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CAFSAC Research Document 79/31

An outline of a method to back calculate the mackerel spawning stock from egg abundance estimates

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Introduction

The idea that egg production can be used to calculate the abundance of adult fish required to produce those eggs appears to have been first expressed by Hensen and Apstein (1897). Several decades later the potential value of fish's planktonic eggs studies was widely recognized and Beverton and Holt (1956) stated that it was probably one of the best methods to study the abundance of the adult population. Simpson (in Graham, 1956) added: "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 practical 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."

Although the concept was appealing abundance estimates derived from egg surveys were never used for management purpose until recently when both the ICES Mackerel Working Group (Anon, 1978) and the CAFSAC Pelagic Subcommittee based their recommendations, at least partly, on such estimates. This paper presents a method to assess abundance of the northern population of northwest Atlantic mackerel based on egg data.

Material and Method

The basic data comes from fish egg and larval surveys that have been initiated in 1965 and conducted since then in the Gulf of St. Lawrence. A detailed account of these surveys is available in Kohler et al. (1974; 1975; 1976; Marine Fish Division files) including tow by tow information on the catch of each species and the associated oceanographic information. Several gears were towed at each station but data from the Meter nets and Miller samplers only were used.

Ichthyoplankton tows made on the Scotian Shelf in 1977 (Lett pers. comm.) as well as earlier studies (Huntsman, 1922; Sparks, 1929; Leim and Scott, 1966) show that mackerel spawning is usually restricted to the Gulf of St. Lawrence from mid-June to mid-July, although MacKay (1976) thinks that, in 1967, the major spawning area might have been the Scotian Shelf.

Saville (1977) gives an expression of the fundamental equation to calculate the number of spawners:

$$(1)\ N_m = \frac{P}{F \times R}$$

where

N_m = number of mature fish in the stock
P = annual egg production of the stock
F = average number of eggs produced annually per female
R = sex ratio in the mature stock

The critical parameter in this equation is P, F and R being easier to determine, although determination of F can cause some problems for batch spawners. P can be calculated in a variety of ways but the data available lead to calculate the daily egg production for one date first and then, using the shape and duration of the spawning cycle, calculate the total egg production during the season. Another strategy would have been, rather than averaging over time and space to find one value of daily egg production, to average over space for subsets of stations to find the daily egg production of several days. However the egg production is spacially so variable that this path yielded too high a variability to be feasible.

The basic information to determine the total abundance of eggs in a given area is the abundance of eggs under a square meter of sea surface which multiplied by the surface area of the region gives the total abundance. When oblique tows are done that data can be obtained directly by dividing the total catch of eggs by the amount of water strained and then multiplying by the depth to which the gear was towed. However oblique tows were not part of the regular protocol of the cruises we get our data from and this type of tow is not suitable when most of the eggs are close to the surface. This problem can be circumvented by combining data from two gears, the surface Meter nets and the Miller samplers. The Miller sampler is a gear type smaller than the Meter net with a torpedo shaped plastic body and a 10.8 cm diameter mouth opening. The Miller samplers were stacked at 10 m intervals on a wire and were towed at the same time as the Meter nets. The maximum tow depth for the Millers was 50 m. Unfortunately the flow is not recorded for this gear type making it impossible to use this data alone to find the abundance of eggs per cubic meter at each depth. However, the assumption that the amount of water strained at each depth is equal is very realistic since all the samplers are set in a very short period of time. The profile of eggs over depth can be determined from the Miller sampler as a percentage composition. If the abundance of eggs per m^3 from the surface Meter net is taken as the true abundance of eggs at the surface, the percentage catch in the surface Miller sampler can be used to calculate the theoretical total quantity of eggs that would have been caught if Meter nets, rather than Miller samplers, had been towed at each depth. From this theoretical total catch and the percentage of eggs at each depth the theoretical catch at each depth can be calculated and then plotted on graph paper. Integrating over depth, using a planimeter or weighting a piece of paper representing the distribution of eggs over depth, the number of eggs under a square meter of sea can be calculated. It must be assumed that this value of eggs per meter square is representative of an area surrounding the station for which it was calculated.

In order to minimize the variation due to the fact that the stations locations vary slightly from year to year it was decided to define a set of standard stations (Fig. 1). The cruise track for each year was plotted on a map and the midpoint of neighbouring stations of different cruises was taken as the standard position location for that station. The station standard areas were then defined by joining adjacent stations with straight lines and constructing a perimeter around the station by joining lines that are perpendicular to the midpoint of the lines between stations. Because the surface areas of the stations on the margin of the grid cannot be defined objectively the 10 fathom isobath was taken as the inshore boundary and the 50 fathom isobath was taken as the offshore one. The choice of the 10 fathom isobath is an aribitary decision while outside the 50 fathom isobath the water temperature is usually too cold for mackerel to spawn. Each area was then cut out and the individual pieces of paper weighted on a Mettler balance to find the station surface area. The abundance of egg per square meter previously calculated multiplied by the surface area (m^2) gives the total abundance of eggs for each station. The value obtained represents several days of spawning activity and as stated earlier we are interested in finding daily egg production.

Egg catches, while sorted, were staged according to the following classification:

stage 1: fertilization to formation of embryonic shield
stage 2: embryonic shield to closure of blastopore; embryo covers half the egg circumference
stage 3: lifting of tail from yolk
stage 4: tail curves back and touches head
stage 5: deformed eggs

At 11°C stage 1 lasts 30 hours (Worley, 1933). Thus one can state that the number of stage 1 eggs found at a given station represents the production of 1.25 days and from that value finds the daily egg production. But depending on when the sampling was done during the spawning cycle, local changes in water masses characteristics, (stratification, temperature) or distribution of the mackerel schools, there may be very few stage 1 eggs during one particular cruise. The spawning population abundance derived from such egg data would then be unduly underestimated. Assuming that the eggs sampled are at the midpoint of their development time, knowing the development time and the rate of disappearance of the eggs from the water column the original number of eggs spawned can be back calculated for each stage by the following formula:

$$(2)\ E_0 = \frac{Ei}{e^{-M \times T_s}}$$

where:

E_0 = number of stage 1 eggs spawned at each station
E_i = number of eggs sampled at each stage at station
M = instantaneous mortality rate
T_s = incubation time for each stage in days

It is realized that eggs will tend to be before the midpoint of their development stage when spawning is increasing, the contrary being true when spawning is decreasing, however it is felt that this assumption is of minor importance.

Ware (pers. comm.) sampled the mackerel spawning cycle in St. Georges Bay for several years and found that the daily rate of disappearance of eggs from the water column was between 30 and 50% which gives a minimum instantaneous mortality rate (M) of 0.36 over all stages.

Worley (1933) studied in laboratory the relationship between the development of mackerel eggs and temperature. He does not give a mathematical expression for the relationship but he gives some values that can be used to do a regression of incubation time versus temperature. The best representation of the relation is an expontentially decreasing function of temperature represented by the following equation;

$$(3)\ IT = e^{-(6.58096\ -\ 0.12961\ \times\ TEMP)}$$

$$(r^2 = .99),\ F = 342.67\ (1,3/34.12)$$

where:

IT = total incubation time.
TEMP = sea surface temperature at each station.

Assuming that the relative duration of each stage remains constant and equal to (Worley, 1933):

stage 1: 17% of the incubation time
stage 2: 43% of the incubation time
stage 3: 29% of the incubation time
stage 4: 11% of the incubation time

The total incubation time can be partitioned into each stage's duration and the original number of eggs spawned can be back calculated. This gives four estimates of the daily egg production at each station. These are averaged to get the daily egg production at each station and added up to find the total daily egg production for the entire Gulf of St. Lawrence. In order to expand the daily egg production to the total seasonal egg production the duration and shape of the spawning cycle must now be investigated.

As stated earlier a different path could have been followed. Rather than averaging the four estimates of daily egg production over stations the egg production could have been averaged over dates. This would have given information on daily egg production for a period starting before the cruise and ending on or the day before the last day of the cruise. The spawning cycle shape and duration could then have been determined for each individual year from that data. But because only part of the Gulf would have been sampled on a given date, the average egg production on that day must be corrected for the total Gulf surface area. The analysis showed that this aerial correction brings so much variability that the total egg production cannot be determined that way. Such a treatment of the data could yield a false sense of precision.

Mackerel eggs were caught on three cruises in 1967 and 1968, two cruises in 1969 and one cruise in 1976, 1977 and 1978. A plot of the average catch of eggs per cubic metre on each cruise versus the midpoint date of the cruise suggest that the spawning cycle of mackerel has a standard normal shape. A regression of the natural logarithm of the average egg catches versus time and time square when retransformed to linear scale approximate a normal curve. The equation of the regression is:

$$(4)\ E = e^{-242.0627 + 2.85314\ TM - 0.00792\ TM^2}$$

where

E = average egg catch
TM = midpoint date of the cruise (in Julian days).

The reduction in the total sums of squares due to the regression is 79.29% with an F (significant at 1%) of 15.31 ($F_{2,\ 8/8.65}$). Figure 2 represents the spawning cycle calculated from that equation and shows clearly that 95% of the spawning acitivity takes place within a 40 day period. This result agrees with the work of Ware (1977) and Lett and Marshall (1978).

If the purpose of this work was to search for a minimal estimate of the spawning population it could be stopped here. Assuming that the daily egg production calculated earlier applies to the peak spawning day, the total egg production of the whole spawning period could be found and equation (1) applied to obtain the total number of spawners. But this would probably not be realistic, because there is no reason to expect that the value calculated corresponds to peak spawning. Therefore its exact location on the egg production cycle has to be determined.

Mackerel is highly temperature dependent in its activity (Sette, 1943: MacKay 1967, 1976; Olla _et al._, 1976) and several studies (Lett and Marshall, 1978; Ware, 1977; MacKay, 1976) have shown that mackerel spawning is related to temperature. This dependence could act as a regulatory mechanism to match the production cycle (Cushing, 1972). The data used to investigate the dependency between spawning cycle and time can also be used to study the relationship between spawning activity and temperature. It appears here again that the cycle has a normal shape.

The equation of the regression is:

$$(5)\ \ln E = -16.36666 + 4.78925\ T_C - 0.19322\ T_{C2}$$

where ($r^2 = .64$, $F = 6.33$ signifiant at 5% ($F_{2,7}/4.74$)

E = average cruise egg catch
T_C = average cruise temperature.

Taking the first derivative of this equation and setting it equal to zero gives the optimal spawning temperature, in this case 12.4°C (Fig. 3) which can be compared very well with 13°C found by Ware (pers. comm.) in St. Georges Bay. Unfortunately the cruises last only for 7 - 10 days and do not provide a long enough temperature record to determine how many days there is between the peak spawning day and the day to which the total egg production is applied.

There is a good correlation between the Gulf of St. Lawrence cruise temperature and Entry Island (Magdalen Island, P.Q.) temperature (Figure. 4).

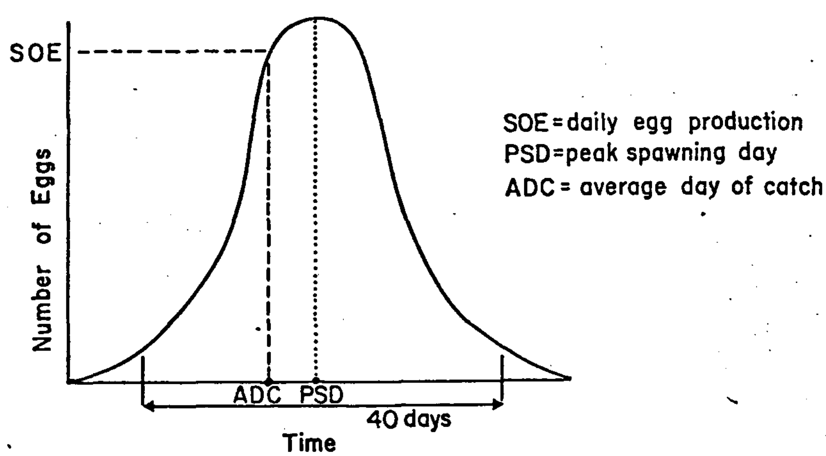
$$(6)\ T_C = 1.074 + 0.87734\ T_{E.I.}$$

($r^2 = .91$, $F = 273.76$ significant at 1% ($F_{1,28}=6.64$))

where
T_O = cruise temperature
$T_{E.I}$ = Entry Island temperature

This relationship can be used to find the interval of time between peak spawning day and the day to which the total egg production applies. Peak spawning is taken as the date at which Entry Island has a temperature of 12.9°C (corresponding to 12.4°C on the cruise). The daily egg production is assigned to the date when Entry Island has a temperature corresponding to the average cruise temperature.

The data necessary to calculate the total egg production for the whole spawning season, is now available. It can be summarized in the following manner:



From a standard normal probability distribution of standard deviations 10 (2 standard deviations equals 40 days equals 95% of spawning) the probability of ADC can be found. The daily egg production can now be calculated for each day (or 1.25 day) of the spawning cycle by the following formula:

$$(7)\ E_{TM} = (PRE + PRO) \times SOE$$

where

E_{TM} = egg abundance at time TM
PRE = probability of a given point
PRO = probability of average day of catch
SOE = daily egg production for the entire Gulf of St. Lawrence.

These daily egg productions added together give the egg production for the whole spawning season.

Given information on maturity, fecundity (Maguire, unpublished data) and population structure the spawning population abundance can be calculated by:

$$(8)\ N_m = \frac{E}{P_i \times M_i \times F_i} \times \frac{1}{R}$$

where

N_m = number of mature individuals
P_i = percentage of age group "i" in the population
M_i = percentage mature of age group "i" in the population
F_i = fecundity of age group "i" in the population
R = sex ratio

The method can be summarized as follows:

1. Find the abundance per metre square at each station

   - combine Miller sampler and surface Meter net data

2. Find the egg production at each station

   - multiply by surface area
   - calculate incubation time
   - partition incubation time and egg abundance into stages
   - back calculate to stage 1 for each stage
   - average these four estimates

3. Find egg production for Gulf

   - adding the values calculated in 2 for each station

4. Find peak spawning temperature, duration and shape of spawning cycle

5. Find values for each day of spawning cycle

   - find probability of ADC
   - apply equation 7

6. Add up to find total seasonal production

Results

The method described was applied to the data from cruises made in 1969, 1976 and 1977. The results of the calculations are summarized below.

Year	Cruise No.	Stage One egg	Average day of Catch	Peak spawning day	Total egg prod.	Spawning stock estimate	Anderson and Paciorkowski estimate
1969	P047	1.1x10	167	181	8.28x10	5247.3x10	5315x10
1976	P167	2.16x10	178	180	3.07x10	2484.3x10	1819.8x10
1977	P184	2.41x10	178.5	184	4.94x10	3667.37x10	1377.2x10

These results show that the northern population spawning stock reached a minimum in 1976 and has increased in 1977 to about 70% of the 1969 level. It would seem that in 1969 the northern population comprised most of the Northwest Atlantic stock. This contradicts Sette (1943) who stated that there was two distinct spawning populations and that the southern one was more important. Sette reached the conclusion that the southern population was more important by comparing the average catch of eggs of Meter nets towed at the surface for 20 minutes for the seasons 1927-32 on the Continental Shelf between Cape Cod and Cape Hatteras (3000-5000 eggs/successful tow) with the catch of eggs given by Sparks (1922) for the Canadian Fisheries Expedition of 1915-16 (300 eggs/tow). However the mackerel egg catches in the Gulf of St. Lawrence are not of that order nowadays. In 1977 the average catch per tow (surface Meter nets, 30 minute tows) was approximately 110,000 eggs/tow which would mean in the order of 70,000 eggs/20 minute tows. It should also be noted that the total egg production calculated for 1977 is 4.94×10^{14} eggs compared with an estimate of 2.67×10^{14} eggs for the southern population obtained by Berrien *et al.* (1979). It would thus appear that if there are two separate spawning populations the northern one is now more important.

Sensitivity Analysis and Confidence Interval

An estimate of the error associated with this method was made. The true value was taken as the one given in the preceding section for each year and the effect of changing the value of the parameters was investigated.

The rate of disappearance of eggs from the water column is a major assumption of this model. The value we used was communicated to us by Dr. Dan Ware and as he pointed out should be considered as an average value for average conditions. The analysis of the importance of this factor shows that variations from the value we used are not critical to the model. A variation of 22% in the rate of disappearance (from 0.36 to 0.45) caused a variation of only 16% in the back calculated number of stage one eggs. However, it is obvious that this rate is likely to change from year to year and if an estimate for each individual year could be obtained the model would certainly be improved.

It can be argued that the spawning cycle length varies from year to year. But the variation is probably not greater than a few days each year and this analysis shows that a variation of 30% in the length of the spawning cycle (from 40 days to 28 days) produced a change of only 24% in the total abundance of eggs. Since the modifications in the duration of the spawning period are likely to be rather small (smaller than 30%) this factor should be considered negligible.

The single most important factor is probably the location of the average day of catch compared to the peak spawning day. To evaluate the importance of this parameter the standard of comparison must be changed. The results of increasing the period of time between peak spawning and average day of catch were compared with the value obtained when the two days were the same. This shows that a change of 6 days in that period causes a change of 52% in the estimated egg production. This means that the sampling strategy should be designed in order to cope with this problem. This year there will be a one month cruise to sample mackerel spawning, which will allow covering the whole Gulf of St. Lawrence at least twice and maybe three times. This will hopefully improve the estimates.

Confidence intervals for the population estimated is a common oversight of assessment papers. Any unconventional assessment ought to consider the reliability of the estimate. In addition to the sensitivity analysis presented earlier an index of the coefficient of variation of the egg production, and thus population estimate, is calculated.

Considering the patchy distribution of mackerel eggs, the assumption that the abundance of eggs/m^2 calculated applies to the whole station's area might not always be true. The choice of a particular set of stations may also influence the estimate obtained. To assess the error due to these factors the abundance of eggs for the whole Gulf was estimated with a number of subset of stations of different sizes. Subsets of 14, 21, 28, 35, 42, 49, 56 and 63 stations each were used. For a given year and subset size the stations were randomly chosen, their production added up and prorated up to the total Gulf surface area giving one estimate of egg production. This process was repeated a hundred (100) times for each subset size and year. Then the average egg production and standard deviation were computed from this vector of egg production estimates. A plot of the coefficient of variation ((standard deviation by mean) x 100) against the size of the subset, showed (Fig. 8) that the coefficient of variation is an exponentially decreasing function of the subset size. Because seventy (70) stations only were used, the coefficient of variation for the subset size sixty-three (63) is underestimated because too large a share of the seventy (70) stations were used. But it is believed that the first seven (7) subsets give reliable estimates of the real coefficient of variation. A regression of the coefficient of variation for the first seven (7) subsets versus subset size was performed using the three years data. The resulting equation is:

$$CV = e^{4.34499 - 0.3214SS} \qquad (9)$$

with $r^2 = .88$ and $F = 127.44$ significant at 1% ($F_{1,18} = 8.28$)

where
CV = coefficient of variation
SS = subset size

Equation (9) was used to predict the coefficient of variation for subset sizes greater than 56. The results given in Fig. 9, show that the value for seventy (70) stations is smaller than ten (10) percent. This suggests that the grid of stations used gives a representative sample of the area covered.

A confidence interval for the rate of disappearance of eggs from the column of water cannot be found.

The 95% confidence limits for optimal spawning temperature can be found by using the standard errors of the coefficients of the regression of abundance of eggs versus temperature and temperature squared. The lower estimate being

$$\frac{-(b + \Delta b)}{2(c - \Delta c)}$$

and the upper one being

$$\frac{-(b - \Delta b)}{2(c + \Delta c)}$$

where b and c are the coefficient of equation (5), relating abundance of eggs to temperature, and Δb and Δc are the standard errors of these coefficients. The limits calculated are 4.94°C and 29.67°C. This is obviously much too large. But it should be noticed that, the average day of catch always staying the same, using another peak spawning day would only increase the total egg production estimated.

A confidence interval can be drawn around the temperature cycle at Entry Island using the stardard error of the estimates from the regression of temperature versus time. But since both peak spawning dates and average day of catch will move together inside that interval its size is irrelevant.

Errors in the gonad weight-fecundity relationship can also be of importance in this method. The relationship used was (Maguire unpublished data)

$$\text{FECUNDITY} = -19817 + 5215 \text{ GONAD WEIGHT}$$

$r^2 = .74$, $F = 59.95$ significant at 99% $(F_{1,23}/7.88))$

The standard error of the estimate being 33,837 eggs/female. The population abundances estimated with fecundity plus or minus the standard errors are given below:

Year	Population estimate	Fecundity plus Standard error	Fecundity minus Standard error
1969	5247.3	4183.0	7037.8
1976	2484.3	1887.8	3633.8
1977	3667.4	2861.3	5106.4

It thus appears that the two single most important factors in this analysis, with the data that are presently available, are the length of time between peak spawning day and average day of catch and the gonad-weight-fecundity relationship. Research planned for 1979 are likely to diminish the variability associated with these parameters.

The rationale used in this work is that whenever a range of values for a parameter was available the value giving the lowest population estimate was used. The population estimated is then a minimum one. Given the variability due to patchiness and to the gonad-weight-fecundity relationship, the population abundance for each year should be between -35% and + 56% of the values calculated.

Conclusion

Except the previously mentioned selection of values giving the lowest estimate no bias could be identified in this method. However, a few assumptions are made. The major one is probably the normality of the spawning cycle. But there is evidence showing that this assumption is realistic. Other assumptions are:

- There is no extrusion of eggs from the net.
- The egg abundance estimated at one station applies to the whole station area.
- The eggs are at the midpoint of their development stages.
- The fecundity estimates are representative of the population's real fecundity.
- The population structure estimated is representative of the real population structure.
- The relationship between incubation time and temperature calculated for the southern population applies to the northern area as well.
- The Miller sampler distribution of eggs is representative of the real distribution of eggs over depth.
- The estimate of the rate of disappearance of eggs from the water column is realistic.

None of these assumptions are unrealistic and most of them are of minor importance. While some are untestable the others have been tested. This showed that the confidence limits put on the estimates were usually rather narrow.

Acknowledgement

This work was realized while working under the direction of Dr. P.F. Lett. His help and patient guidance are gratefully acknowledged. Dr. M. Sinclair and R.N. O'Boyle made very useful comments on an earlier draft of the manuscript. B. Swan helped in the determination of eggs per metre square for 1976.

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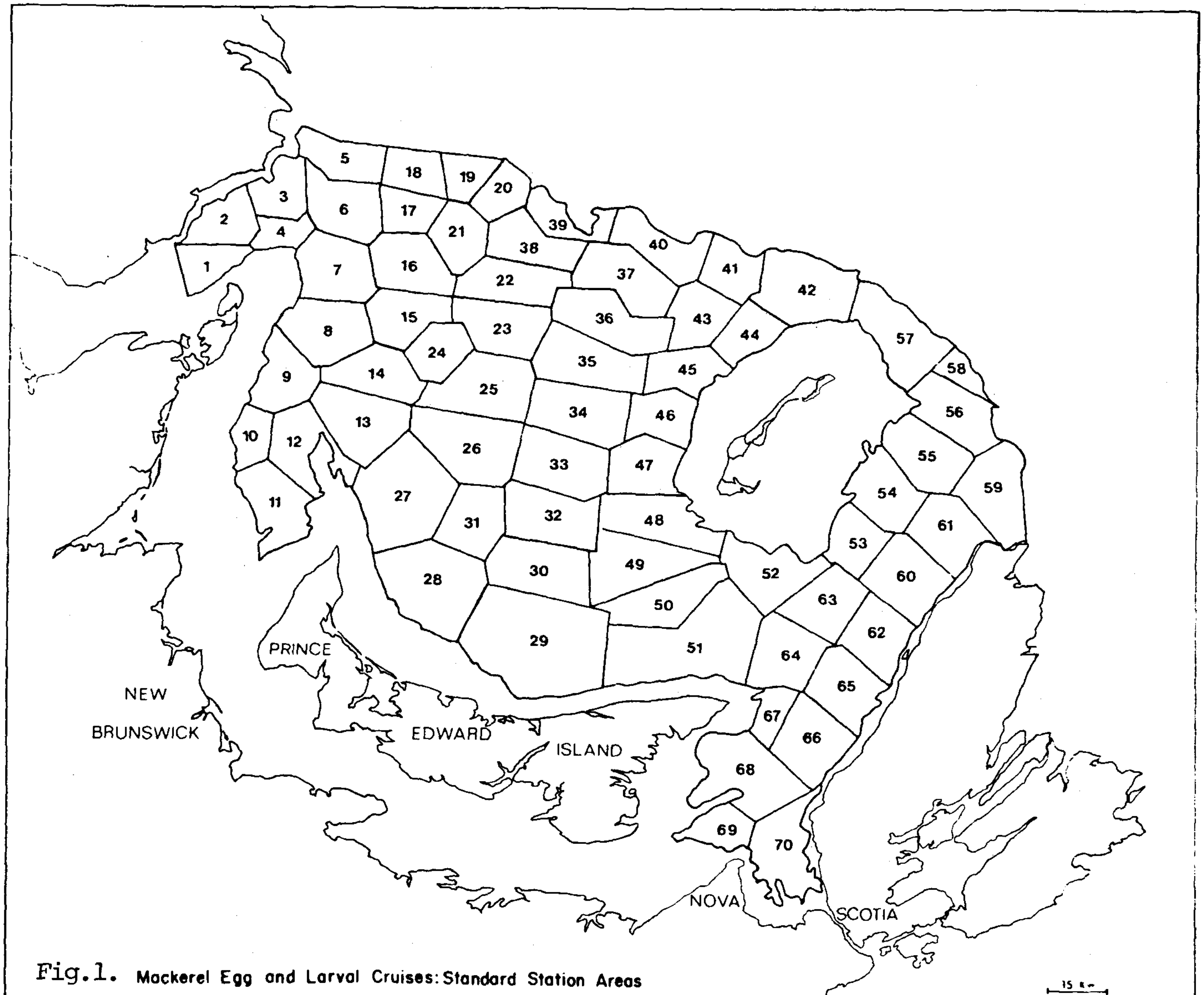

Fig.1. Mackerel Egg and Larval Cruises: Standard Station Areas

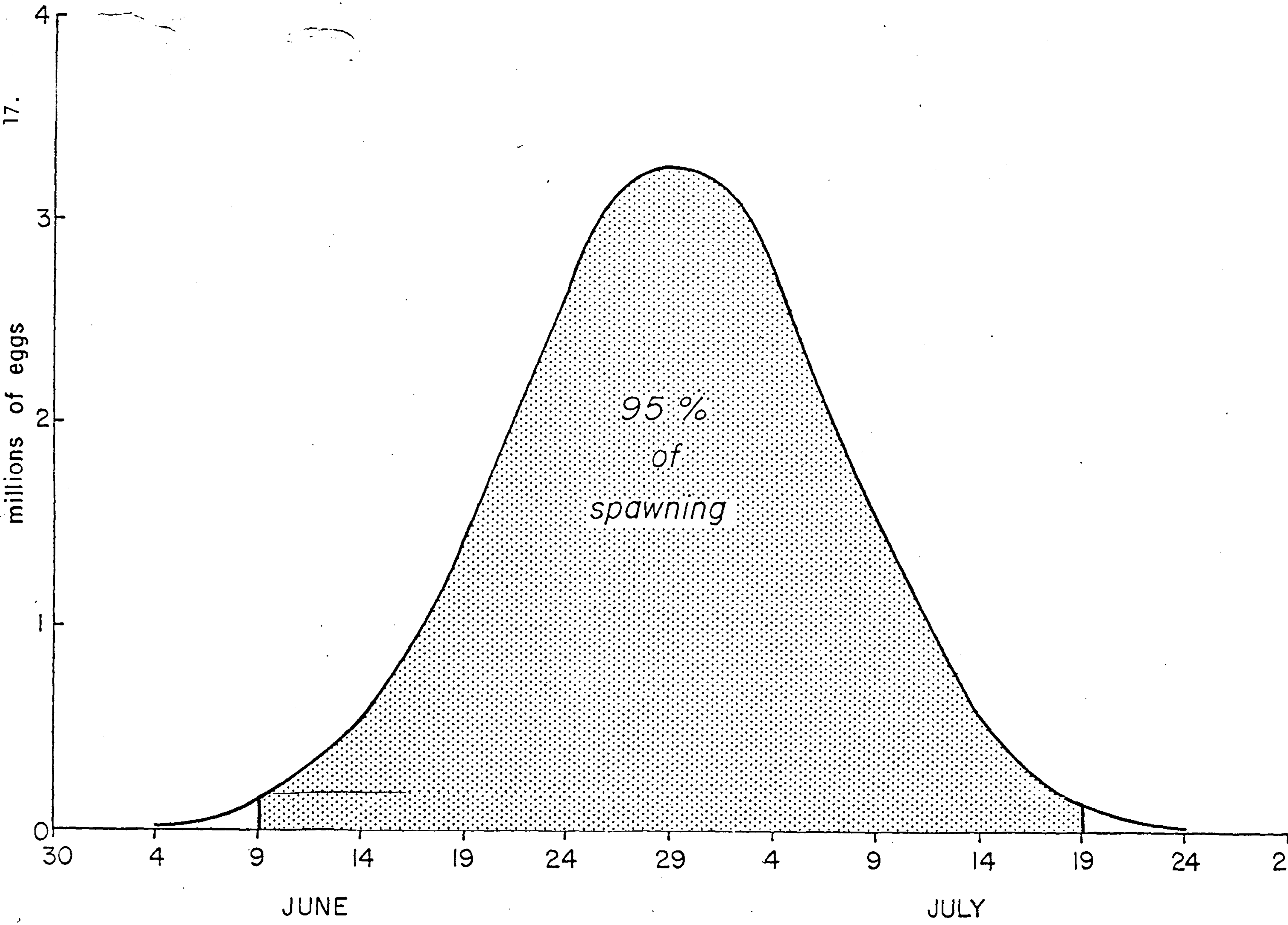

Fig. 2.Shape and duration of spawning cycle calculated from equation 4

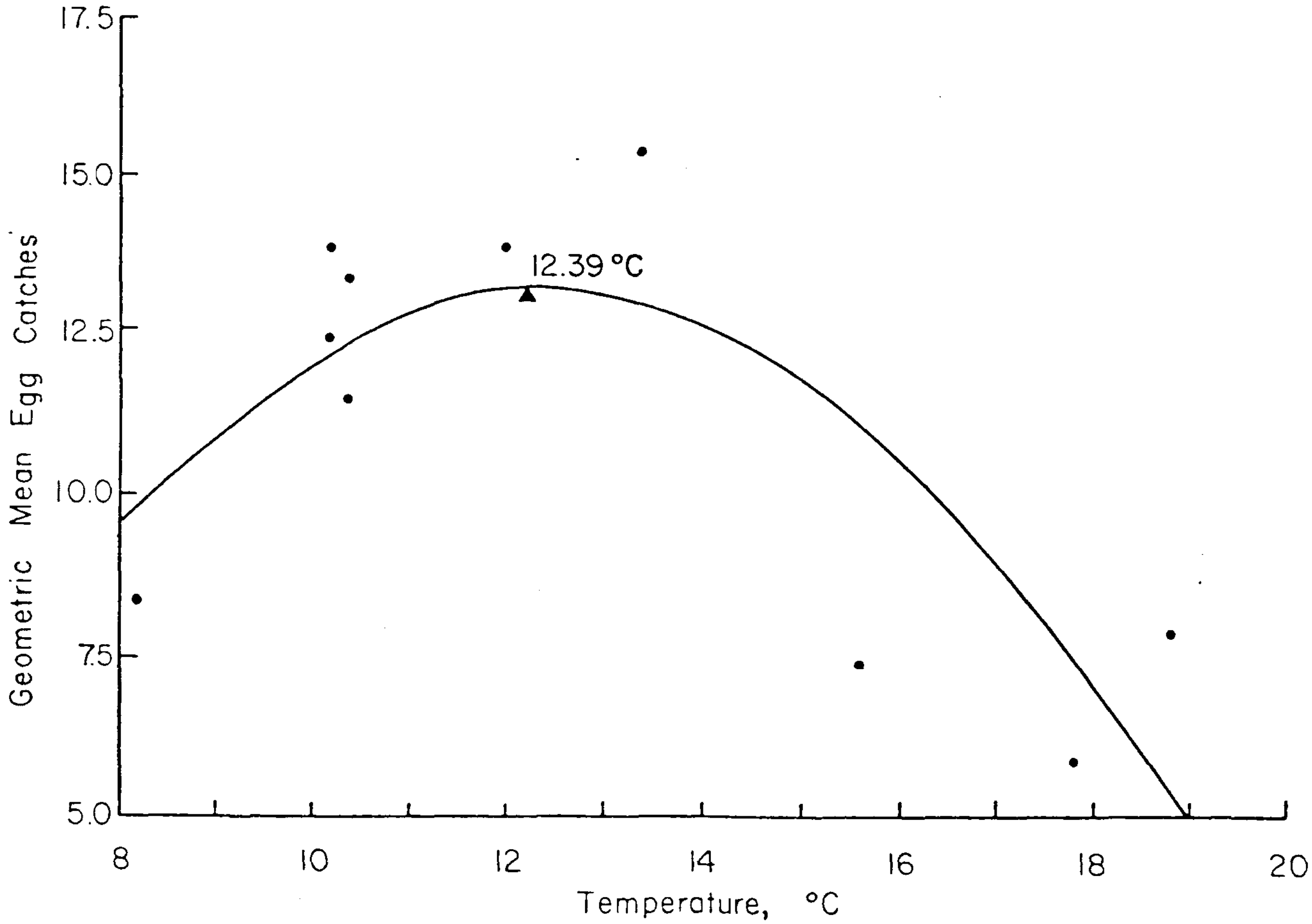

Fig. 3 Spawning cycle versus temperature

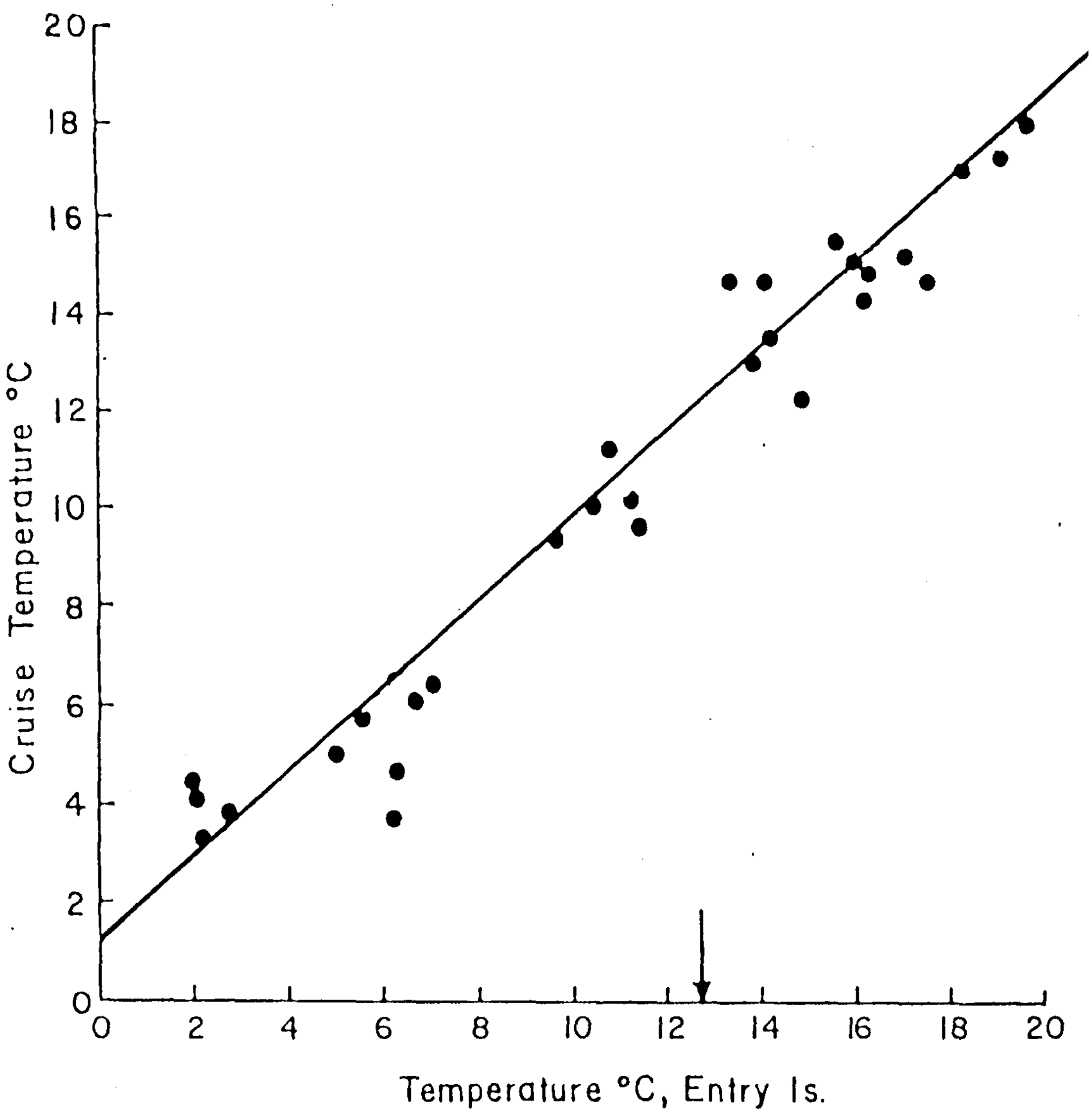

Fig. 4. Relationship between cruise temperature and Entry Island temperature.

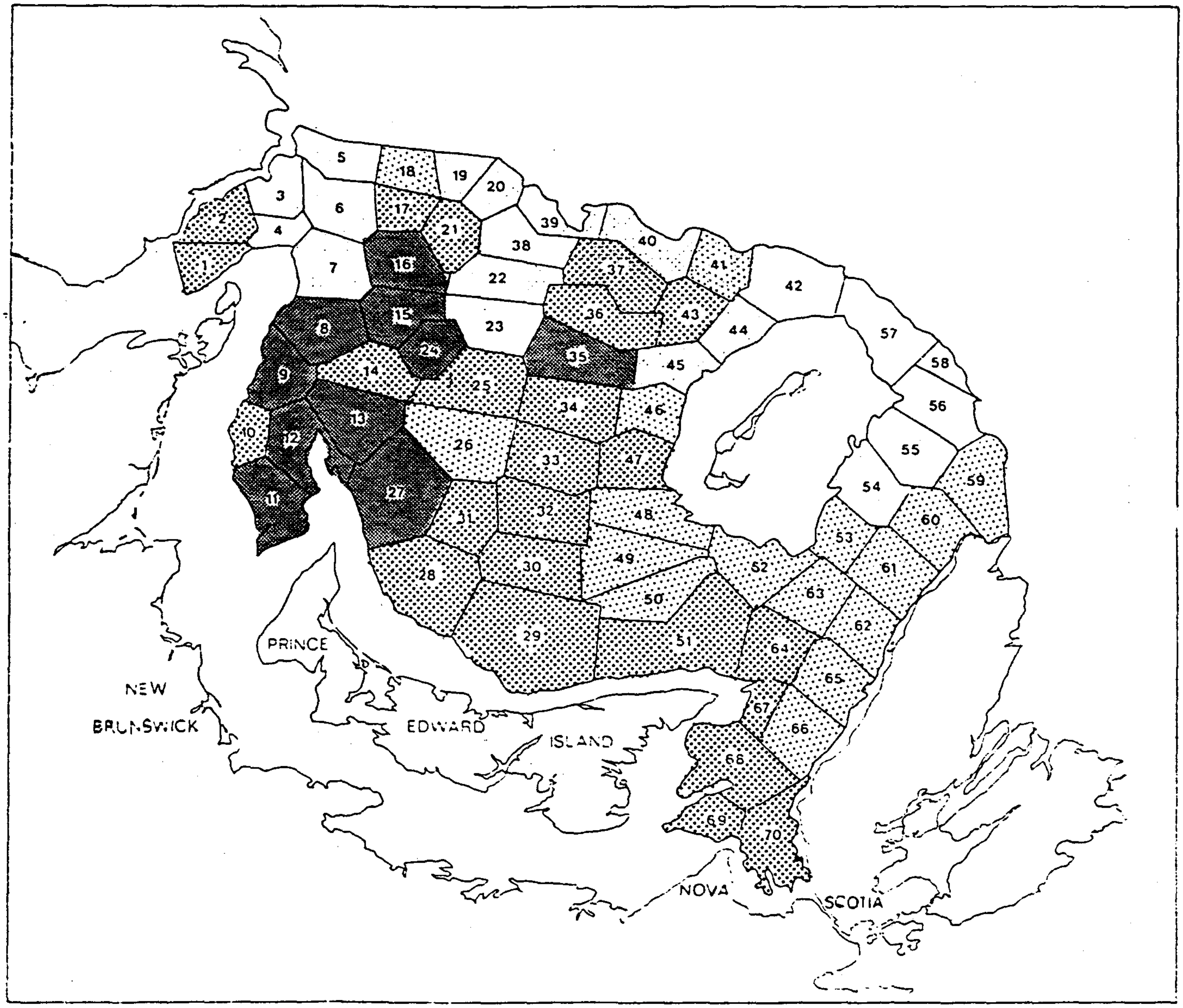

Fig. 5. Mackerel Egg and Larval Cruises: Eggs per meter square. Standard Areas, 1969 .

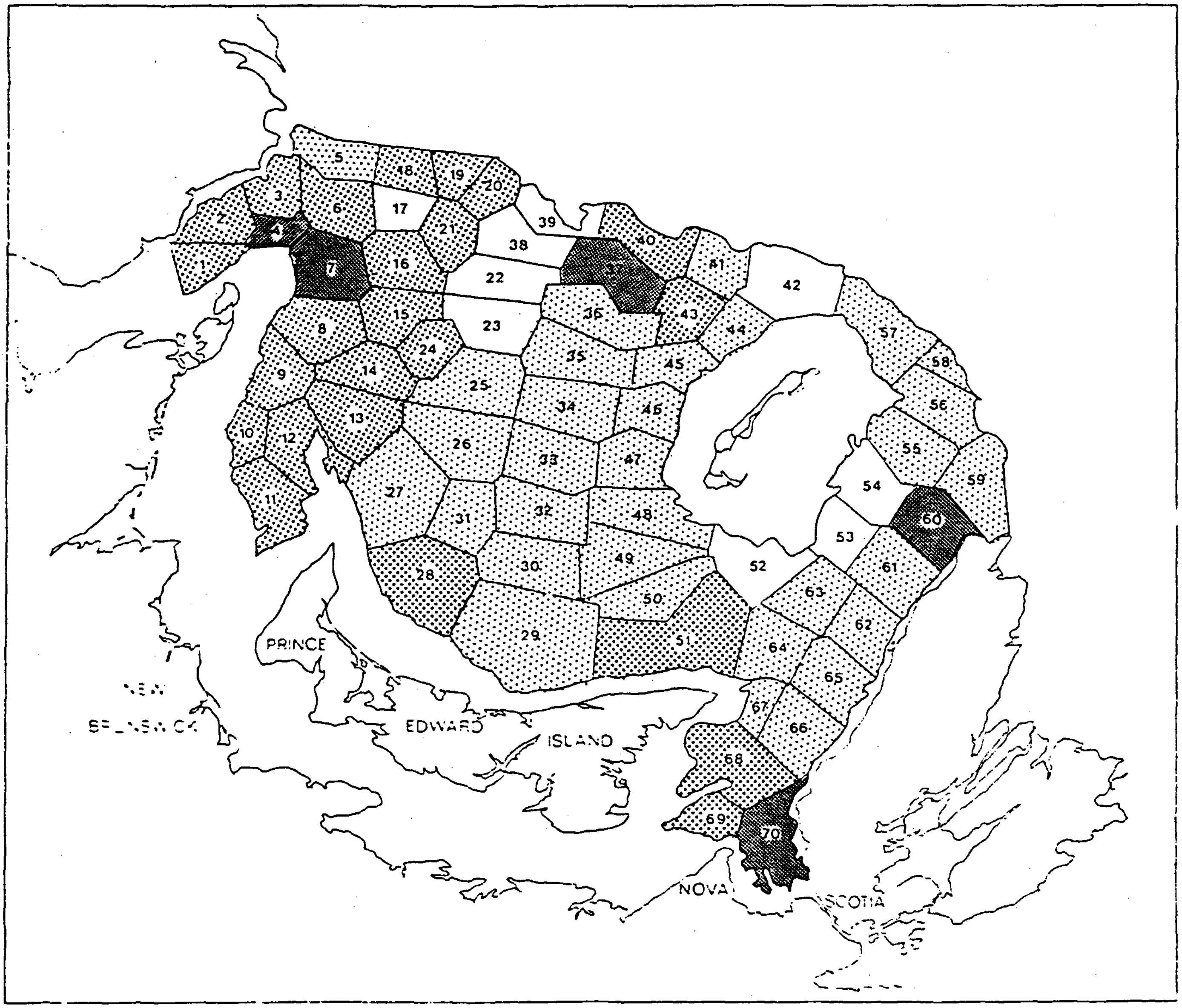

Fig. 6. Mackerel Egg and Larval Cruises: Eggs per meter square.
Standard Areas, 1976 .

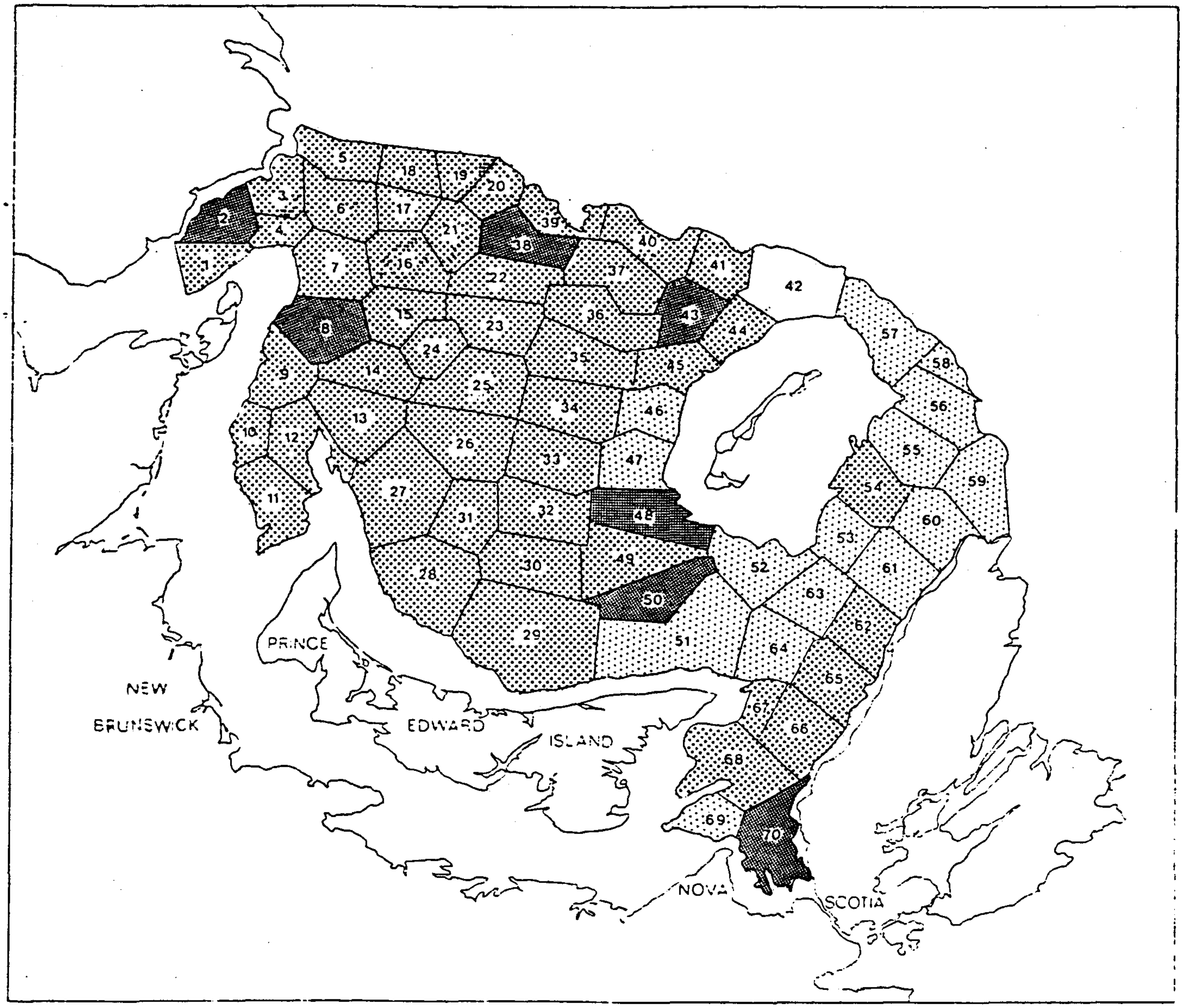

Fig. 7. Mackerel Egg and Larval Cruises: Eggs per meter square. Standard Areas, 1977.

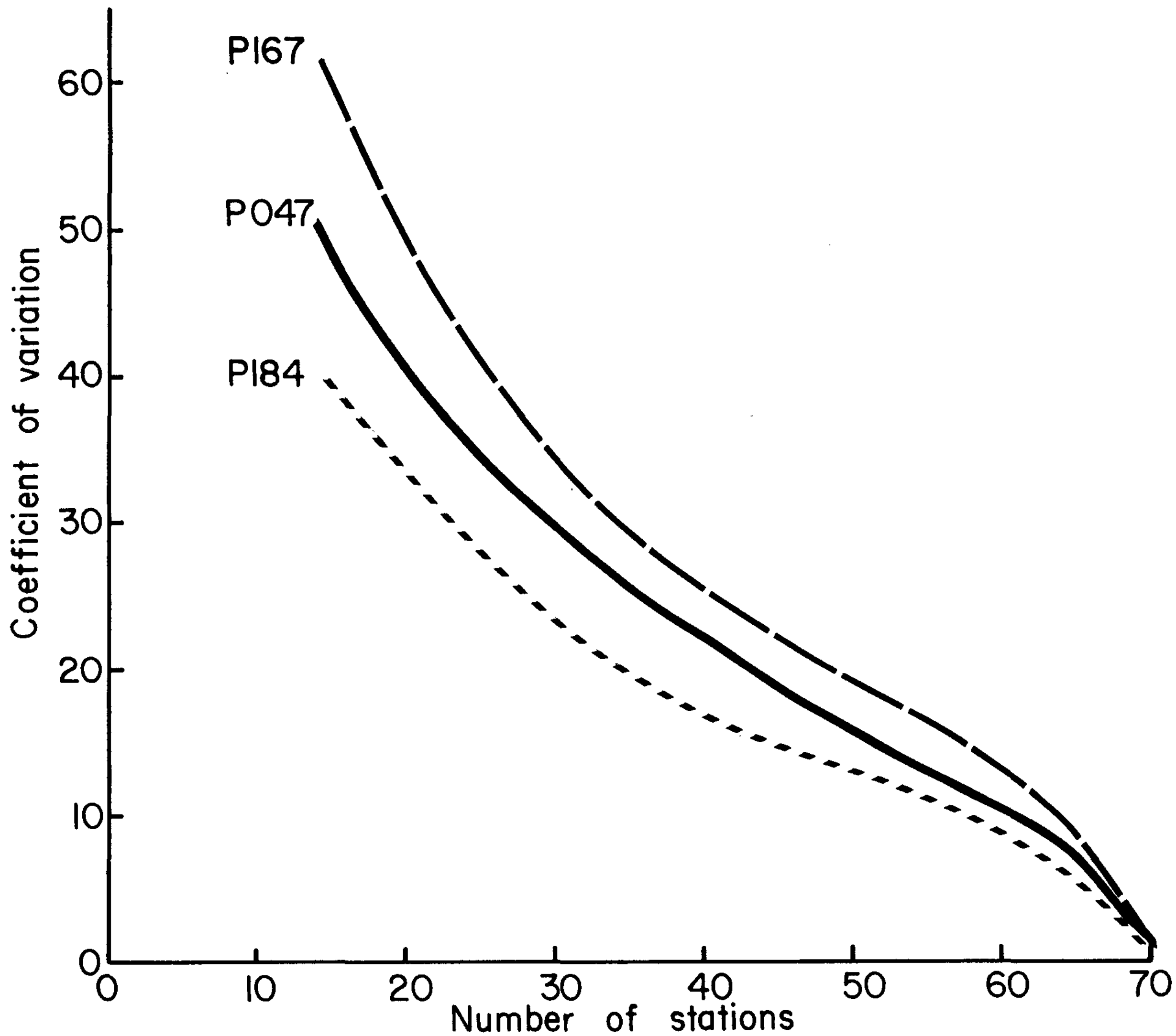

Figure 8. Observed relationship between the number of stations and the associated coefficient of variation.

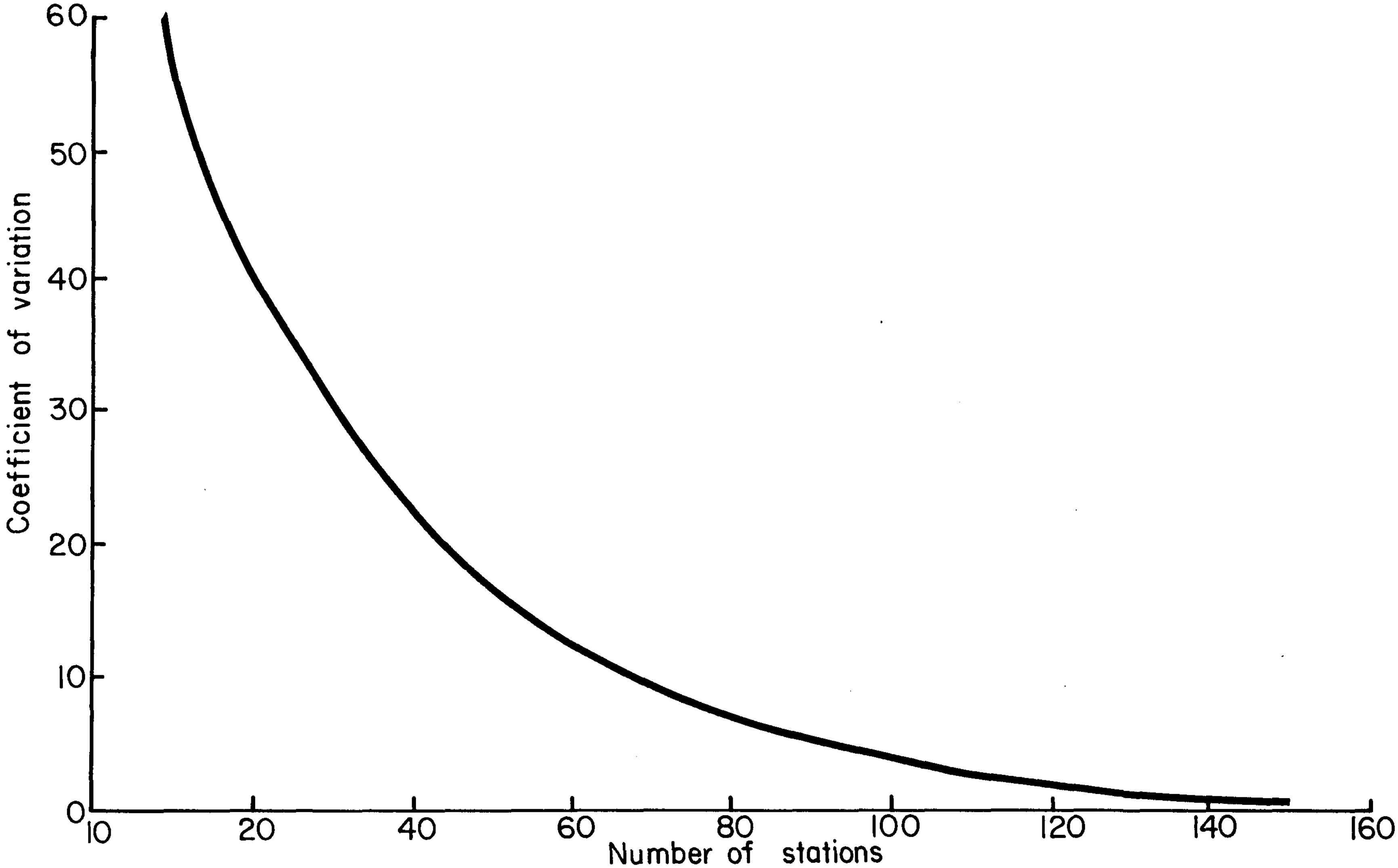

Fig. 9. Calculated relationship between the number of stations and the associated coefficient of variation.