The Reproductive Biology of the Georges Bank Haddock (*Melanogrammus aeglefinus* L.): Fecundity

by

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ALL FIGURES ARE MISSING

INTRODUCTION

Research on various phases of the biology and population dynamics of the Georges Bank haddock stock has been carried on by American investigators for more than 50 years (Anon., 1932; Grosslein and Hennemuth, 1973), yet not a single paper exists on the important aspects of reproductive biology dealing with fecundity (Blacker, 1971). The Woods Hole Laboratory in the 1950's (then North Atlantic Fisheries Investigations, U.S. Fish and Wildlife Service) began a study of the reproductive biology of the haddock including fecundity, and one of the principal investigators, John R. Clark, collected over 500 ovaries and associated lengths, ages, and maturities from Georges and Browns Banks and the Gulf of Maine. Clark and his associates conducted a number of experiments to determine the proportion of "ripe" to "unripe" eggs[1] in the ovary and estimated the fecundity of 11 females (Clark, 1957, 1958, and from notes on file at the Northeast Fisheries Center, Woods Hole, Massachusetts). Unfortunately, the U.S. commitments to ICNAF (International Commission for the Northwest Atlantic Fisheries) to engage in mesh-selectivity experiments (Clark, 1963) resulted in abandoning the study of reproductive biology, and little now can be salvaged from this earlier study or the collection of samples.

Other fecundity studies for the Northwest Atlantic region include: Earll (1880) who estimated fecundity for seven females captured in the line-trawl-fishery of Cape Ann, Massachusetts (Gulf of Maine), and Rojo (1959) and Hodder (1963, 1965) who studied fecundity for haddock of the Grand Bank of Newfoundland. Earll's data have been used as recently as 1968 by Posgay

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[1] We use the term "egg" for all prespawning phases in the ovary of the mature female. But we also call the reader's attention to Helge (1975) who properly defines (1) the "oocyte" and its stages up to the time of ovulation and (2) the "egg," the stage ready for fertilization by the sperm.

and Marak (1971) to estimate total egg production on eastern Georges Bank. Lastly, Garrod (1973) used unpublished data, furnished by the Northeast Fisheries Center, to compare fecundity, age, and recruitment in a number of fish stocks.

In 1969, collection of fecundity samples was added to a study in progress of the sexual maturity and spawning structure of the Georges Bank haddock stock (see Marak and Livingstone, 1970). The Fisheries Research Board of Canada, Biological Station, St. Andrews, New Brunswick, and the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, Massachusetts, agreed to a joint study of the spawning structure and fecundity relationships of the Georges Bank and Scotian Shelf haddock stocks (personal communication, January 14, 1969, R. G. Halliday, FRB, St. Andrews)[1]. The Northeast Fisheries Center (NEFC), was to collect sexual maturity and fecundity samples from Georges Bank (ICNAF Subarea 5Z); the Canadian Biological Station (FRB, St. Andrews) was to collect similar data for the Scotian Shelf (ICNAF Subarea 4X, W). The preparation and counting of samples was to be done by FRB, St. Andrews; however, by 1971, because of a backlog of unprocessed samples, NEFC, Woods Hole, processed the Georges Bank samples collected in 1972 and 1973. In this paper we deal only with those samples collected on Georges Bank.

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[1] And the suggestion of A. C. Kohler at an informal meeting of ICNAF advisors on cooperative research in Subareas 4 and 5 at Boothbay Harbor, Maine, December, 1968. ICNAF Res. Doc., 69/1 Ser. No. 2142, 5 p.

In particular it is shown that the absolute fecundity (the number of eggs produced by a fish of a given length) appears to have increased nearly 25% in 1972 and 1973 from its level in 1970 and 1971. Though the age structure of the stock changed significantly over the period considered and hence the distribution of ages for a given length, the increase in absolute fecundity appears to be independent of the change in age composition.

MATERIALS AND METHODS

Collection of Samples

Between 50 to 100 whole ungutted haddock were collected during the winter-spring period by commercial otter trawlers fishing out of the port of Boston, Massachusetts, from 1968 to 1973 and also out of New Bedford, Massachusetts, in 1969. Besides commercial samples, the R/V ALBATROSS IV collected haddock for the fecundity study on its routine spring groundfish surveys and made a special cruise (C725) to eastern Georges Bank from February 26 to March 3, 1972 to sample the prespawning population. The distribution of all samples used in fecundity analysis is shown by Georges Bank sampling strata (Grosslein, 1969) and time period (Table).

The commercial samples were collected near the end of the trip, and kept separate from the rest of the catch. They were landed at the port in relatively fresh condition and the samples worked up at one of the fish processing plants. The data collected from each fish included: length, total wet weight, fork length, sex, maturity stages, ovary weight, and scales and/or otoliths for individuals over 70 cm in length. Identification of maturity stage was by a color scale developed by the senior author (Livingstone, unpubl., 1978). Females were selected after examination of

the ovary; those ovaries containing ripe transparent eggs or liquid eggs were rejected. The data collected on research cruises did not include fish weight or ovary weight.

Preservation and Preparation

1. FRB, St. Andrews

Ovaries collected for processing at FRB, St. Andrews, were preserved in Gilson's fluid (Bagenal and Braum, 1968). The whole ovary was placed in a jar or jars depending on size, and then covered by Gilson's fluid. Ovaries were sliced to allow full penetration of the preservative and shaken before being stored, and later (up to four months) transported to FRB, St. Andrews.

Preparation of whole ovaries for counting was similar to the procedure followed by May (1967), Hodder (1963), Pitt (1964), and others. The process consisted of vigorous shaking in an Equipoise shaker[/] at intervals to further the breakdown in Gilson's fluid, cleaning in water and decanting off bits of membranes and other unwanted matter, repeated washing through a fine mesh funnel, dry,and storage either dry in small jars or in jars containing formalin.

2. NEFC, Woods Hole

Beginning in 1972 Davidson's solution, a preservative used in histology (Henderson, 1963), was used in place of Gilson's fluid. We had been concerned over the amount of mercuric chloride, 20 g per liter (Bagenal and Braum, 1968), in Gilson's fluid and on recommendation of M. W. Newman, NMFS, Oxford, Maryland, we decided to experiment with Davidson's solution. Ovaries were preserved whole and usually in one jar. Ovaries of large females, which might weigh over 500 g, were cut apart and preserved in separate jars. Large ovaries were slit in several locations to ensure pene-

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[/] The use of product names does not constitute endorsement by NMFS.

tration of the preservative. Ovaries remained in the preservative until the time of cleaning and subsampling.

Because ovaries were preserved whole, a somewhat different method of cleaning and subsampling had to be developed. Whole ovaries were removed from the jar or jars depending on their size. Some of the larger ovaries, because of the action of the preservative in shaping and hardening them to the contour of the jar, had to be removed by sawing the jar in half. Ovaries were next placed in a fine mesh funnel for several minutes to allow the preservative to drain off. They were then damp blotted and weighed on a Mettler balance to the nearest gram. Large ovaries were weighed in plastic bags to help retain all eggs. After weighing, the ovary was placed in a dissecting tray and two plugs were removed from near the center of either the left or right ovary by means of a standard cork borer 7 and 11 mm in diameter (Figure). The plugs were shoved free of the cork borer by a

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Figure . Haddock ovary with small and large plug subsamples removed. The example was used in special study of egg diameters and densities at the six locations (see Results p.).

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smaller diameter cork borer which had the end plugged. Immediately after coring, the plugs were weighed damp in an analytical Mettler balance. The plugs were placed in vials containing Davidson's solution where they were allowed to harden in the preservative for several weeks before cleaning and counting.

To clean and separate the eggs from membranes and tissues, the plugs were homogenized by a Sorvall Omni-mixer homogenizer in distilled water at speeds of between 4,000 and 5,000 rpm for periods up to five minutes depending on size. The homogenized contents were washed into a beaker, wherein after repeated washings and stirrings the lighter recruitment eggs[/] and bits of membrane floated to the surface while the heavier eggs sank to the bottom of the beaker. Finally, the entire mass of eggs was stirred rapidly for several seconds, and allowed to settle, and then transferred into small vials where they were stored in Davidson's solution until time of counting.

Subsampling and Counting

1. FRB St. Andrews

The whirling vessel, as modified by Pitt (1965), was used for the Georges Bank samples in 1970 and 1971. Subsampling the entire mass of eggs in the whirling vessel was similar to the approach followed by May (1967) for cod and by Hodder (1963) for haddock. The Fisheries Research Board of Canada, St. Andrews, rewashed the preserved mass of eggs in a fine mesh funnel as a final step in cleaning. Next the entire mass of eggs was dumped into the bowl of the whirling vessel which was half filled with water. The whirling vessel, was spun initially to observe the settling behavior of the eggs and their distribution in the ten compartments. Once this test was completed the vessel was spun vigorously by hand and allowed to spin freely for 10 to 30 seconds before it was stopped abruptly and the eggs allowed to settle out at

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[/] These recruitment "eggs" are generally thought to be the egg stock of future spawnings. They are small, less than 0.10 mm, far outnumber the larger developing eggs, and are not included in the fecundity estimates.

random into the ten compartments. Two compartments were chosen at random and the eggs washed into small beakers. The process was repeated with each subsample, resulting in four subsamples and again with the four resulting in a total of eight subsamples with a resulting fractioning of 1/1000. The eight subsamples were placed in small absorbent paper containers to dry before being counted. Counting was by eye. Geometric means (Ricker, 1973) and coefficients of variation were calculated for each of the eight samples. Geometric means were expanded by 1,000 to get estimated fecundity.

2. NEFC, Woods Hole

Plug subsamples were counted in a electronic system designed by Crossen (1961) and modified by us in 1971 (Schultz, 1968). In both systems the eggs are streamed in water single file through a light beam which triggers an electronic counter. The system we modified from Schultz (1968) shown diagrammatically (Figure), consisted of three plastic reservoirs, one equipped with a stirrer, a submersible pump that pumped water to a supply reservoir (Figure), and an electronic package that contained photomultiplier unit, photo cell counting chamber and the electronic counter. Small diameter glass tubes[/], usually 1½ to 2 times the average egg diameter and from 5-8 inches in length were positioned centrally in the photocell chamber by small corks at each end of the glass tube. During the actual counting the eggs sank by gravity and were guided single file down narrow (diameter) tygon tubing to the glass tube in the counting chamber and finally to a fine mesh screen (0.016 mm) where the sample could be saved for recounting if need be.

[/] Glass tubes were custom hand drawn by the Glass Blowing Department, Marine Biological Laboratory, Woods Hole, Massachusetts.

Test samples were first run through the system to check the accuracy of the electronic count. A random sample of mixed eggs was removed from the vial by eye dropper. They were squirted single file onto a grooved plastic slide. The first 50 encountered were measured by a dissecting scope equipped with an ocular micrometer. Measurements were converted to millimeters and average egg diameters were calculated. These average diameters were used as a guide in selecting the glass tube for the counting chamber. In addition to the measured sample between 300 to 500 eggs were counted out and set aside to be used in a test of the electronic counter.

Usually two or three trial runs were made to check accuracy of the electronic counter and to make any adjustments to senstivity that might be necessary. The trial counts were averaged, and the electronic count was checked against the hand count. The difference between the two counts, called the "counting error," was used to correct the total number of eggs in the ovarian plug sample. Estimated fecundity by the ovarian plug technique was derived from:

$$\frac{\text{Total ovary weight (g)}}{\text{Large plug weight (g)}} \times \text{corrected number of eggs counted in plug}$$

Tests of Sampling Methods

Several preliminary questions on technique needed to be answered. It had to be determined if a single ovarian plug could be used to estimate the entire population of eggs in the ovary. A comparison was also needed of the fecundity estimates obtained by the whirling vessel method and the electronic count of the eggs in a plug subsample. To answer the first question we compared egg diameters and densities at three different locations in the left

and right ovary (Figure), and for three haddocks of different lengths. To compare fecundity estimates by the two techniques, we exchanged 11 whole ovaries and 17 plug samples with the Fisheries Research Board of Canada, St. Andrews. Each sample was counted by whirling vessel and by our electronic count.

1. A Single Sample Plug vs. Several

Bagenal (1967) has warned of the possible error generated in counting 'thousands' of eggs. For this reason fecundity studies have generally favored counting fewer numbers of eggs in replicate samples (see also Bagenal and Braum, 1968). That a single sample, however, can be representative of all the eggs in the ovary has been determined in studies of intraovarian egg diameters and densities in a number of species (Topp, 1968; Shehadeh et al., 1973; Martinez and Houde, 1975). In the study of three females, we examined the differences in egg diameters and densities at six locations in the ovary. From an analysis of variance we concluded that the egg diameters for a given maturity stage were not significantly different throughout the ovary. We also determined from a 3-way analysis of variance that egg density (expressed as number of eggs per gram) was not noticeably different at the six locations (F - 1.174; F 0.05 2, = 3.59) or between the left and right ovary (F = 3.08 F; $F_{0.05\ 1,12}$ =) but did differ significantly (F = 363.636) between fish. This experiment justifies using a single ovarian plug subsample.

2. Comparison of Canadian and United States Fecundity Estimates

To determine the comparability of the estimates obtained by the two different subsampling and counting procedures, we exchanged 17 ovarian plug samples and 11 whole ovaries with the Fisheries Research Board of Canada, St. Andrews. The plugs were subsampled by whirling vessel and counted at

the Fisheries Research Board of Canada, St. Andrews; likewise the 11 whole ovaries were counted by the wet electronic system at the Northeast Fisheries Center, Woods Hole. The total number of eggs counted in each sample are plotted (Figure) and compared by linear regression. The plotted points

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Figure .

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indicate a very close one to one relationship for both plus ($r = 0.96$, $b = 0.995$) and whole ovaries ($r = 0.99$, $b = 0.979$). Thus, the fecundity estimates by the whirling vessel and by the wet electronic count gave nearly identical estimates of fecundity.

ABSOLUTE FECUNDITY

Absolute Fecundity and Length

Bagenal (1973) defined the absolute fecundity as the number of eggs in the ovary just prior to spawning. To compare the fecundity of haddock between years, it needed to be decided what should be compared, either the total number of eggs produced by the population or the number of eggs produced by haddock of either fixed age, length, or weight. If the absolute fecundity of fish of all lengths is known, then total egg production can be easily calculated from the distribution of lengths of females in the population. We thus compare the number of eggs produced by haddock of a fixed length from year to year. Length is chosen rather than age since maturity appears to be more a function of length than age and, furthermore, length is much easier to determine in practice than age. Weight was not used since it is not clear to us what one would be comparing; the weight of the fish includes the weight of the eggs, thus, in general, the greater the absolute fecundity for fish say of the same length, the greater the weight.

To obtain estimates of absolute fecundity from samples consisting of a range of lengths a curve of the form (Bagenal, 1973; Daan, 1974)

$$F = aL^b \tag{1}$$

was fitted to the data where F is the number of eggs and L is the length, and a and b are constants. To make the model more precise it is assumed that the fecundity of the population can be modeled by

$$F = L^b \varepsilon \tag{2}$$

where ε is lognormally distributed. Hence

$$E[F|L] = L^b e^{\mu + \sigma^2/2} \tag{3}$$

where μ and σ^2 are the mean and the variance, respectively, of $\ln\varepsilon$. If b is constant from year to year then $E[F|L]$ will be a function only of μ and σ^2. Taking the log of both sides of equation (2), the relationship can be rewritten as

$$\ln F = a + b \ln L + \varepsilon' \tag{4}$$

where $a = E[\ln\varepsilon]$ and $\varepsilon' = \ln\varepsilon - a$. Thus the absolute fecundity increases if either the intercept or the var (ε') increases. The assumption that b is constant implies that whatever factors are causing absolute fecundity at length to change from one year to the next affects all lengths proportionately, i.e.,

$$E[F|L] = E[\varepsilon]\ L^b$$

and hence $E_1\ [F|L]_1/E[F|L]_2$ is a constant independent of L. If b is not constant then interpretation is more difficult; the estimated functions (1) may intersect which would say, for example, that the fecundity for small fish decreased while increasing for larger ones.

To determine whether the variances (σ^2) can be assumed to be homogeneous over time, equation (3) was fitted separately to each year (Table 1).

Table 1.

Bartlett's test was applied, and the variances were found to be significantly different at the .01 level. Though Bartlett's test is sensitive to departures from normality, the residuals appear to be normally distributed, and hence the results of the test were taken to indicate heteroscedasticity. The variances were nearly equal for the years 1970 and 1972, and 1971 and 1973 (Table 1). Thus an analysis of covariance (which assumes equal variances) violations of this assumption can cause problems in the interpretation of the significance of the test (see Scheffé, 1959) was applied separately to each pair of years. The results of the analyses are given in Tables 2 and 3.

Table 2.

Table 3.

For each pair, it could not be rejected that the slopes b are equal, but for both pairs the intercepts were significantly different. The question remains whether the pooled estimates of the slope obtained from each pair of years are equal. To test this the statistic

$$t' = \frac{b_1 - b_2}{\sqrt{S^2_{b_1} + S^2_{b_2}}}$$

was calculated (see Snedecor and Cochran, 1967, p. 437). The value of t' obtained is 2.270 and the approximate 2.5% level is t' = 2.274. Due to the multiplicity of tests performed in the analysis, it is deemed that the test does not give strong evidence that the slopes are unequal, or at the least, the magnitude of the probable difference is small, and hence the model with b constant fits the data fairly well. A weighted average of the slopes estimated for each pair of years is used to estimate the joint slope for all years. Or

$$\hat{b} = \frac{\omega_1 b_1 + \omega_1 \quad 2}{\omega_1 + \omega_2}$$

where $\omega_1 = 1/S^2_b$ and $\omega_2 = 1/S^2_{b_2}$. The standard error of $\hat{b}$ is approximately

$$\frac{1}{\omega_1 + \omega_2} \sqrt{1 + \frac{4\omega_1 \quad \omega_2}{(\omega_1 + \omega_2)^2} \quad \frac{(f_1 + f_2)}{f_1 \quad f_2}}$$

(see Snedecor and Cochran, 1967). The joint estimate of b along with its standard error is given in Table 4. Table 4 also lists the estimates of

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Table 4.

$e^{\mu+\sigma 2/2}$ with approximate confidence limits for each year. Figures 1-4 show plots of the data for each year with the estimated log fecundity line (eq. (4), b is the joint estimate). Figure 7 is a combined plot for 1971 and 1972

Figure 7.

from which it can be seen that the fecundity level for 1971 is generally lower than that of 1972 for all lengths.

Absolute Fecundity and Age

To determine whether the changing age structure of the population, as reflected in the samples, caused the apparent increase in absolute fecundity, the number of eggs produced by each fish was adjusted to remove the effect of length. This adjustment was made by regressing log fecundity on log length for all four years combined (Figure 5); the residuals were used as a measure of each individual's deviation in fecundity from the 4-year average as represented by the regression line. Figures 8-11 show the plots of

Figures 8 - 11. Age fecundity relationship adjusted for length for Georges Bank female haddock, 1970-1973.

fecundity adjusted for length versus age for each of the four years. From these figures it can be seen that fecundity has increased over this period for all ages though perhaps slightly more for the younger fish. It can also be seen from Figures 8-11 that the addition of age as an exploratory variable for the observed variability in fecundity would account for little, if any, additional variability in production than that already attributed to length.

DISCUSSION

Table 4 shows that the absolute fecundity was nearly 25% higher in 1972 and 1973 than in 1970 and 1971. That is fish of a given length were producing an average of 25% more eggs than in the earlier period. The mean level of egg production is both a function of the long-mean μ and the log-variance σ^2. Thus if either μ or σ^2 increases, mean production increases, or for a fixed length, and log-mean, the more variable production is the higher the mean production will be. The coefficient of variance of the egg production for fish of a fixed length is

$$e^{\sigma^2} - 1$$

which is only a function of σ^2 and may be looked upon loosely as a measure of egg production variability irrespectively of the mean production level.

It should be stressed that the model more or less assumes that b is constant from year to year, i.e., there are some varying factors that affect fecundity proportionately at all lengths. Since the varying age composition of the population did not seem to be the cause of this proportional rise in fecundity at length, it can be speculated that other factors such as a change in population density or environmental conditions may have been the cause of the rise in fecundity observed. Figure 5, the composite plot for the four years, may possibly be interpreted as being the fecundity relationship for a much broader distribution of ages and environmental conditions at each length. The slope for the combined regression is very close (b = 3.27) to the above weighted estimate, and the residual variance of $\ln F|_L$ is homogeneous.

Lastly, when comparing years for which the sample range of the distribution of lengths vary widely, the use of equation (2) may produce a biased

comparison due to the lack of fit of the model. In his study of the fecundity of Grand Bank haddock, Hodder (1963) estimated b to be about 5, but the lengths of the fish in his sample were much shorter an average than ours. There seems to be a strong correlation between the percentage of small fish in the sample and the estimate of b (Hodder, 1963, Figure 2). Also, there appears to be a jump in residual variance at about 42 cm (Hodder, Figure 2) which seems to occur for other species at about the same length (e.g., plaice, Simpson, 1951, Figure 1; witch flounder, Bowering, 1978, Figure 2). In the present analysis care was taken so that the range of lengths were as nearly the same for each year as feasible. Furthermore, fish of less than 42 cm were not included in the analysis. Thus, any misinterpretation of the results due to model misspecification is lessened.

Figure____. Relationship of total number of eggs counted in ovarian plug (.) and whole ovary (x) samples by electronic wet count, Woods Hole and by whirling vessel, St. Andrews.

Table 1. Number of fecundity estimates for Georges Bank sampling strata, 1969-1973.[1/]

Year	Date	Stratum													
		10	13	16	17	18	19	20	21	22	23	24	25[2/]	29	Total
1969	Mar 17-Apr 23	1	1	15	5		22	1		13		8			66
1970	Feb 22-Mar 14			9			6	12		7			26	13	73
1971	Jan 30-Mar 22		1	30			33			16		1			81
1972	Jan 18-Apr 26		1	6	8	4	11	1	11	36			1	42	121
1973	Feb 18-Apr 22			16				2		3			1		22
	Total	1	3	76	13	4	72	16	11	75		9	28	55	363

[1]Samples from line-trawl fishery, Chatham, Massachusetts, 1955 data not included.

[2]1955 data not included in table.

Table 2. Estimates of lna, b and σ^2 obtained by regressing lnF on lnL separately for each year.

Year	Number of fish	$\hat{\ln a}$	$\hat{b}$	Residual mean square
1970	72	-7.459	3.503	.0565
1971	75	-9.871	4.069	.1065
1972	117	-5.182	2.995	.0641
1973	20	-4.921	2.964	.1223

Bartlett's test for equality of variances: $\underline{\bar{X}}^2(3) = 11.5$, x^2 (.99, 3) = 11.35

Table 3. Summary statistics for the results of an analysis of covariance for the years 1970 and 1972.

F - test for a common slope:

$F(1,185) = 1.70$, $F(.95, 1,185) = 3.9$

F-test for a common intercept:

$F(1,186) = 31.2$, $F(.999, 1,186) = 11$

Estimate of the common slope b.,

$\hat{b}, = 3.084$

Estimated residual variance, σ_1^2.

$S^2 = .0615$

Table 4. Summary statistics for the results of an analysis of covariance for the years 1971 and 1973.

F-test for a common slope:

$F(1, 92) = 1.71$, $F(.95, 1, 92) = 3.95$

F-test for a common intercept:

$F(1, 93) = 15.02$, $F(.999, 1, 93) = 13$

Estimate of the common slope b_2 ;

$\hat{b}_1 = 3.885$

Estimated residual variance, σ^2:

$S^2 = .1104$

Table 5. Estimates of the parameters of the model $E[F|L] = e^{M+\sigma^2/2} L^b$ with a constant b.

Year	Estimate of $e^{M+\frac{\sigma^2}{2}}$	95% (approximate) confidence limits
1970	.001952	$\pm$ .0001
1971	.001910	$\pm$ .0002
1972	.002401	$\pm$ .0001
1973	.002699	$\pm$ .0004

$\hat{b} = 3.215 \pm .2617$