neither smooth nor symmetrical. Van Cleve & Seymour (1953) presented a composite seasonal curve based on all catches in all years of sampling halibut eggs. The increase and decrease of abundance were not as abrupt as indicated by the data of Nordgaard; the difference might be attributed to the effect of combining many spawning seasons.

The available information about the nature of egg abundance with time suggests several shortcomings of earlier methods of estimating annual egg abundance. When the sampling was confined to a relatively short period, the brief maximum of abundance might have been missed; samples might have reflected widely different segments of the annual cycle. Buchanan-Wollaston (1926) sampled only for several short periods each season and had almost no basis for determining the shape of the curve of egg abundance with time. Even when the survey was conducted throughout the spawning season, the distribution of eggs in time and space could have affected greatly the apparent egg abundance when relatively few samples could be taken. Van Cleve & Seymour (1953) were forced to cover a large area for many weeks, sampling most stations only once; they might have been widely different distances from centers of egg abundance at the peak of the spawning season in different years.

Time-Location Interactions

The analyses of variance for the nine sets of data in the Puget Sound studies revealed a consistent pattern of statistically significant interactions between time and location (Table 1). The interactions were statistically significant even where the main effects of time and location were not. The interactions, beyond the o.ol probability level, implied a greater complexity than a simple additivity of main effects.

The interaction term was especially large when the distribution of egg abundance with depth was investigated. Such a result is expected when mixing of the water column varies with wind speed. When significant interactions occur, each depth should be sampled at each location on each cruise. The difficulty of establishing an index of abundance by sampling at a few selected locations or times when the effects of time and location are not additive is obvious. Until the interactions can be reduced, the interpretation of the effects of times and locations will be questionable.

Model

A model was sought which would allow the estimation of egg abundance in three dimensions with time, with confidence intervals about annual egg abundance and any other mean of interest. A partially hierarchical analysis of variance model with fixed and random factors met the requirements (Scheffé, 1959).

The spawning season can be divided into periods; cruises will be made within the periods. The region where eggs occur can be divided into areas; several locations will be sampled within each area. Several depths will be sampled at each location to develop a three-dimensional representation of egg distribution. Duplicate samples can be nested at each depth. The curve of egg abundance with time will be constructed from the estimates of mean egg abundance during periods; shifts in centers of egg abundance can be detected and measured.

The general model is:

$$X_{jkmnqr} = \mu + P_j + C(P)_{k(j)} + A_m + AP_{mj} + AC(P)_{mk(j)}$$
$$+ L(A(C(P)_{n(m(k(j)} + D_q + DP_{qj} + DA_{qm}$$
$$+ DAP_{qmj} + DC(P)_{qk(j)} + DA(C(P)_{qm(k(j)}$$
$$+ DL(A(C(P)_{qn(m(k(j)} + e_{jkmnqr},$$

where: X_{jkmnqr} is the number of eggs per standard volume in any sample subjected to the logarithmic transformation; μ is the overall mean; P_j is the period effect, $j = 1, . . . J$; $C(P)_{k(j)}$ is cruises within periods, $k = 1, . . K$; A_m is the area effect, $m = 1, . . M$; AP_{mj} is the interaction between areas and periods; $AC(P)_{mk(j)}$ is the interaction between areas and cruises-within-periods; $L(A(C(P)_{n(m(k(j)}$ is locations within areas within cruises within periods, $n = 1, . . N$; D_q is the depth effect, $q = 1, . . Q$; DP_{qj} is the interaction between depths and periods; DA_{qm} is the interaction between depths and areas; DAP_{qmj} is the interaction between depths and areas and periods; $DC(P)_{qk(j)}$ is the interaction between depths and cruises-within-periods; $DA(C(P)_{qm(k(j)}$ is the interaction between depths and areas-within-cruises-within-periods; $DL(A(C(P)_{qn(m(k(j))}$ is the interaction between depths and locations-within-areas-within-cruises-within-periods; and e_{jkmnqr} is the error term, $r = 1, \ldots R$. Further terms, such as replications in the field and aliquots in the laboratory, could be nested within the model (Table 2).

The assumptions implicit in the model are: $P. = 0$; $C(P)_{k(j)} = \underline{N}(0, \underline{s}^2_{C(P)})$; $A. = 0$; $AP_{.j} = AP_{m.} = 0$; $AC(P)_{.k(j)} = 0$, $\underline{N}(0, \underline{s}^2_{AC(P)})$;

$L(A(C(P)_{n(m(k(j))} = \underline{N}(0, \underline{s}^2_{L(A(C(P))})$; $D. = 0$; $DP_{.j} = DP_{q.} = 0$; $DA_{.m} = DA_{q.} = 0$;

$DA_{.m} = DA_{q.} = 0$; $DAP_{.mj} = DAP_{q.j} = DAP_{qm.} = 0$; $DC(P)_{.k(j)} = 0, \underline{N}(0, \underline{s}^2_{DC(P)})$;

$DA(C(P)_{.m(k(j)} = DA(C(P)_{q.(k(j)} = 0$, $\underline{N}(0, \underline{s}^2_{DA(C(P)})$; $DL(A(C(P)_{.n(m(k(j)} = 0$,

$\underline{N}(0, \underline{s}^2_{DL(A(C(P)})$; and $e_{jkmnqr} = \underline{N}(0, \underline{s}^2_{e})$; where the dot (.) notation indicates a sum and $\underline{N}$ indicates a normal population with mean and variance in parantheses.

The model is quite flexible, so that a survey program can be designed for the most efficient estimate from any combination of expected variability and available resources. It is possible to follow the consequences of the model in one hypothetical situation, given \$ 5,ooo to obtain an estimate of the annual egg production. The costs of the survey can be set at \$ 2oo for a cruise and \$ 2o for a day of sorting and counting in the laboratory. This cruise is a relatively expensive and inflexible unit which must be used carefully.

We are unwilling to assume that any interaction is zero until it has been evaluated; R = 2 allows an evaluation of the interaction between depths and locations-within-areas-within-cruises-within-periods. The depths chosen for sampling might be o.1, 5, 1o, and z - 1 metres, where z is the depth; therefore Q = 4.

The choice of areas and locations can affect the apparent variability appreciably. The inefficient estimates obtained by including stations of widely divergent egg abundance in one mean can be improved when observations provide a basis for stratifying by expected abundance. Lacking observational guidance, locations within areas will be determined by dividing each area into halves across its longest dimension, choosing the sampling location in the center of each half as a centric systematic area-sample treated as a random sample (Milne, 1959); therefore N = 2. We have specified NQR = 16 samples in each area and can next maximize the number of areas which could be sampled on a cruise, estimated to be K = 8. Eight areas of approximately equal surface extent and similar shape will be chosen in a convenient configuration. The number of cruises within a period will be set at K = 2. Therefore, the number of samples obtained would be 2 per depth at each location, or 8 per location, 16 per area, 128 per cruise, 256 per period, reaching a maximum of 3,o72 samples if 24 cruises were made.

A balance between the periods which could be sampled and the days available for analysis with \$ 5,ooo available can be computed. If the samples could be handled at the rate of 5 per hour, or 4o per day, then 1o periods could be sampled to provide 2,56o samples with laboratory time available to examine 2,8oo samples. Under this scheme, the duplication increases the number of samples by 1,4oo, a cost equivalent to more than 3 cruises. The experiments in the Puget Sound studies suggest that the cost of duplications is disproportionately high for any expected increase in the precision of the estimate of annual egg abundance. However, there should be a study of the minimal amount of water which must be filtered to provide an adequate sample. Minimizing the volume filtered would reduce the time necessary to make each sample and increase the number of samples; it is entirely possible that less cumbersome and expensive equipment could be used to take the samples. Further, sub-sampling in the laboratory, as aliquots or aliquants, could also increase the number of samples which could be handled. Such studies could be added to the analysis of variance model with no difficulty.

At the start the periods would be distributed symmetrically about the probable time of maximum egg abundance. In the early years of the program, the periods must be distributed so that secondary maxima or shifts in the date of the maximum will be detected and measured. A suitable distribution of periods for the Puget Sound studies might be: one in December and one in June; two in January, February, March, April, and May. The procedure is realistic in that the precise date on which the cruise can be made is not critical.

The procedure for estimating the annual egg abundance considers that at least two cruises estimate the mean egg abundance for each period. The mean egg abundance for each period can be expressed as:-

$$\bar{X}_{j\cdots\cdots} = + P_j + \overline{C(P)}_{\cdot(j)} + L(A(C(P)_{\cdot(\cdot(\cdot(j)} + \bar{e}_{j\cdots\cdots},$$

with variance:

$$\mathrm{Var}\,(\bar{X}_{j\cdots\cdots}) = \frac{s^2_{C(P)}}{K} + \frac{s^2_{L(A(C(P)}}{NMK} + \frac{s^2_{e}}{KMNQR},$$

which can be shown algebraically to be equalto the mean square for cruises within periods. Therefore, confidence limits may be set for the mean egg abundance for each period:

$$C.L.\ P_j = \bar{X}_{j\cdots\cdots} \pm t_{0.10}\ \frac{M.S.\ C(P)}{KMNQR},$$

where "t" has been taken at the o.lo probability level and the appropriate degrees of freedom are those for cruises within periods. The estimated annual egg abundance is:

$$\text{Annual egg abundance} = \sum_{j=1}^{J} \bar{X}_{j\cdots\cdots}\ \frac{T_j}{E_j},$$

where T_j is the number of days in period j and E_j is the length, in days, an egg is in the plankton during period j. Minimal confidence limits may be set about the estimated annual egg abundance by substituting first the upper and then the lower confidence limits computed for each period. The confidence limits are minimal because the variance of E_j has been neglected. There must be wide variations in the length of time eggs remain in the plankton, but there is no observational evidence for useful estimates.

Discussion

The common procedures for estimating the annual abundance of planktonic fish eggs were found to be unsatisfactory, both because of unrealistic assumptions and because the error of the estimate was unknown. In the Puget Sound studies, data from a fish egg survey were examined with a random model of analysis of variance. The confidence limits for the estimate of annual egg abundance were 12 and 849% at the o.o5 probability level. The large number of cruises needed to reduce the confidence interval to an acceptable length suggests an expensive program. Multiple-ship operations would probably be necessary for a population distributed over a wide sea area.

The shape of the curve of egg abundance with time is an indication of the magnitude of the temporal changes. The considerable range of abundance over a spawning season indicated the inefficiency of the random model which treated egg abundance independent of time. The variance of the annual mean egg abundance could be reduced by regression techniques, but observations are too few to support any assumption about the shape of the curve. The expected normal curve might be distorted into a polymodal or unsymmetrical form by environmental factors or an incomplete separation of spawning stocks. An empirical curve can be established by far more intensive observations. It is conceivable that eventually environmental observations can be used to predict changes in the spawning activities of fish populations, but until then it seems prudent to avoid assumptions which cannot be tested against observations.

The location of the center of egg abundance, as well as the time, can differ between years. The futility of establishing representative sampling times or locations to obtain an index of abundance is obvious. The large time-location interactions encountered are to be expected if the eggs are spawned in a geographic pattern which is altered by hydrographic factors. The interactions might be reduced if samples could be taken in water of known origin and history. Sampling at geographic locations may continue to be necessary in large annual surveys, but is clearly unsatisfactory in most shorter experiments.

The model for a partially hierarchical analysis of variance has sufficient generality to be of broad applicability for studies of annual egg abundance. Years and groups of years could be added as fixed factors; sub-sampling within any fixed factor could be added as a random factor to increase the precision with which any mean is estimated.

Improvements in a program of estimating the annual egg abundance can be based upon information acquired during the study. In later surveys the costs of vessel operations and laboratory analyses can be allocated in a more efficient experimental design than can be constructed before the variance of the main effects is known. A continual program of balancing variability against costs would allow refinement of the sampling scheme within available resources. Some interactions might be found to be undetectable and the sampling could become more efficient with more knowledge of hydrography and the biology of the population. The decision to continue such a program could be based upon the adequacy of the confidence interval estimate which could be attained for the funds available.

The analysis of variance model can be readily programmed for computer analysis. In the Puget Sound studies two transformations of the original data were attempted; other transformations have been suggested and their use should be explored. Transformations and test of their effectiveness on large groups of data become more reasonable when a computer is available for the tedious computations.

The model for the partially hierarchical analysis of variance is a powerful tool in a program for estimating the annual abundance of a population of planktonic fish eggs. However, the estimate of annual egg abundance can be no better than the observations upon which it is based; the variability will continue to be underestimated by an unknown amount until the time eggs remain in the plankton can be estimated. Difficult problems associated with equipment and field procedures, hydrography, and biological factors, such as the identification of spawning stock, mortality rates, and adult spawning behaviour, still require further study.

The Puget Sound studies and the literature indicate the large and complex variability of distributions of egg abundance in time and space. The large variability associated with the time eggs remain in the plankton has not been estimated and will be most difficult to assess. These considerations suggest that the measurement of abundance of fish stocks by planktonic egg surveys is not yet a practical undertaking.

Abstract

Data from surveys in Puget Sound and the literature are used to examine some common procedures for estimating the annual production of planktonic fish eggs. Methods of integrating areas within contour lines to obtain an index of abundance appear unsatisfactory. Indices based on comparisons of abundance during short periods in successive years or relying on one or a few samples at each location during the spawning season are rejected, both because of unknown fluctuations in the time and location of maximum egg abundance and because of the lack of probability statements to accompany such indices.

The complex distributions in time and space encountered in estimating populations of planktonic fish eggs can be treated with a partially hierarchical analysis of variance. Periods, areas, and depths of sampling can be considered to be fixed factors; cruises within periods, locations within areas, and replications can be considered to be random factors. The confidence limits set for any mean can be used to establish meaningful contour intervals for depicting distributions. Procedures for allocating resources, choosing times and places of sampling, and setting confidence limits about estimated annual production can be established. The approximate cost of detecting specified fluctuations in egg abundance with a known probability of error can be determined.

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Table 1. Summary of analyses of variance for time, location, and duplication effects in the Puget Sound studies. The size of each experiment is indicated by the levels of main effects.

Probability Level[1)]

Main Effects			Interactions		
Time	Location	Duplication	T x L	T x D	L x D
xx 5	xx lo	NS 2	xx	x	NS
xx 5	xx 7	NS 2	xx	x	NS
x 12	xx 3	NS 2	xx	NS	NS
NS 4	xx lo	NS 2	xx	NS	NS
xx 16	x 8	NS 2	xx	NS	NS
xx 15		NS 2			
NS 3	NS 5	NS 2	xx	NS	NS
NS 2	NS 4	NS 2	NS	NS	NS
NS 3	NS 3	NS 2	xx	NS	NS

1) NS = P > o.o5; x = P ≤ o.o5; xx = P ≤ o.ol

Table 2. Partially hierarchical analysis of variance for surveys of annual egg abundance.

Source of Variation	Degrees of Freedom	Parameters estimated by Mean Squares
Periods	(J-1)	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)} + MNQR\ \underline{s}^2_{C(P)} + KMNQR\ \underline{s}^2_{P}$
Cruises (P)	(K-1)J	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)} + MNQR\ \underline{s}^2_{C(P)}$
Areas	(M-1)	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)} + JKNQR\ \underline{s}^2_{A}$
A X P	(M-1) (J-1)	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)} + KNQR\ \underline{s}^2_{AP}$
A X C(P)	(M-1) (K-1)J	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)} + NQR\ \underline{s}^2_{AC(P)}$
Locations (A(C(P)	(N-1)MKJ	$\underline{s}^2 + QR\ \underline{s}^2_{L(A(C(P)}$
Depths	(Q-1)	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + JKMNR\ \underline{s}^2_{D}$
D X P	(P-1)(J-1)	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + KMNR\ \underline{s}^2_{DP}$
D X A	(Q-1)(K-1)	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + JKNR\ \underline{s}^2_{DA}$
D X A X P	(Q-1)(K-1)(J-1)	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + KLR\ \underline{s}^2_{DAP}$
D X C(P)	(Q-1)(K-1)J	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + MNR\ \underline{s}^2_{DC(P)}$
D X A(C(P)	(Q-1)(M-1)(K-1)J	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)} + NR\ \underline{s}^2_{DA(C(P)}$
D X L(A(C(P)	(Q-1)(N-1)MKJ	$\underline{s}^2 + R\ \underline{s}^2_{DL(A(C(P)}$
Error	JKMNQ(R-1)	$\underline{s}^2$
Total	JKMNQR-1	

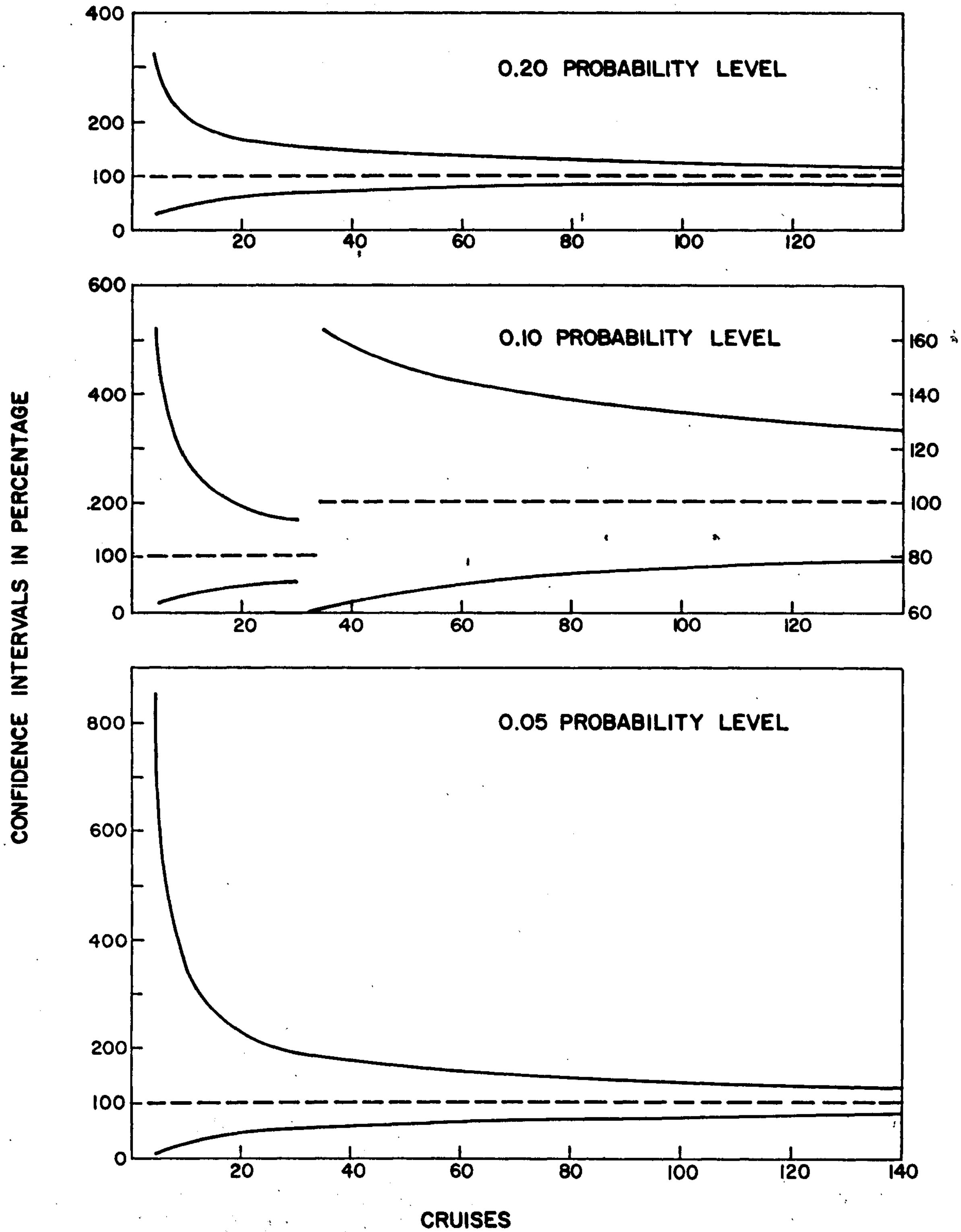

Figure 1. Relationship between percentage confidence intervals and the number of cruises used to estimate mean annual egg abundance.

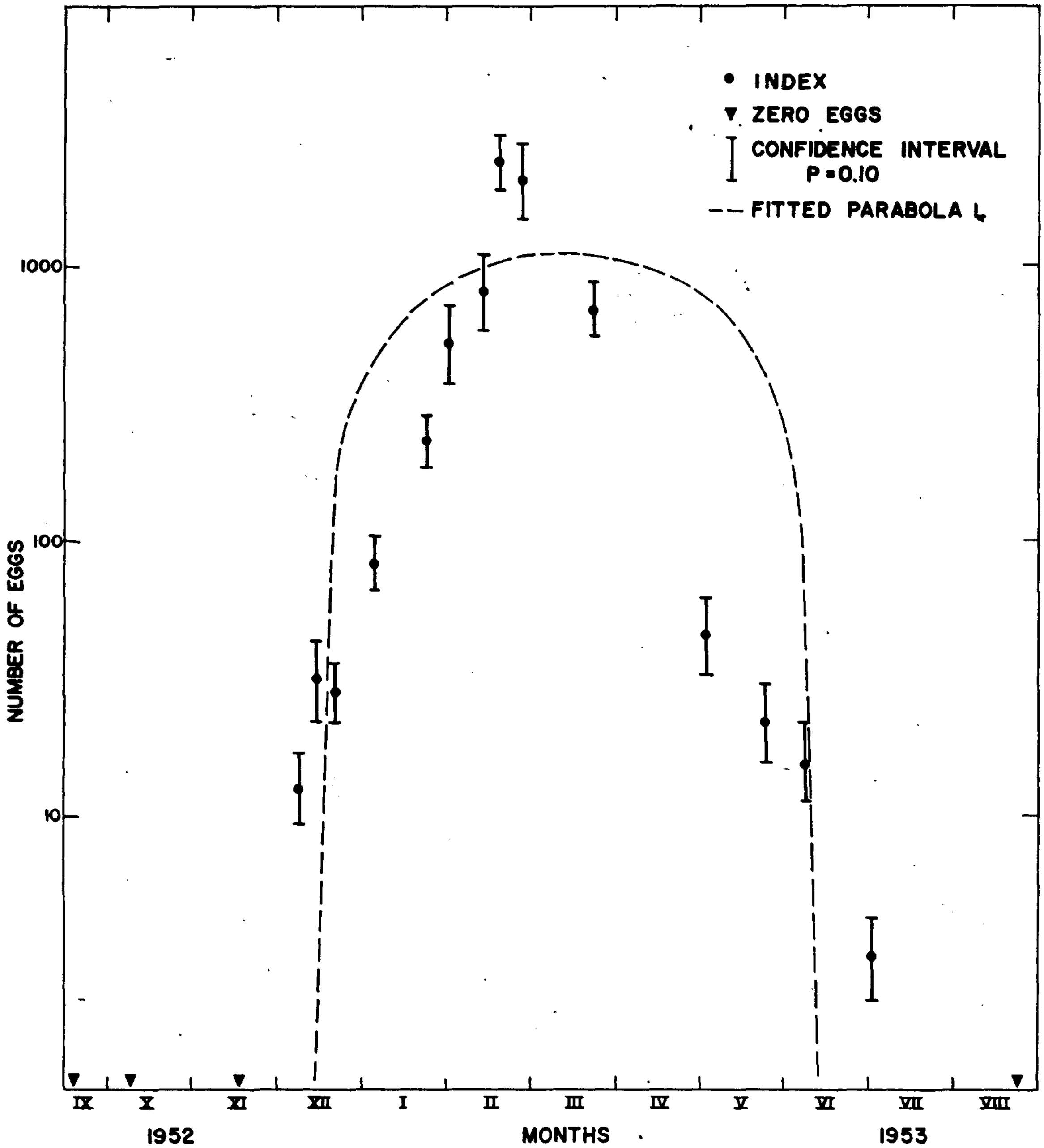

Figure 2. Index of egg abundance in standard hauls at three stations.