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Methods of Assessing the Effect of Regulation on Georges Bank Haddock

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Introduction

A preliminary assessment of the effect of mesh regulation on the yield of the 1952 year class of haddock on Georges Bank was presented to the ICNAF Committee on Research and Statistics at Lisbon in 1957 (Taylor, 1957). This assessment indicated that the 1952 year class was about 90 percent as large as the 1948 and about equal to the 1950 year class. The latter year classes having been fished by the pre-regulation small mesh net, it was then possible, on the basis of these comparative sizes, to estimate the effect of large mesh on the yield of the 1952 year class. It was estimated that the 1952 year class yielded between 18 and 45 percent more pounds of fish during its first three years in the fishery than it would have under small mesh fishing.

At a meeting of Scientific Advisors to Panels 4 and 5, Quebec City, December 3-5, Paloheimo reviewed Taylor's estimates. Using a modification of the "virtual population" method (Fry, 1957), Paloheimo's analysis indicated that the .952 year class was "far greater" in size than the 1950 year class and about equal to the 1948 year class. If these estimates are correct, it cannot be demonstrated that landings from the 1952 year class increased as a direct result of mesh regulation.

The data used by Paloheimo are essentially the same as those used by Taylor. He included in his calculations estimates of the numbers of small 2-year-old fish discarded at sea from the three year classes, which Taylor did not. The effect, however, of including these discards is to make the 1952 year class appear smaller relative to the 1948 and 1950 year classes, since relatively large numbers of fish were discarded from the latter. It is, therefore, obvious that the omission of these discards from Taylor's computations does not account for the substantial discrepancies in the estimates but tends rather to increase them.

Since the data used were otherwise essentially similar, one must conclude that there is a basic error in one of the two methods or an error in application, or an error in interpretation of the data and results.

This paper will show that the method used by Paloheimo does not differ in principle from that used by Taylor but is an extension and generalization of the same basic equation, and that the apparent discrepancies result (1) primarily from the comparison of absolute population sizes estimated over unequal time periods and (2) from underestimation of the value of q[1/] at age 2 for the 1952 year class.

1/ q is the international notation recommended at Lisbon in 1957 for the ratio between the best index of effective overall fishing intensity and the resulting instantaneous fishing mortality coefficient. Earlier papers (Beverton, Taylor, Paloheimo, etc.) have used c.

The latter is less serious if comparisons are made over equal periods of time, but depends to some extent on how great the error in q is and whether or not a similar error is made in the other year class being compared. The discrepancies in question result from a comparison of 3 year's catches of the 1952 year class, 5 year's catches of the 1950 year class, and 7 year's catches of the 1948 year class. The consequences of such comparisons under certain conditions will be examined below.

Methods used in comparing year class size

The methods of analysis used by Taylor and Paloheimo derive from the same basic equation:

$$C_t = \frac{qf_tR_t}{qf_t+M}\left(1 - e^{-(qf_t + M)}\right) \qquad (1)$$

or

$$C_t = \frac{qf_t}{qf_t - M}\left(N_t - N_{t+1}\right) \qquad (2)$$

where $N_{t+1} = N_t e^{-(qf_t + M)}$.

$N_t = R_t$ = number of fish in a year class at the beginning of year t; C_t = catch in numbers during year t; f = fishing intensity in days; q = factor of proportionality between f and F, the instantaneous fishing mortality rate; and M = the instantaneous natural mortality rate.

In his comparisons, Taylor restricted the value of t to 2 and considered R_t as recruitment to age 2, or equivalent to N_2. Using the subscripts x and y to identify the values of parameters pertaining to year classes x and y, thus enabling us to express the general case where the parameters may be different in two different years, we may write (1) for year class x at age 2 as:

$$C_x = \frac{q_xf_xR_x}{q_xf_x + M_x}\left(1 - e^{-(q_xf_x + M_x)}\right) \qquad (3)$$

and for year class y at age 2:

$$C_y = \frac{q_yf_yR_y}{q_yf_y + M_y}\left(1 - e^{-(q_yf_y + M_y)}\right) \qquad (4)$$

Since the problem is to determine R_y relative to R_x, dividing (4) by (3) and rearranging, we have:

$$R_y/R_x = \frac{C_y/f_y}{C_x/f_x} \cdot \frac{q_x}{q_y} \cdot \frac{q_yf_y + M_y}{q_xf_x + M_x} \cdot \frac{1 - e^{-(q_xf_x + M_x)}}{1 - e^{-(q_yf_y + M_y)}} \qquad (5)$$

Except for subscripts, equation (5) is identical to equation (7) in Taylor, 1957.

The characteristics of equation (5) need special emphasis to avoid various misunderstandings which have arisen with regard to its use.

In the first place, one sees that if q, f, and M do not differ between the two years being compared, the relative magnitude of year classes x and y is expressed by the ratio of their catches per day $\left(\frac{C_y/f_y}{C_x/f_x}\right)$. This accords with the popular idea that catches per day are true measures of relative abundance. Furthermore, we see that if f and M are the same in the two years, and if q may be assumed to be same in the two years, q may be assigned any value we choose except zero without affecting the result.

If, however, f differs between the two years while q and M remain constant, the ratio of catches per day no longer gives a true measure of the relative sizes of year classes but must be corrected by the term

$$\frac{qf_y + M}{qf_x + M} \cdot \frac{1 - e^{-(qf_x + M)}}{1 - e^{-(qf_y + M)}} \qquad (6)$$

This term becomes increasingly important as the differences in f increase.

Again we note from (6) that, provided the value of q may be assumed to be the same, q may be in error through a fairly wide range without disturbing the correction term greatly, even though the amounts of fishing are different. The following table shows values of R_y/R_x where it is assumed that the catch per day is the same in the two years, f_x equals 5,000 days, f_y equals 6,000 days, and q_x equals q_y through values ranging from 0.06 to 0.12 per thousand days fished. The value of $M_x = M_y$ is taken as 0.1. These values are all within the range of possible values for the Georges Bank fishery.

Table 1.--Variations in the value of R_y/R_x, q = 0.06 to 0.12

q	0.06	0.08	0.10	0.12
R_y/R_x	1.028	1.037	1.046	1.053

For these values, no serious error in the estimation of the relative size is introduced through a possible 100 percent error in the value taken from q.

The error increases as the difference in the amount of fishing between the two years increases. If, in the above example, we let f_x equal 4,000 days and f_y 6,000, the difference in estimate of the relative sizes of the two year classes amounts to about 5 percent between q = 0.06 and q = 0.12, about twice as great a discrepancy as in the example in table 1, but still somewhat smaller than one might, a priori, expect.

An alternate method of estimation

Paloheimo develops his method of assessment from equation (2), which is identical to equation (1). Letting $a_t = \dfrac{qf_t + M}{qf_t}$, equation (2) is then written:

$$a_t C_t = N_t - N_{t + 1} \qquad (7)$$

Letting t = 1 be the year when the year class is two or three years old, and t = n be the last year for which we have statistics:

$$\Sigma\, a_t C_t = N_1 - N_{n + 1} \qquad (8)$$

With certain assumptions, it is thus possible to estimate N_1 for any period over which statistics of the fishery are available. If we substitute back into equation (8) the values of a_t and N_{n+1}, the form of the equation becomes more familiar and some of its implications more clear:

$$\Sigma \left[C_t \cdot \frac{qf_t + M}{qf_t} \right] = N_t(1 - e^{-(q\Sigma f_t + \Sigma M)}) \qquad (9)$$

Since we are interested in the magnitude of N_1 for year class x as compared to N_1 for year class y, we introduce subscripts to identify the year classes and year parameters and derive the following equation in the same manner as (5) was derived:

$$ {}_yN_1 / {}_xN_1 = \frac{\Sigma\left[\frac{C_y}{f_y}(qf_y + M)\right]}{\Sigma\left[\frac{C_x}{f_x}(qf_x + M)\right]} \cdot \frac{1 - e^{-(q\Sigma f_x + \Sigma M)}}{1 - e^{-(q\Sigma f_y + \Sigma M)}} \qquad (10) $$

Equation (10) has some rather obvious advantages over equation (5). If q may be assumed <u>constant over the periods of summation</u>, it permits utilization of all the available data in comparing the magnitude of two year classes, as contrasted to the data of a single year for each year class (equation 5). With q constant, it does not matter whether or not we compare for equal periods of time. If, however, q is assumed constant for comparable ages but actually varies in some consistent way with age, equation (10) may give strongly biased estimates for comparisons not made over equal periods. Inspection of (10) also shows that if q varies with age but may be assumed the same at each age, a good estimate of the relative sizes of the year classes is obtained only if the amount of fishing is about the same in corresponding years of the year classes in question. The term $q\Sigma f$, for example will weight correctly for differences in q with age, only if f is exactly the same from year to year.

We thus see that equation (8), which in application to the problem of comparing two year classes, x and y, becomes in practice equation (10), involves certain assumptions which must be carefully examined before any firm conclusions may result from its application. Although some of the same assumptions are implied in equation (5), we have seen that the errors involved are relatively small because equation (5) applies to one and the same year of life of the year classes in question. In using equation (5), the primary concern is whether there are or not random variations in q from year to year for a given age of fish. These are probably less serious than systematic variation of q with age of fish although trends in gear efficiency would make comparison of year classes widely separated in time invalid.

The effect of errors in q on equations (8) or (10) summations and estimates

Although inspection of the foregoing equations indicates their general characteristics, the consequences of assuming untrue values of q become more obvious with numerical examples:

Case 1. Values of q increasing with age

Let us suppose two year classes, x and y, consisting of 50 million fish at t = 1 (N_1 = 50). Let us further suppose that q is the same at corresponding ages in the two year classes but that it increases during the first three years from q_1 = 0.05, q_2 = 0.075, q_3 = 0.10, after which it remains constant at 0.10 per thousand days fished. Let M = 0.1. Let f_1 to f_8 be constant at 5,000 days per year for year class x and at 6,000 days for year class y.

With the foregoing information, we can compute the catches from each year class from t = 1 to t = 8. Then let us suppose that we lack information about q at early ages, although we have reason to believe it is about 0.10 at later ages. Therefore, let us assume that q is 0.10 for all ages. The summations and estimates of N_1 at each age are shown in table 2 for year classes x and y.

Table 2 shows at once that the assumption of constant q results in an underestimation of N_1 at all ages, but that the estimate improves as more and more data are included. The error by age 8 has decreased to about 6 percent from the true value.

We also note that if we compare the estimated N_1's of year classes x and y at corresponding ages and, therefore, over equal periods of time, the relative sizes estimated are in error by a maximum of only 2 percent even though, at the early ages, the absolute estimates are grossly in error.

The danger of making comparisons over unequal intervals of time (v. Paloheimo, 1958) is obvious. If, for example, one compares year class x at age 1 with year class y at age 4, we estimate y to be 25 percent larger. Freedom in such comparisons, in fact, permits us to make the year classes appear equal, larger or smaller, as suits our fancy.

Table 2.--Estimates of N_1 using equation (8) when q increases from ages 1 to 3 but is assumed constant (C_t and $\hat{N}_1$ are expressed in millions of fish). The true value of N_1 is 50 million fish

	Year class x						Year class y					
Age	C_t	$\hat{F}$	a_t	$1-e^{-\Sigma(F+M)}$	$\Sigma a_t C_t$	$\hat{N}_1$	C_t	$\hat{F}$	a_t	$1-e^{-\Sigma(F+M)}$	$\Sigma a_t C_t$	$\hat{N}_1$
1	10.54	.50	1.200	.4512	12.65	28.03	12.36	.60	1.167	.5034	14.42	28.64
2	10.52	.50	1.200	.6988	25.27	36.16	11.60	.60	1.167	.7534	27.96	37.11
3	8.24	.50	1.200	.8347	35.16	42.12	8.34	.60	1.167	.8775	37.69	42.96
4	4.52	.50	1.200	.9093	40.58	44.63	4.14	.60	1.167	.9392	42.52	45.28
5	2.48	.50	1.200	.9502	43.56	45.84	2.06	.60	1.167	.9698	44.93	46.33
6	1.36	.50	1.200	.9727	45.19	46.46	1.02	.60	1.167	.9850	46.12	46.82
7	.75	.50	1.200	.9850	46.09	46.79	.51	.60	1.167	.9926	46.72	47.06
8	.41	.50	1.200	.9918	46.58	46.97	.25	.60	1.167	.9963	47.01	47.18

We note, of course, that if the true values of q are known, we obtain a constant true estimate of N_1 at 50 million fish at any age.

Figure 1, curve A, shows graphically the errors of estimate arising from assuming q constant when it is actually increasing in value. The data are from table 2 for year class x.

Case 2. Values of q decreasing with age

Now let us examine a case in which, perhaps because of greater vulnerability to the gear at younger ages, q decreases from ages 1 to 3. As before, let N_1 be 50 million fish, M = 0.1, f = 5,000 days per year, q_1 = 0.15, q_2 = 0.125, and q_3 = 0.10 after which it remains constant. From these values we calculate the catches and enter them in table 3. Then, assuming we don't know the true values of q, we construct the remainder of the table on the assumption that q has a constant value of 0.10.

The estimated values of N_1 in table 3 and their departure from the true N_1, 50 million fish, are shown graphically in figure 1, curve B.

Table 3.--Case 2. Effect of q decreasing with age. Fishing intensity constant at 5,000 days

Age	C_t	$\hat{F}$	a_t	$1-e^{-\Sigma(F+M)}$	$\Sigma a_t C_t$	$\hat{N}_1$
1	25.26	.50	1.200	.4512	30.32	67.20
2	8.34	.50	1.200	.6988	40.33	57.71
3	4.30	.50	1.200	.8347	45.49	54.50
4	2.36	.50	1.200	.9093	48.32	53.14
5	1.30	.50	1.200	.9502	49.87	52.49
6	.71	.50	1.200	.9727	50.73	52.15
7	.39	.50	1.200	.9850	51.20	51.97
8	.21	.50	1.200	.9918	51.45	51.88

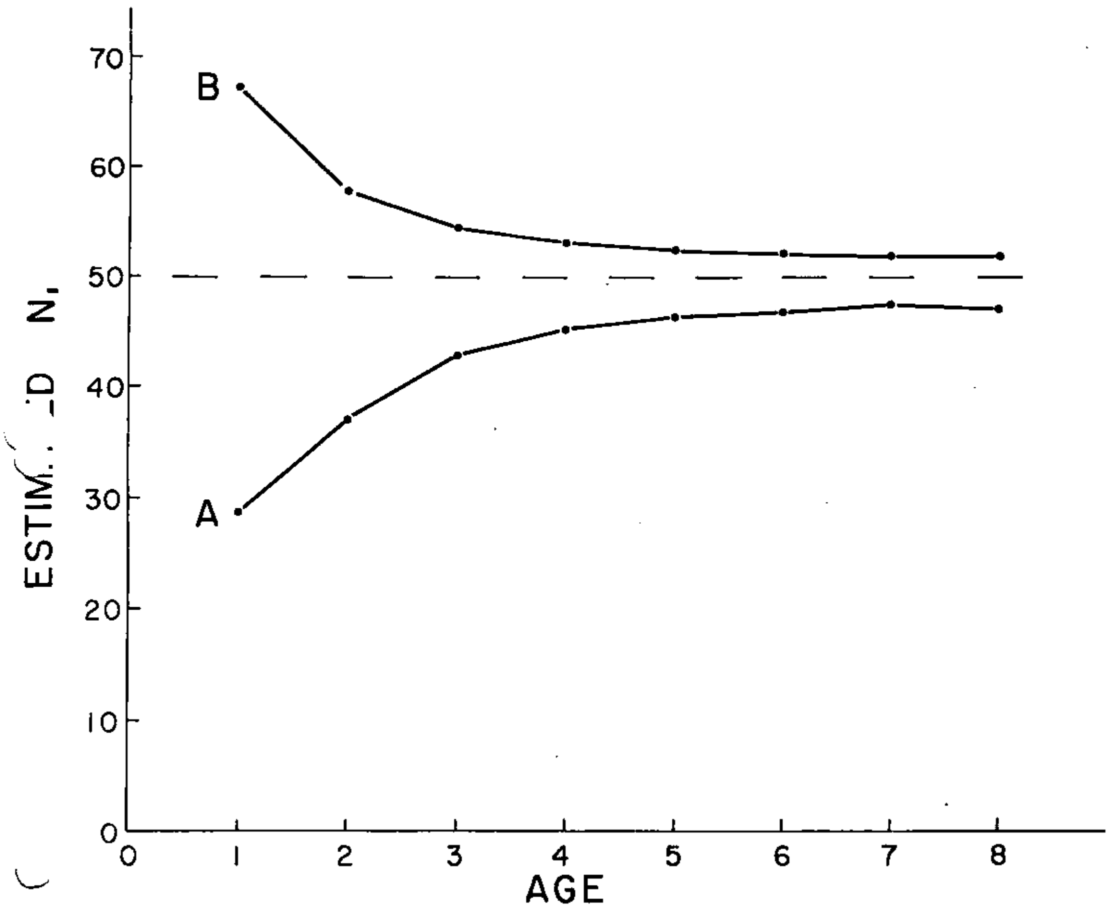

Figure 1. --Estimated values of N_1 when q actually increases from ages 1 to 3 but is assumed to be constant (Curve A) and when q decreases from ages 1 to 3 (Curve B). The true value of N_1 is 50 million fish.

It is hardly necessary to point out that Case 2, in the same manner as Case 1, gives rise to reasonably accurate estimates of relative population size only when comparisons are made over equal time periods. But it is most important to point out the gross errors which arise in comparing a Case 2 situation for one year class to a Case 1 situation for another. This, indeed, seems to have happened in attempting to establish a value of q for large mesh nets in the Georges Bank haddock fishery. There is in this instance some argument for "using all the available data," for the discrepancies become less the more information that is used. It is, however, easy to determine from the trend in estimates whether or not this situation exists and if it does, no conclusions from such estimates should be seriously set forth.

The application of equation (8) to the Georges Bank haddock data

Tables 4, 5, and 6 are taken from Paloheimo's table 2 (Paloheimo, 1958) for the 1948, 1950 and 1952 year classes. The original table has been extended to show the summations $1 - e^{\Sigma(F+M)}$, $\sum a_t C_t$, and $\hat{N}_1$ at each age. The estimated N_1's for each year class are shown graphically in figure 2.

Table 4.--Computations of N_1 for the 1948 year class

Age	C_t $\times 10^{-6}$	F min.	F max.	a_t min.	a_t max.	$1-e^{-\Sigma(F+M)}$ min.	$1-e^{-\Sigma(F+M)}$ max.	$\Sigma a_t C_t$ min.	$\Sigma a_t C_t$ max.	$\hat{N}_1$ min.	$\hat{N}_1$ max.
2	35.7	.49	.54	1.204	1.185	.4457	.4173	43.0	42.3	96.4	101.4
3	26.7	.58		1.172		.7192	.7329	74.3	73.6	103.3	100.4
4	8.5	.53		1.189		.8504	.8577	84.4	83.7	99.2	97.6
5	3.8	.59		1.169		.9250	.9286	88.8	88.1	96.0	94.9
6	2.1	.52		1.192		.9592	.9632	91.3	90.6	95.2	94.8
7	.8	.46		1.217		.9776	.9776	92.3	91.6	94.4	93.7
8	.4	.59		1.169		.9889	.9889	92.8	92.1	93.8	93.1

Table 5.--Computations of N_1 for the 1950 year class

Age	C_t x10^{-6}	F min.	F max.	a_t min.	a_t max.	$1-e^{-\Sigma(F+M)}$ min.	$1-e^{-\Sigma(F+M)}$ max.	$\Sigma a_t C_t$ min.	$\Sigma a_t C_t$ max.	$\hat{N}_1$ min.	$\hat{N}_1$ max.
2	29.6	.53	.63	1.189	1.159	.4674	.5181	35.2	34.3	75.3	66.2
3	17.6	.59		1.169		.7329	.7583	55.8	54.9	76.1	72.4
4	5.6	.52		1.192		.8563	.8700	62.4	61.6	72.9	70.8
5	2.7	.46		1.217		.9179	.9257	65.7	64.8	71.8	70.0
6	2.7	.59		1.169		.9592	.9632	68.9	68.0	71.8	70.6

Table 6.--Computations of N_1 for the 1952 year class

Age	C_t	F min.	F max.	a_t min.	a_t max.	$1-e^{-\Sigma(F+M)}$ min.	$1-e^{-\Sigma(F+M)}$ max.	$\Sigma a_t C_t$ min.	$\Sigma a_t C_t$ max.	$\hat{N}_1$ min.	$\hat{N}_1$ max.
2	33.0	.39	.46	1.256	1.217	.3874	.4288	41.4	40.2	106.9	93.8
3	18.2	.46		1.217		.6501	.6737	63.6	62.3	97.8	92.5
4	11.3	.59		1.169		.8245	.8363	76.8	75.5	93.1	90.3

The estimated N_1's for the 1952 year class are quite different in character from those for the 1948 and 1950 year classes. The rapid decline in the estimated N_1's from 107 million at age 2 to 93 million at age 4 suggests a Case 2 situation in which the assumed value of q at age 2 is lower than its true value (cf. curve B, figure 1). The estimates of N_1 for the 1952 year class are obviously approaching their true value from above and will always be overestimated.

The discrepancy in estimates between the 1948 and 1952 year classes, compared over unequal periods, is clear from figure 2. Comparing the age 8 estimate for the 1948 year class to the age 2 estimate for the 1952 year class, the latter appears to be 15 percent larger; at age 3, about 4 percent larger, and at age 4 about equal. Our analysis of the effects of errors in the assumed value of q eads us to believe that in subsequent years the estimates of the 1952 year class will continue to decline.

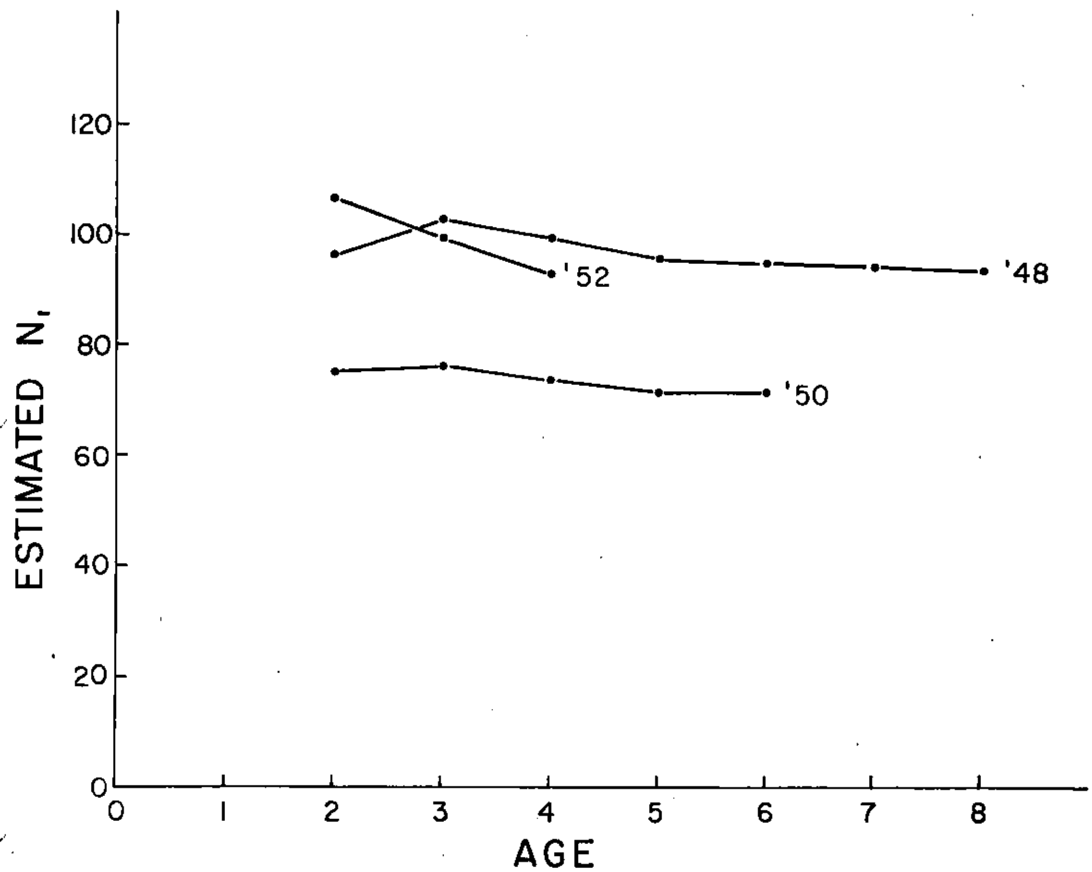

Figure 2. --Variations in estimated N_1's with age for the 1948, 1950, and 1952 year classes. Data from Paloheimo's (1958) "minimum" estimates.

On the other hand, if we compare the 1948 year class at age 4 to the 1952 year class at the same age, a comparison the virtues of which have already been pointed out, the 1952 year class appears to be less than 94 percent of the 1948. This estimate is not seriously at variance with Taylor's (91 percent) and, taking into account the fact that underestimation of q results in a persistent overestimation of N_1 (Case 2 above), it is not unlikely that the 1952 year class actually is close to 90 percent of the 1948.

Variations in q with age in the haddock data

If we apply equation (8) to the data on landings and annual effort for the Georges Bank haddock fishery from 1931 to 1952, that is, during the period of small mesh fishing, and assume that q is constant at 0.09 at all ages, we invariably obtain a type A curve (fig. 1) for estimates of N_1, ages 2 to 9, for each year class. A typical computation is shown in table 7 for the 1939 year class.

Table 7.--Estimated N_1's for the 1939 year class assuming q = 0.09. Catch in millions of fish, fishing intensity in thousands of days. M = 0.10

Age	C_t	f	F	a_t	$1-e^{-\Sigma(F+M)}$	$\Sigma a_t C_t$	$\hat{N}_1$
2	23.464	7.326	.659	1.152	.5323	27.030	50.78
3	16.348	5.732	.516	1.194	.7484	46.550	62.20
4	8.364	4.882	.439	1.228	.8519	56.821	66.70
5	5.689	5.656	.509	1.196	.9195	63.625	69.20
6	2.315	4.892	.440	1.227	.9550	66.466	69.60
7	1.827	7.283	.655	1.153	.9776	68.572	70.14
8	.745	8.223	.740	1.135	.9899	69.418	70.13
9	.369	7.714	.694	1.144	.9955	69.840	70.16

As we have seen, this indicates that q is less than 0.09 at age 2, and possibly later ages. We have also seen that if we know the true value of q, we should obtain a constant estimate of N_1.

It is possible, by iteration, to estimate values of q at age 2 or later ages which will make our estimates of N_1 constant. We find by iteration, for example, that a value of q at age 2 for the 1939 year class of 0.056 gives us a nearly constant estimate of about 72 million fish, ages 2 to 9 (fig. 3).

Table 8 shows estimated values of q, ages 2 to 4, which will give fairly constant estimates of N_1 for each year class, 1931 to 1952. Adjustment of q is necessary in all year classes at age 2, only the 1948, 1950 and 1952 year classes approaching our first estimate of 0.09. Some adjustment is necessary in about half the cases at age 3, and only one at age 4.

Remembering that the period 1931 to 1952 was one during which small mesh nets were used, we note that the average value of q at age 2 is about half that from age 4 on, and at age 3 it is only slightly less than at later ages.

Variations in q at age 2

Table 8 shows variations in q at age 2 ranging from 0.011 to 0.085 per thousand days fished. This extreme variation seems unusual until we plot q against the estimated N_1's (fig. 4). Clearly there is a relation between q and population size. The regression equation is $q = 0.000578N_1 + 0.019$ (11) and the correlation coefficient is 0.626 (1 percent significance, 20 d.f. is 0.537).

Recent studies, to be reported elsewhere, show that a large part of the apparent variation in q at age 2 results from variations in the sizes of fish landed and discarded. There is a marked tendency toward greater landings of the smaller two year olds in years when this age is more abundant. Thus with the larger year classes q, as measured from numbers landed, appears larger (fig. 4). The mortality effected, however, is probably rather constant, approaching the highest values indicated in figure 4, since the gear actually catches these smaller fish and they die, whether they are landed or discarded.

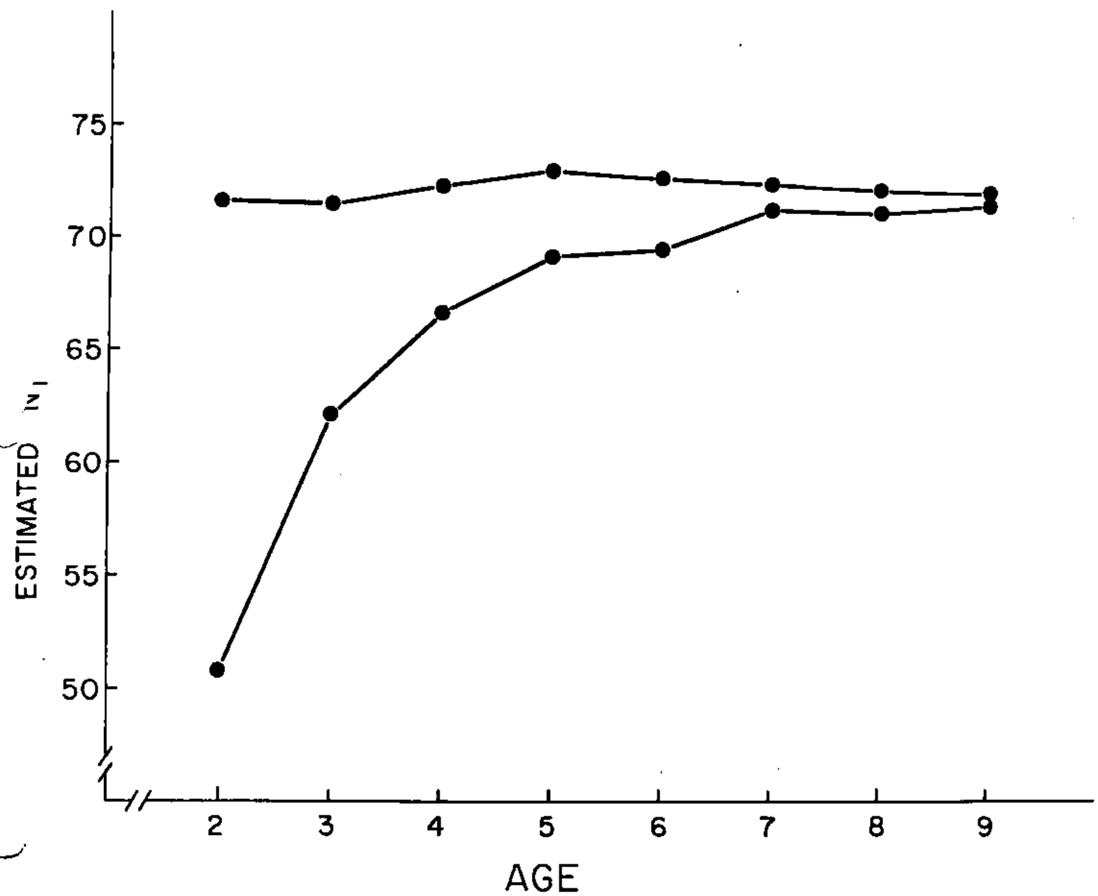

Figure 3.--Estimated N_1's for the 1939 year class. Lower curve assumes a q constant at 0.09 per thousand days fished. Upper curve results from assuming q = 0.056 at age 2.

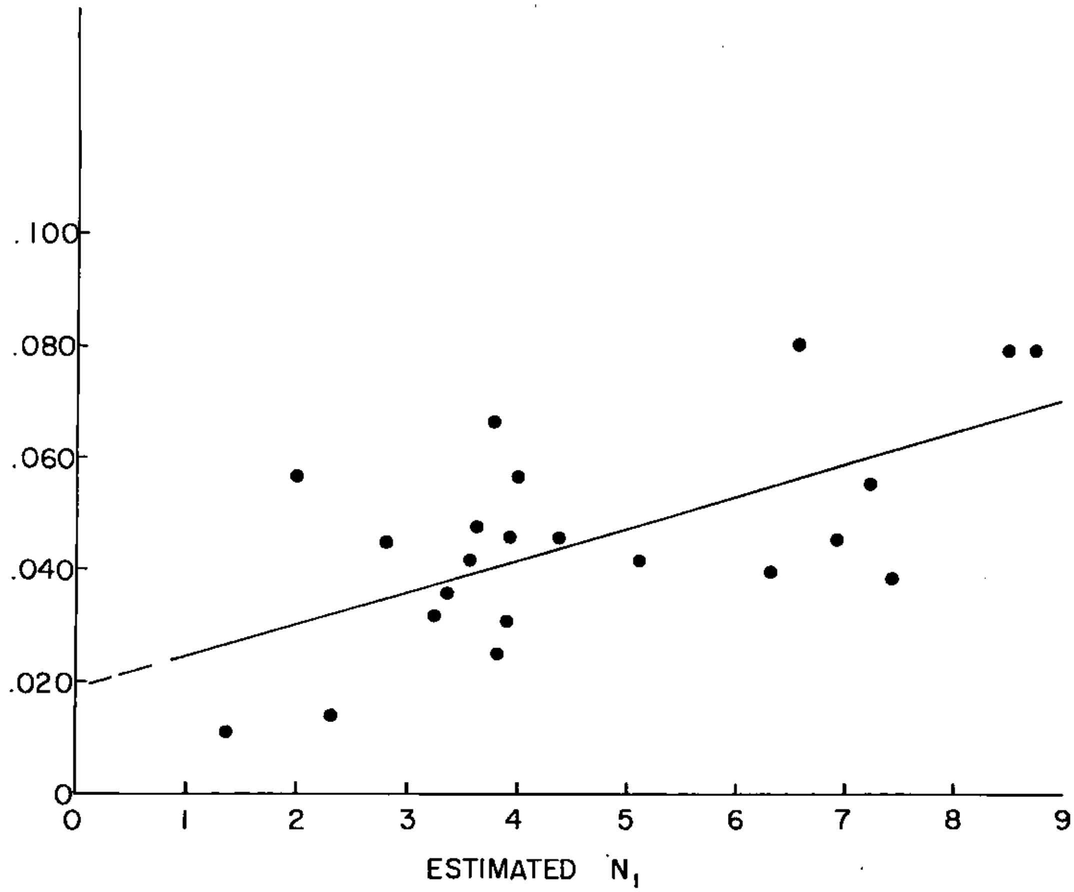

Figure 4.--Variations in q at age 2 plotted against estimated N_1, 1931 to 1948 year classes.

Table 8.--Estimates of q at ages 2, 3, and 4 which give nearly constant estimates of N_1, 1931 to 1952

Year class	q_2	q_3	q_4
1931	.045	.09	.09
2	.032	.09	.09
3	.057	.09	.09
4	.067	.09	.09
5	.048	.055	.09
6	.046	.077	.09
7	.042	.075	.09
8	.031	.065	.09
9	.056	.09	.09
1940	.039	.084	.12
1	.025	.060	.09
2	.011	.039	.09
3	.046	.09	.09
4	.036	.085	.09
5	.038	.089	.09
6	.046	.104	.09
7	.057	.09	.09
8	.080	.129	.09
9	.042	.09	.09
1950	.085	.09	.09
1	.014	.059	.09
2	.080	.093	.09
Mean	.0465	.0829	.0914

Comparison of landings from the 1948 and 1952 year classes

Although the purpose of this paper is to compare methods of assessing the effect of mesh regulation, some evaluation of the validity of conclusions resulting from the use of various methods may be made by comparing the crude statistics of landings from the 1948 and 1952 year classes. It is stated (ICNAF Document 2, page 1, 1958) that the study by Paloheimo (Document 2, Appendix V, 1958) "fails to demonstrate that landings increased as a direct result of regulation."

Table 9 shows landings in numbers and pounds, together with annual fishing effort, for the 1948 and 1952 year classes at ages 2, 3, and 4. We note that although nearly 3,000,000 less fish were landed from the 1952 year classes between ages 2 and 4, these landings exceeded those of the 1948 year class by about

5,000,000 pounds. Assuming, for the moment that these year classes are equal in size (Paloheimo, Document 2, Appendix V, 1958), table 9 indicates a minimum benefit resulting from the use of the large mesh net of about 2,000,000 pounds of haddock per year between the ages of 2 and 4. If the 1952 year class is actually smaller than the 1948, the benefit is correspondingly greater.

Table 9.--Statistics of landings from the 1948 and 1952 year classes

	1948 year class			1952 year class		
Age	Numbers landed (millions)	Weight landed (millions)	Days fished	Numbers landed (millions)	Weight landed (millions)	Days fished
2	29.0	38.3	5486	31.8	47.5	5807
3	26.7	49.3	6490	18.2	38.2	5334
4	8.4	21.2	5933	11.3	29.4	6569
Totals	64.1	108.8	17,909	61.3	115.1	17,710

Summary

A comparison of methods of estimating the absolute or relative sizes of populations entering the fishery used by Taylor (1957) and Paloheimo (1958) shows hat both methods are valid and are, in fact, derived from the same basic equation. It is shown that the method used by Taylor (equation 5) gives unbiased estimates of relative population size even when erroneous values of q are assumed, provided it can be assumed that q is constant at corresponding ages. It is further shown that Paloheimo's method (equation 8) also gives unbiased estimates of relative population size under the same conditions, but only if applied over time periods of the same length for the year classes in question.

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