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A COMPARISON OF METHODS FOR ESTIMATING AGE-SPECIFIC FISHING MORTALITY RATES FROM CATCH-AT-AGE DATA

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INTRODUCTION

In an earlier paper (Wetherall and Yong 1975)[2] we presented results of a first-cut cohort analysis and yield per recruit assessment of the North Pacific albacore, Thunnus alalunga, population. We regarded these results as strictly provisional, and pointed out that several key assumptions needed to be tested and verified. Among these were:

(1) The albacore catch histories, as derived from the catch and length composition statistics and a particular age-length relation, were reasonably accurate. The catch histories may be significantly altered if new information becomes available concerning length composition of catches, particularly catches south of 25°N. Further, the cohort analysis may yield different results if ages are assigned in another manner; for example, by separation of modal length groups (which allows for variation in birth date and growth rate for each cohort) rather than by application of a common length-age relationship (which allows for variation in birth date, but assumes a constant growth pattern for each cohort).

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[2]Wetherall, J. A., and M. Y. Y. Yong. 1975. A cohort analysis of the North Pacific albacore stock and an assessment of yield per recruit in the American and Japanese fisheries. Working paper for the North Pacific albacore population dynamics workshop, December 1975. SWFC Admin. Rep. 16H, 1975, 55 p. 19 tables, 36 figs. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

(2) A second major assumption was that natural mortality coefficients used in the cohort analysis were approximately correct. Considering the difficulties in estimating natural mortality rates, this assumption will likely have to stand unverified, although the robustness of the cohort analysis and other assessments to departures from our assumed conditions should be studied.

(3) A third critical assumption was that the fishing mortality rates on 10-year old albacore during the 4th quarter of each year, 1959-72, were known, or rather that our guesses of these parameters were accurate. In the reverse iterative solution of the catch equation, the sequence of age-specific fishing mortality coefficients is scaled by the value we assign to the fishing mortality rate on this oldest age group, F_n. Error in our guesstimate of F_n leads to biased estimates of F_i, $i = 1, 2, \ldots, n-1$. The errors diminish progressively from F_n to F_1, but in any case the estimate of average fishing mortality rate over the life of each cohort, $\bar{F}$, is biased in the same direction as the error in F_n. To use cohort analysis effectively we therefore need to (a) determine F_n accurately at the outset, or (b) be able to select among alternative values of F_n and their associated sequences of F_i on the basis of independent information, such as tag return statistics. Without an independent and accurate fix on exploitation rate, only the age-specific pattern of fishing mortality may be correctly discerned, and the absolute values of F_i estimates must be viewed cautiously. Further, since we usually must adopt the same estimate of F_n for each cohort, we are severely restricted in drawing inferences about trends in the F_i or in $\bar{F}$ over time.

In the remainder of this paper we set aside the first two major assumptions and focus on the third one. In particular, we wish to compare the usual Gulland-Murphy method of cohort analysis with (a) a newer least squares technique due to Doubleday (1975, 1976), and (b) a simple nonlinear regression method which we developed to estimate parameters of a general age-specific fishing mortality model. After briefly outlining each method, we compare the three techniques using sets of artificially generated catch-at-age data, where the true underlying parameters are known. The parameters, or at least the age-specific patterns, were chosen to mimic approximately the fishery dynamics of North Pacific albacore. Then we apply the three techniques to actual catch-at-age data for the albacore population, as given in our earlier paper.

Outline of Methods

I. Cohort Analysis (Gulland-Murphy Method)

In the reverse iterative solution of the catch equation (Murphy 1964; Gulland 1965), catch-at-age data for each individual cohort (or pooled data from several year classes) are used to yield estimates of the initial cohort size, R, and the age-specific fishing mortality rates for all but the oldest age group (i.e., F_i, $i = 1, 2, \ldots, n-1$). The method requires that we specify the age-specific natural mortality coefficients M_i, $i = 1, 2, \ldots, n$, and the fishing mortality rate of the oldest age group, F_n.

In this procedure the estimates of F_i depend critically on the fixed value of F_n, and since F_n is usually difficult to establish, the absolute values of the F_i estimates are often questionable, particularly for the older age groups.

II. Doubleday Method

One way to circumvent the problem of having to fix F_n is to reduce the number of other parameters to be estimated. An obvious way to do this is to specify some structure in the age-specific fishing mortality vector, so that different elements are the same or have factors in common. We can then use the same data set to estimate a reduced set of parameters. We avoid having to specify F_n by making the extra structural assumptions. Pope (1974)[3] first suggested this could be done by decomposing the fishing mortality rate for the ith age group in the jth fishing period, F_{ij}, into two factors; one representing age-specific effects and another period-specific effects. He suggested the following model:

$$F_{ij} = \exp(s_i + f_j) \qquad i = 1, 2, \ldots, n$$
$$j = 1, 2, \ldots, m$$

where the s_i are assumed constant over time periods and the f_j are constant over age groups.

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[3]Pope, J. G. 1974. A possible alternative method to virtual population analysis for the calculation of fishing mortality from catch at age data. Manuscript for Annu. Meet. Int. Comm. Northwest Atl. Fish. 1974, Res. Doc. No. 20, Serial No. 3166 (mimeogr.)

Doubleday (1976) developed an estimation procedure based on Pope's model which uses the (m x n) table of the catches, C_{ij}, and a specified constant natural mortality coefficient, M, to produce estimates of [2(n + m) - 1] parameters:

(1) s_i and f_j $\quad i = 1, 2, \ldots, n$

$j = 1, 2, \ldots, m$

and (2) $N_{i,1}$ $\quad i = 1, 2, \ldots, n$

$N_{1,j}$ $\quad j = 2, 3, \ldots, m$

The latter are estimates of the population sizes for each of the (m + n - 1) year classes at the age when they first enter the catch table.

The estimates are found by an iterative least-squares solution of the nonlinear regression model

$$\ln C_{ij} = \ln \left[\begin{matrix} N \\ k \; j-(i-k) \end{matrix} \right] - (i-k)M + (s_i + f_j)$$

$$- \sum_{\ell = k}^{i-1} \exp\left[s_i + f_{j-(i-\ell)} \right] - \ln\left[\exp(s_i + f_j) + M \right]$$

$$+ \ln\{ 1 - \exp\left[- \exp(s_i + f_j) - M \right] \} + \varepsilon_{ij}$$

where k is the age at entry to the catch table for the year class from which the catch, C_{ij}, was taken.

Note that the assumption of constant M could be relaxed; we could instead specify values for the individual M_{ij}.

III. Our Regression Method

As Doubleday points out, the Pope model may not be appropriate for many fisheries, particularly those where age-specific factors of fishing mortality vary over time, or equivalently, time-specific factors vary over age. This may well be the case for North Pacific albacore. For example, nominal fishing effort has increased substantially in recent years, but this has been directed more at younger albacore than at the older fish.

We have recently experimented with an alternative approach which involves the estimation of a parametric age-dependent fishing mortality function using catch-at-age data from individual cohorts. Consider the general deterministic catch equation

$$C_i = \int_{t_i}^{t_i + \Delta_i} F(u)\, R \exp\left\{ - \int_{o}^{u} [M(x) + F(x)]\, dx \right\} du$$

$$= H(t_i + \Delta_i) - H(t_i)$$

where C_i = catch in the ith age interval $(t_i, t_i + \Delta_i)$

t_i = age at beginning of ith interval

Δ_i = length of ith interval

$F(u)$ = instantaneous fishing mortality rate at age u

$M(x)$ = instantaneous natural mortality rate at age x

R = initial cohort size

$H(u)$ = cumulative catch from the cohort at age u

Assume that $M(u) = M$ = constant and that the differential $dH(u)$ is linear over each age interval, i.e., piecewise linear over the exploited life of the cohort. Under these conditions,

$$C_i = \Delta_i \, R \, F(\tau_i) \exp\left[- M\tau_i - \int_0^{\tau_i} f(u)\, du \right]$$

where $\tau_i = t_i + \Delta_i/2$.

This leads to a general nonlinear regression model

$$\ln(C_i/\Delta_i) = \ln R + \ln F(\tau_i) - M\tau_i - \int_0^{\tau_i} F(u)\, du + \varepsilon_i \qquad (1)$$

where ε_i is a random error term.

To apply this model we need to specify the form of $F(u)$. For example, if we let $F(u) = F$ = constant, the linearity assumption is satisfied and equation 1 reduces to the well-known catch curve model

$$\ln(C_i/\Delta_i) = \ln(RF) - (F + M)\,\tau_i + \varepsilon_i$$

which may be used to yield a least squares estimate of the total mortality rate, $Z = F + M$, and, if M is specified, estimates of F and R.

Of course, our main concern is to explore more complicated fishing mortality functions, ones for which equation 1 is only an approximation. For many tunas, including North Pacific albacore, cohort analyses suggest a fishing mortality sequence typified by Figure 1. Fishing mortality rates show an erratic seasonal fluctuation around a basically dome-shaped curve. Because of phase-shifts in the mortality cycles a detailed model of $F(u)$ would likely be quite cumbersome. For

Fig. 1

many purposes, we can show that it is sufficient to model only the main underlying trend. Specifically, for North Pacific albacore we examined the model

$$F(u) = \alpha(u + \theta) \exp(-\beta u)$$

which faithfully traces the trend in Figure 1. Substituting in equation 1, we have

$$\ln(C_i/\Delta_i) = \ln(R\alpha) - (\beta + M)\tau_i + \ln(\tau_i + \theta) \qquad (2)$$

$$- (\alpha/\beta^2)\Big[1 - \exp(-\beta\tau_i) - \beta\tau_i \exp(-\beta\tau_i)$$

$$+ \beta\theta\Big(1 - \exp(-\beta\tau_i)\Big)\Big] + \varepsilon_i$$

To better isolate fishing mortality we assume M is known, and then estimate just R, θ, α, and β.

We note here that our assumption of constant natural mortality rate, M, was for convenience only. Equations 1 and 2 may be modified if information is available on age-specific M.

COMPARISONS USING ARTIFICIAL DATA

The Generated Data Sets

We generated two sets of deterministic catch-at-age data for use in comparing the three procedures. In each case we specified Pope's age-specific and period-specific components, s_i and f_j, of the age-specific fishing mortality rates, F_{ij}. All rates were computed on a quarterly basis over 20 fishing years. Tables 1 and 2 list the mortality

Tables 1,2

components for data set D1, in which the rates are constant over all quarters in each year, satisfying the assumptions of Doubleday's method.

Tables 3,4 Tables 3 and 4 give the elemental rates for data set D2, in which the rates vary quarterly. In all cases the catch-at-age data were generated for 8 year-groups (32 quarter-year age groups), with R = 1,000 and M = 0.20 for each cohort. Example catch data for one fishing year in each data set are shown in Tables 5 and 6. The average annual age-specific fishing mortality rates for each fishing year are given in Table 7 for set D1 and Table 8 for set D2.

Tables 5,6
Table 7
Table 8

The standard cohort analysis and our new regression technique employ individual year-class catch histories. One of these from each data set, D1 and D2, is given in Tables 9 and 10 (picked arbitrarily). The associated age-specific fishing mortality rates from which the selected data were generated are listed in Tables 11 and 12. In Figure 2 we plot the quarterly fishing mortality coefficients for the selected year class in set D1. The rates for the D2 year class are in Figure 3.

Tables 9,10
Tables 11, 12
Fig. 2
Fig. 3

Results of Cohort Analysis

Cohort analysis was done on the selected year-class catch histories of sets D1 and D2, using the FORTRAN program COHORT (W. W. Fox, SWFC, La Jolla, California). Natural mortality was set to 0.20 for all ages. The resulting age-specific fishing mortality estimates are given in Figures 4 and 5 for different values of F_n. Both quarterly and

Figs. 4,5

annual catch data were analyzed. In addition, the average fishing mortality rate over the life of each cohort, $\bar{F}$, was computed:

$$\bar{F} = \sum_{i=1}^{n} F_i \bar{N}_i \Big/ \sum_{i=1}^{n} \bar{N}_i \quad = \quad \sum_{i=1}^{n} C_i \Big/ \sum_{i=1}^{n} \bar{N}_i$$

where $\bar{N}_i$ is the average size of the chort during the ith age interval. The estimates of $\bar{F}$ are also indicated on Figures 4 and 5.

As expected, the actual sequence of F_i is estimated accurately provided F_n is on the mark. Otherwise the estimates of F_i are in error, the error being greater for older age groups.

Results of Analysis Using Doubleday Method

Doubleday's method was applied to the (20 x 8) catch-at-age tables for sets D1 and D2, using the FORTRAN programs POPI and POPO (Doubleday 1975). POPI was used initially with M = 0.20, with s_8 set to -1.0 and with all other parameters set to zero. Results of POPI were then input to POPO. POPO was applied repeatedly until convergence was achieved.

Estimates of the F_{ij} for data set D1 were very accurate;
Table 13 compare the POPO output in Table 13 with the actual values of Table 7. On the other hand, estimates of F_{ij} for data set D2 have a fairly large
Table 14 positive bias; compare Table 14 with the true values in Table 8. It is doubtful whether different initial estimates would improve the estimation. The bias probably arises from the failure of Doubleday's basic assumptions

that the age-specific fishing mortality factors are constant over time. However, our conclusion here is not final, and we intend to explore the matter further.

Results of Analysis Using Our Regression Model

The nonlinear regression model at equation 2 was applied to annual (8 data points) and quarterly (32 points) series of data from the selected year-class catch histories, both D1 and D2. Natural mortality was fixed at M = 0.20. Figures 6, 7, 8, and 9 show the data and the fitted regression lines. The fit to the annual data is somewhat better than the fit to quarterly data, as expected, especially in case D2.

Figs. 6,7, 8,9

Table 15

Table 15 gives the parameter estimates $\hat{R}$, $\hat{\theta}$, $\hat{\alpha}$, and $\hat{\beta}$ for each fishing mortality function, and lists the true values of R. In addition the table gives true and estimated values of $\bar{F}$ for each case, where

$$\bar{F} = \int_0^8 F(u)\ N(u)\ du \ / \int_0^8 N(u)\ du$$

In all cases the initial cohort size, R, is underestimated, and $\bar{F}$ is overestimated except for the annual data of set D2.

Table 16

Table 16 lists the actual average fishing mortality rates during 5 years of each cohort's life, along with the regression function estimates of $\bar{F}$ at the midpoints of those years (based on annual data). The same information is plotted in Figures 10 and 11. The main trends in fishing

Figs. 10, 11

mortality rate are determined fairly accurately by the regression analysis, but the absolute values generally show a positive bias.

ANALYSIS OF ALBACORE CATCH-AT-AGE DATA

We applied ordinary cohort analysis and our new regression method to two sets of North Pacific albacore data:

(1) the catch-at-age data for the 1961 year class (Wetherall and Yong 1975, Table 6), and

(2) an aggregated catch-at-age vector formed by summing individual catch histories for year classes 1957-61.

Figs. 12,13 The cohort analysis results are given in Figures 12 and 13. For the given values of F_n they show a general dome-shaped pattern, with a peak fishing mortality rate at coded age 3 (true age 5). The main problem is to choose among these alternative curves.

The average fishing mortality rates, $\bar{F}$, over 8 years of the 1961 year class are also given in Figures 12 and 13. In addition,

Table 17 Table 17 lists the average fishing mortality rates over 8 years for each of the individual cohorts, 1957-61, corresponding to four different levels of F_n, the fishing mortality on 10-year olds during the 4th quarter. An order of magnitude difference in F_n results in a similar difference in $\bar{F}$.

Table 18 The results of our regression analysis are given in Table 18, which lists the estimated parameters and associated $\bar{F}$ for each data set. The actual catch curves and estimated regression lines are shown in

Figs. 14, 15,16,17 Figures 14, 15, 16, and 17.

We found in examining the test data of sets D1-YC10 and D2-YC20 that the regression method gave a fairly close but perhaps positively biased estimate of $\bar{F}$. The estimate was best when derived from annual data. On the other hand, the individual age-specific values of F_i might not be estimated quite so well. With these results in mind, we suggest that the regression method can serve as a guide in selecting a "best" age-specific F-vector from the cohort analyses, based on a comparison of $\bar{F}$ values. In the case of YC-1961 and the aggregate YC-1957-61, we compare Tables 16 and 17. Allowing for the presumed positive bias in $\hat{\bar{F}}$, we judge in both cases that the "best" F-vector would be one associated with an F_n equal to about 0.10.

Tables 16, 17

In addition to using cohort analysis and the regression method on data from YC-1961 and YC-1957-61, we applied POPI and POPO to two sets of North Pacific albacore catch-at-age data; one set covering fishing years 1952-65, another spanning 1959-72. In both cases the estimates of age-specific F seemed to have a serious positive bias, and the residual mean squares were substantially larger than Doubleday (1975) allows for reliable results.

CONCLUSIONS

Our very cursory comparison of methods for estimating age-specific fishing mortality rates has led us to conclude provisionally that Pope's model and Doubleday's method of implementing it are not very robust; the method works when its assumptions are satisfied, but not under the conditions likely to be encountered in the North Pacific albacore fisheries.

On the other hand, our results indicate that a more thorough investigation of our regression method would be fruitful, and we are planning a more complete investigation. We particularly feel that the regression procedure can establish a reasonably accurate estimate of the average fishing mortality rate, $\bar{F}$, over a cohort's life. If so, the method would be very useful in sifting through the vectors of F_i computed in ordinary cohort analysis, and choosing the best one, since there is a direct relationship between the guess of F_n and the resulting estimate of $\bar{F}$.

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Table 1.--Age-specific fishing mortality factors, s_i, for data set D1.

Age interval (years)	s_i	$\exp(-s_i)$
2.5-3.5	-0.693	0.50
3.5-4.5	0.406	1.50
4.5-5.5	0.0	1.00
5.5-6.5	-0.693	0.50
6.5-7.5	-1.609	0.20
7.5-8.5	-2.303	0.10
8.5-9.5	-2.303	0.10
9.5-10.5	-2.995	0.05

Table 2.--Year-specific fishing mortality factors, f_j, for data set D1.

Fishing year	f_j	$\exp(-f_j)$
1	-0.223	0.8
2	-0.223	0.8
3	-0.223	0.8
4	-0.223	0.8
5	-0.223	0.8
6	-0.223	0.8
7	-0.223	0.8
8	-0.223	0.8
9	-0.223	0.8
10	-0.223	0.8
11	0.000	1.0
12	0.182	1.2
13	0.336	1.4
14	0.470	1.6
15	0.588	1.8
16	0.693	2.0
17	0.742	2.1
18	0.876	2.4
19	0.876	2.4
20	0.876	2.4

Table 3.--Quarterly age-specific fishing mortality factors, s_i, for data set D2.

Age interval (years)	s_i Quarter 1	Quarter 2	Quarter 3	Quarter 4
2.5-3.5	-3.912	-0.693	-0.223	-1.609
3.5-4.5	-2.303	0.406	-0.916	-1.609
4.5-5.5	-1.609	0.000	-1.609	-1.204
5.5-6.5	-0.916	-0.693	-2.996	-0.916
6.5-7.5	-1.609	-1.609	-4.605	-1.609
7.5-8.5	-2.303	-2.303	$\rightarrow(-\infty)$	-2.303
8.5-9.5	-2.303	-2.303	$\rightarrow(-\infty)$	-2.303
9.5-10.5	-2.303	-2.996	$\rightarrow(-\infty)$	-2.303

Table 4.--Quarterly time-specific fishing mortality factors, f_j, for data set D2.

Fishing year	f_j Quarter 1	Quarter 2	Quarter 3	Quarter 4
1	-0.916	-0.223	-0.223	-0.916
2	-0.916	-0.223	-0.223	-0.916
3	-0.916	-0.223	-0.223	-0.916
4	-0.916	-0.223	-0.223	-0.916
5	-0.916	-0.223	-0.223	-0.916
6	-0.916	-0.223	-0.223	-0.916
7	-0.916	-0.223	-0.223	-0.916
8	-0.916	-0.223	-0.223	-0.916
9	-0.916	-0.223	-0.223	-0.916
10	-0.916	-0.223	-0.223	-0.916
11	-0.916	0.000	-0.223	-0.916
12	-0.916	0.182	-0.223	-0.916
13	-0.916	0.336	-0.223	-0.916
14	-0.916	0.470	-0.223	-0.916
15	-0.916	0.588	-0.223	-0.916
16	-0.916	0.693	-0.223	-0.916
17	-0.916	0.788	-0.223	-0.916
18	-0.916	0.876	-0.223	-0.916
19	-0.916	0.876	-0.223	-0.916
20	-0.916	0.876	-0.223	-0.916

Table 5.--Scaled catch-at-age for fishing year 1, data set D1.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Total
2.5-3.5	92.9	79.9	68.8	59.2	300.8
3.5-4.5	138.9	97.9	69.0	48.6	354.4
4.5-5.5	23.9	18.6	14.5	11.3	68.4
5.5-6.5	4.6	4.0	3.4	2.9	14.9
6.5-7.5	1.0	1.0	0.9	0.8	3.7
7.5-8.5	0.4	0.3	0.3	0.3	1.3
8.5-9.5	0.3	0.3	0.2	0.2	1.0
9.5-10.5	0.1	0.1	0.1	0.1	0.4

Table 6.--Scaled catch-at-age for fishing year 1, data set D2.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Total
2.5-3.5	1.9	88.2	117.9	12.8	220.8
3.5-4.5	6.0	147.2	30.7	7.0	190.9
4.5-5.5	6.5	55.4	9.3	6.4	77.6
5.5-6.5	7.9	17.4	1.6	5.8	32.7
6.5-7.5	2.7	5.0	0.2	2.2	10.1
7.5-8.5	1.0	1.9	0.0	0.9	3.8
8.5-9.5	0.8	1.5	0.0	0.7	3.0
9.5-10.5	0.6	0.6	0.0	0.5	1.7

Table 7.--Actual age-specific fishing mortality rates for data set D1.

Fishing year	Age group (midpoint, years)							
	3	4	5	6	7	8	9	10
1	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
2	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
3	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
4	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
5	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
6	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
7	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
8	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
9	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
10	0.40	1.20	0.80	0.40	0.16	0.08	0.08	0.04
11	0.50	1.50	1.00	0.50	0.20	0.10	0.10	0.05
12	0.60	1.80	1.20	0.60	0.24	0.12	0.12	0.06
13	0.70	2.10	1.40	0.70	0.28	0.14	0.14	0.07
14	0.80	2.40	1.60	0.80	0.32	0.16	0.16	0.08
15	0.90	2.70	1.80	0.90	0.36	0.18	0.18	0.09
16	1.00	3.00	2.00	1.00	0.40	0.20	0.20	0.10
17	1.10	3.30	2.20	1.10	0.44	0.22	0.22	0.11
18	1.20	3.60	2.40	1.20	0.48	0.24	0.24	0.12
19	1.20	3.60	2.40	1.20	0.48	0.24	0.24	0.12
20	1.20	3.60	2.40	1.20	0.48	0.24	0.24	0.12

Table 8.--Actual age-specific fishing mortality rates for data set D2.

Fishing year	Age group (midpoint, years) 3	4	5	6	7	8	9	10
1	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
2	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
3	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
4	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
5	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
6	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
7	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
8	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
9	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
10	0.27	0.42	0.30	0.19	0.08	0.04	0.04	0.03
11	0.30	0.50	0.35	0.22	0.09	0.04	0.04	0.03
12	0.32	0.60	0.40	0.25	0.10	0.05	0.05	0.04
13	0.35	0.66	0.46	0.27	0.11	0.06	0.06	0.04
14	0.38	0.74	0.51	0.30	0.12	0.06	0.06	0.04
15	0.40	0.82	0.56	0.33	0.14	0.07	0.07	0.04
16	0.43	0.90	0.62	0.35	0.14	0.07	0.07	0.04
17	0.46	0.98	0.67	0.38	0.16	0.08	0.08	0.05
18	0.48	1.06	0.73	0.41	0.17	0.08	0.08	0.05
19	0.48	1.06	0.73	0.41	0.17	0.08	0.08	0.05
20	0.48	1.06	0.73	0.41	0.17	0.08	0.08	0.05

Table 9.--Scaled catch-at-age for year-class 10, data set D1.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Total
2.5-3.5	92.9	79.9	68.8	59.2	300.8
3.5-4.5	138.9	97.9	69.0	48.6	354.4
4.5-5.5	23.9	18.6	14.5	11.3	68.4
5.5-6.5	4.6	4.0	3.4	2.9	14.9
6.5-7.5	1.0	1.0	0.9	0.8	3.7
7.5-8.5	0.4	0.3	0.3	0.3	1.3
8.5-9.5	0.3	0.3	0.2	0.2	1.0
9.5-10.5	0.1	0.1	0.1	0.1	0.4

Table 10.--Scaled catch-at-age for year-class 20, data set D2.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Total
2.5-3.5	1.9	148.8	109.4	11.9	272.0
3.5-4.5	5.6	238.0	21.1	4.8	269.5
4.5-5.5	4.4	76.1	5.0	3.4	89.0
5.5-6.5	4.2	21.7	0.7	2.7	29.3
6.5-7.5	1.2	6.1	0.1	0.9	8.3
7.5-8.5	0.4	2.4	0.0	0.4	3.2
8.5-9.5	0.3	1.8	0.0	0.3	2.4
9.5-10.5	0.2	0.7	0.0	0.2	1.1

Table 11.--Age-specific fishing mortality rates for year-class 10, data set D1.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Average
2.5-3.5	0.40	0.40	0.40	0.40	0.40
3.5-4.5	1.20	1.20	1.20	1.20	1.20
4.5-5.5	0.08	0.08	0.08	0.08	0.08
5.5-6.5	0.40	0.40	0.40	0.40	0.40
6.5-7.5	0.16	0.16	0.16	0.16	0.16
7.5-8.5	0.08	0.08	0.08	0.08	0.08
8.5-9.5	0.08	0.08	0.08	0.08	0.08
9.5-10.5	0.04	0.04	0.04	0.04	0.04

Table 12.--Age-specific fishing mortality rates for year-class 20, data set D2.

Age interval	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Average
2.5-3.5	0.01	0.70	0.64	0.08	0.35
3.5-4.5	0.04	2.40	0.32	0.08	0.74
4.5-5.5	0.08	1.80	0.16	0.12	0.56
5.5-6.5	0.16	1.00	0.04	0.16	0.35
5.6-7.5	0.08	0.44	0.01	0.08	0.16
7.5-8.5	0.04	0.24	0.00	0.04	0.08
8.5-9.5	0.04	0.24	0.00	0.04	0.08
9.5-10.5	0.04	0.12	0.00	0.04	0.05

Table 13.--Estimates of F_{ij} to year-class 10, data set D1, using Doubleday's method.

Fishing year	Age group (midpoint, years) 3	4	5	6	7	8	9	10
1	0.41	1.22	0.83	0.42	0.17	0.09	0.09	0.04
2	0.41	1.22	0.83	0.42	0.17	0.09	0.09	0.04
3	0.41	1.22	0.83	0.42	0.17	0.09	0.09	0.04
4	0.41	1.22	0.83	0.42	0.17	0.09	0.09	0.04
5	0.40	1.22	0.82	0.42	0.17	0.09	0.08	0.04
6	0.40	1.22	0.82	0.42	0.17	0.09	0.08	0.04
7	0.40	1.22	0.82	0.42	0.17	0.09	0.08	0.04
8	0.40	1.21	0.82	0.42	0.17	0.09	0.08	0.04
9	0.40	1.21	0.82	0.42	0.17	0.08	0.08	0.04
10	0.40	1.21	0.82	0.42	0.17	0.08	0.08	0.04
11	0.50	1.51	1.02	0.52	0.21	0.11	0.11	0.05
12	0.60	1.80	1.22	0.63	0.25	0.13	0.13	0.06
13	0.70	2.11	1.43	0.73	0.30	0.15	0.15	0.07
14	0.80	2.41	1.63	0.84	0.34	0.17	0.17	0.08
15	0.90	2.71	1.83	0.94	0.38	0.19	0.19	0.09
16	1.00	3.01	2.04	1.05	0.42	0.21	0.21	0.10
17	1.10	3.31	2.24	1.15	0.47	0.23	0.23	0.11
18	1.21	3.63	2.46	1.26	0.51	0.25	0.25	0.13
19	1.23	3.69	2.50	1.28	0.52	0.26	0.26	0.13
20	1.19	3.59	2.43	1.25	0.50	0.25	0.25	0.12

Table 14.--Estimates of F_{ij} for year-class 20, data set D2, using Doubleday's method.

Fishing year	Age group (midpoint, years) 3	4	5	6	7	8	9	10
1	0.37	0.70	0.64	0.56	0.32	0.17	0.19	0.14
2	0.37	0.71	0.64	0.56	0.32	0.18	0.19	0.14
3	0.37	0.70	0.64	0.56	0.32	0.17	0.19	0.14
4	0.37	0.70	0.63	0.55	0.31	0.17	0.19	0.14
5	0.36	0.70	0.63	0.55	0.31	0.17	0.19	0.14
6	0.36	0.69	0.63	0.55	0.31	0.17	0.18	0.14
7	0.36	0.69	0.62	0.54	0.31	0.17	0.18	0.13
8	0.35	0.67	0.61	0.53	0.30	0.17	0.18	0.13
9	0.34	0.65	0.59	0.52	0.29	0.16	0.17	0.13
10	0.33	0.63	0.57	0.50	0.28	0.16	0.17	0.12
11	0.35	0.68	0.62	0.54	0.31	0.17	0.18	0.13
12	0.38	0.73	0.66	0.58	0.33	0.18	0.19	0.14
13	0.41	0.78	0.71	0.62	0.35	0.19	0.21	0.15
14	0.44	0.80	0.76	0.67	0.38	0.21	0.22	0.17
15	0.47	0.90	0.81	0.71	0.40	0.22	0.24	0.18
16	0.51	0.97	0.88	0.77	0.44	0.24	0.26	0.19
17	0.55	1.05	0.96	0.84	0.48	0.26	0.28	0.21
18	0.62	1.19	1.08	0.95	0.54	0.30	0.32	0.23
19	0.70	1.34	1.22	1.07	0.61	0.33	0.36	0.26
20	0.90	1.73	1.57	1.37	0.78	0.43	0.46	0.34

Table 15.--Estimates of regression model parameters for cohorts D1-YC10 and D2-YC20, based on annual and quarterly data.

Cohorts	Parameters $\hat{R}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\bar{F}}$	Data points
D1-YC10						
Annual data	841	1.588	0.560	0.000	0.66	8
Quarterly data	897	1.502	0.574	0.126	0.72	32
True values	1,000	--	--	--	0.60	--
D2-YC20						
Annual data	751	0.724	0.498	0.189	0.43	8
Quarterly data	348	0.982	0.315	0.000	0.58	32
True values	1,000	--	--	--	0.44	--

Table 16.--Estimated and actual fishing mortality rates for cohorts D1-YC10 and D2-YC20, based on regression analysis of annual data.

Cohorts	Coded age interval	Coded age at midpoint	Actual average F during interval	Estimated F at midpoint
D1-YC10	1	0.5	0.400	0.601
	2	1.5	1.200	1.029
	4	3.5	0.400	0.784
	6	5.5	0.080	0.402
	8	7.5	0.040	0.179
D2-YC20	1	0.5	0.351	0.389
	2	1.5	0.740	0.579
	4	3.5	0.354	0.467
	6	5.5	0.082	0.266
	8	7.5	0.051	0.133

Table 17.--Estimated values of $\bar{F}$ for North Pacific albacore year classes 1957-61, corresponding to different values of F_n.

F_n	Year class 1957	1958	1959	1960	1961
0.40	0.52	0.42	0.60	0.49	0.43
0.20	0.44	0.38	0.57	0.44	0.37
0.10	0.34	0.32	0.50	0.35	0.29
0.01	0.07	0.09	0.17	0.08	0.06

Table 18.--Estimates of regression model parameters for two sets of North Pacific albacore catch-at-age statistics.

Cohorts	Parameters $\hat{R}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\bar{F}}$	Data points
YC-1961						
Annual data	998	0.339	0.149	0.276	0.40	8
	1,022	0.150	0.001	0.000	0.24	9
Quarterly data	576	0.380	0.120	0.000	0.38	32
	406	0.146	0.001	0.000	0.24	36
YC-1957-61						
Annual data	837	0.573	0.295	0.000	0.44	8
	793	0.160	0.010	0.000	0.25	9
Quarterly data	506	0.630	0.259	0.000	0.45	32
	384	0.161	0.001	0.000	0.25	36

Figure 1. Sequence of quarterly F_i for combined catch histories of albacore year-classes 1957-61, based on cohort analysis with $F_n = .10$.

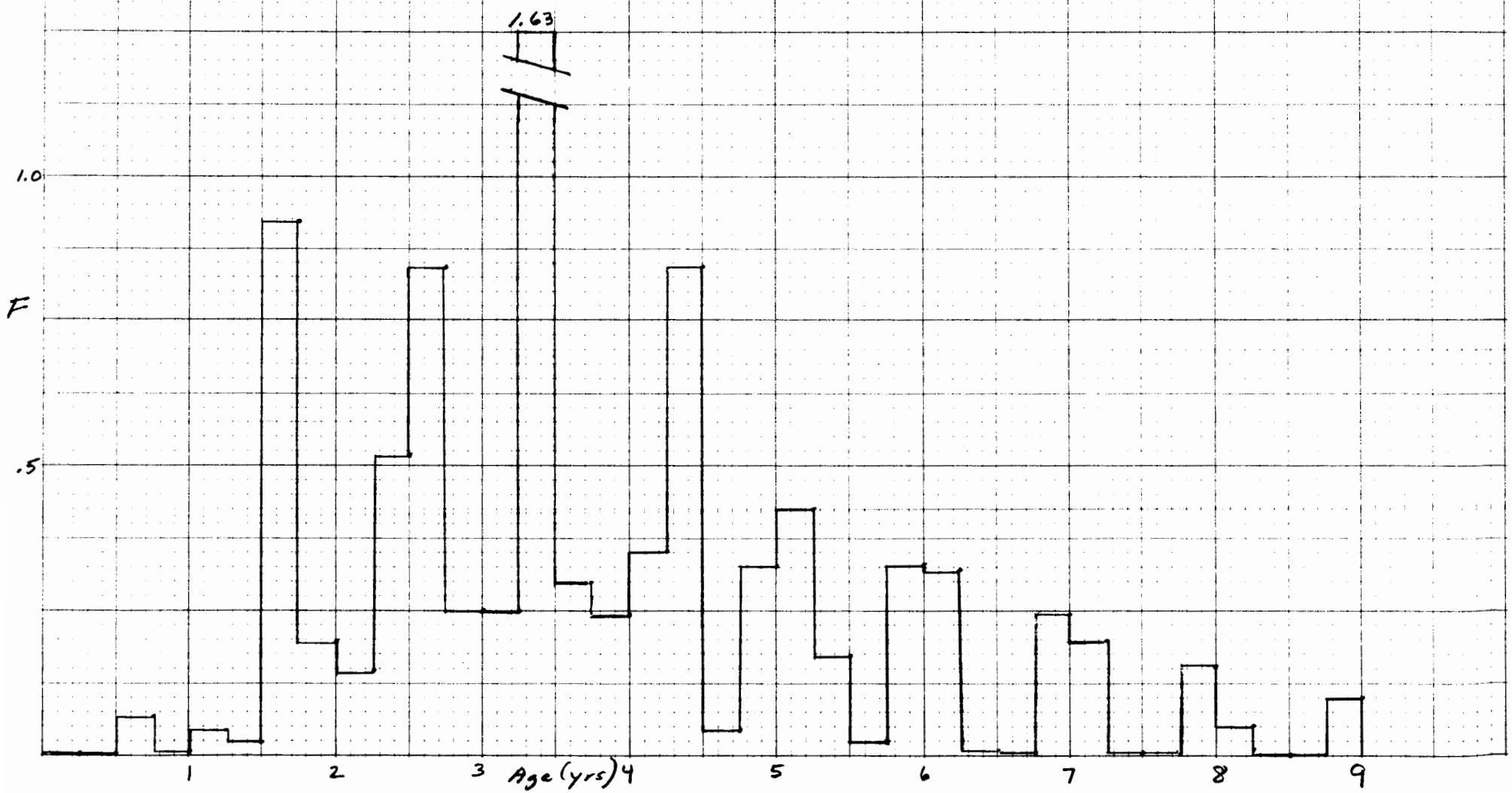

Figure 2. Actual F_i for D1-YC20, annual.

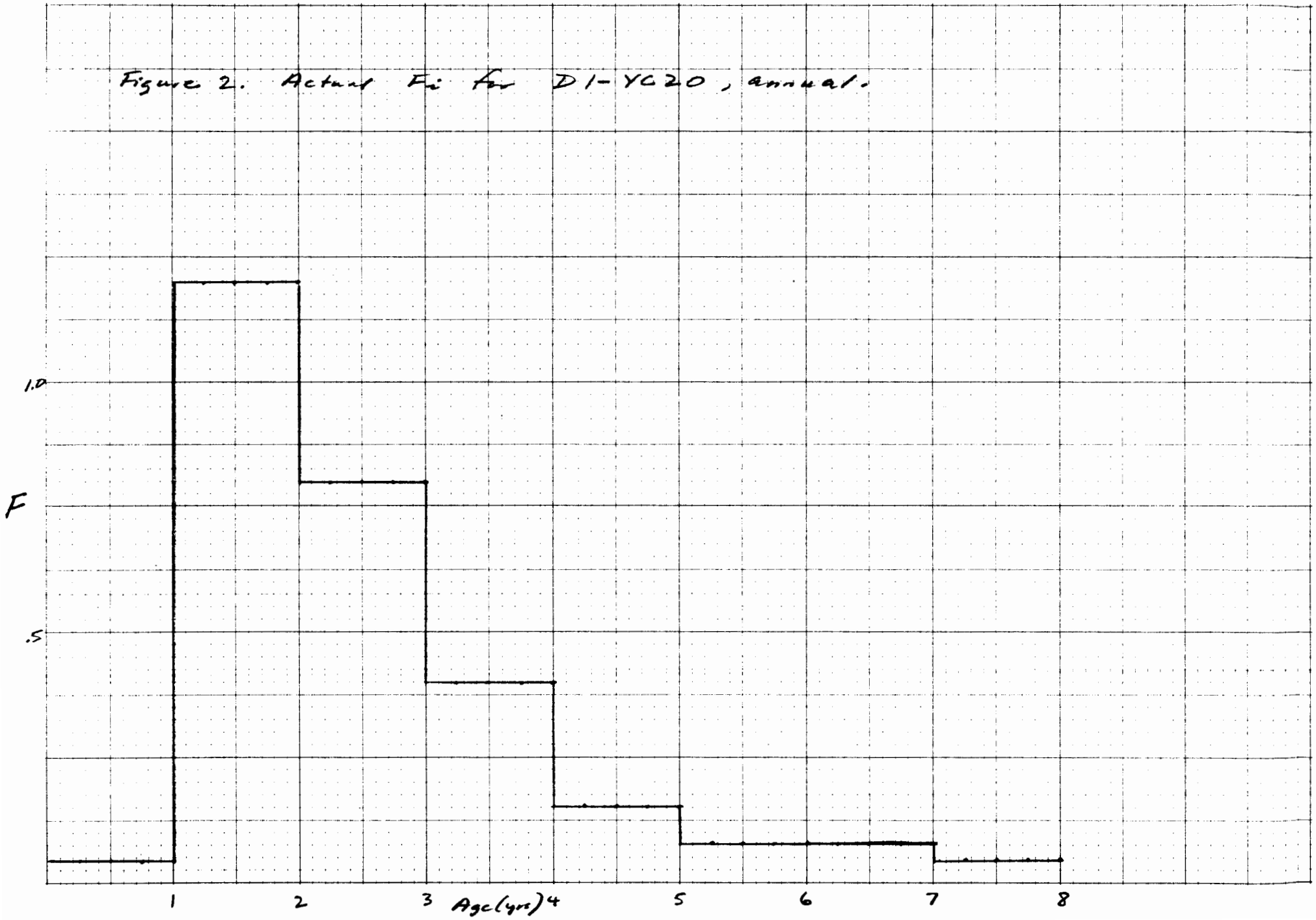

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Figure 3. Actual F_i for D2-YC20, quarterly.

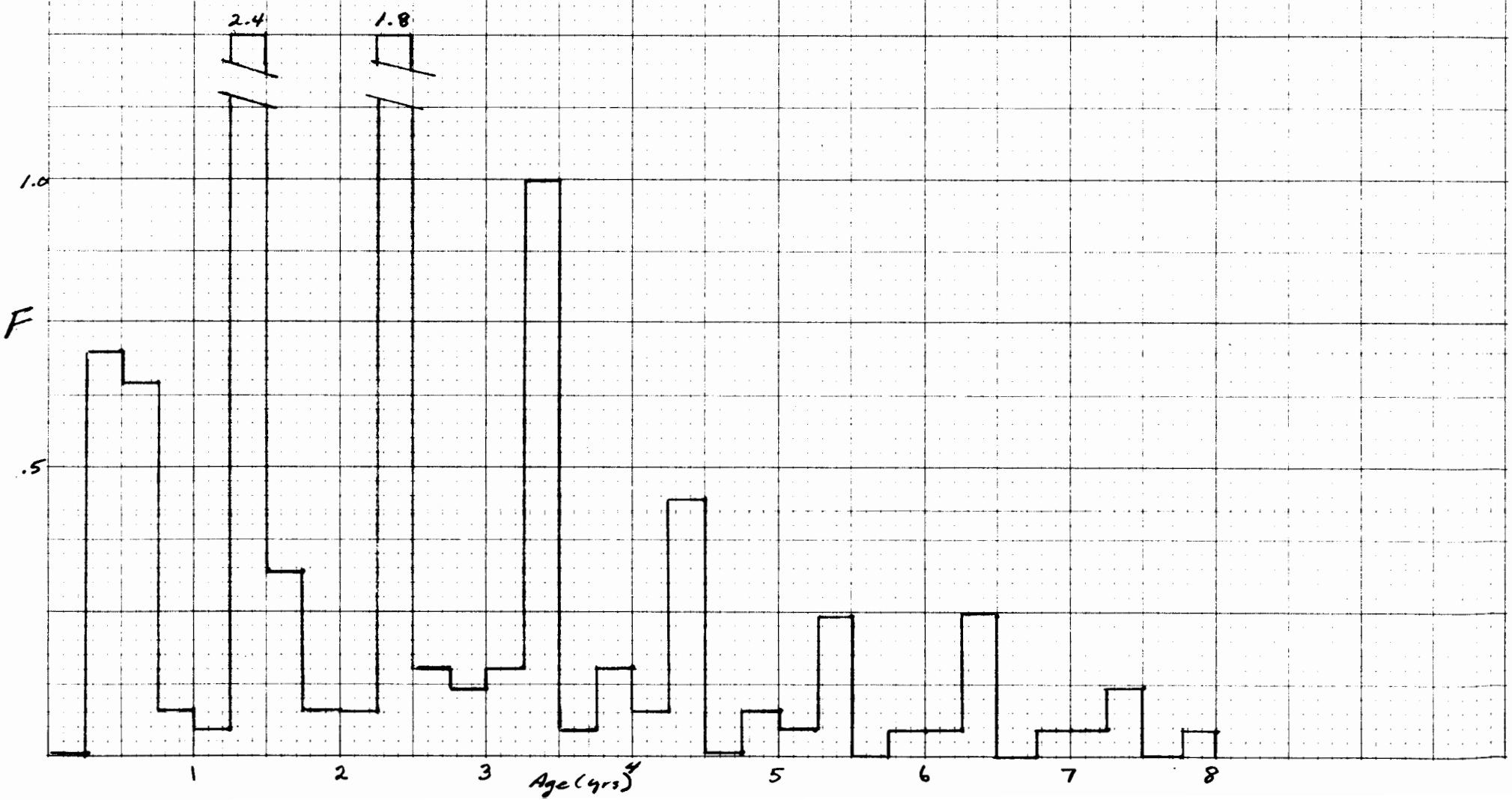


Figure 4a. Cohort analysis estimates of F_i, quarterly, for D1-YC10

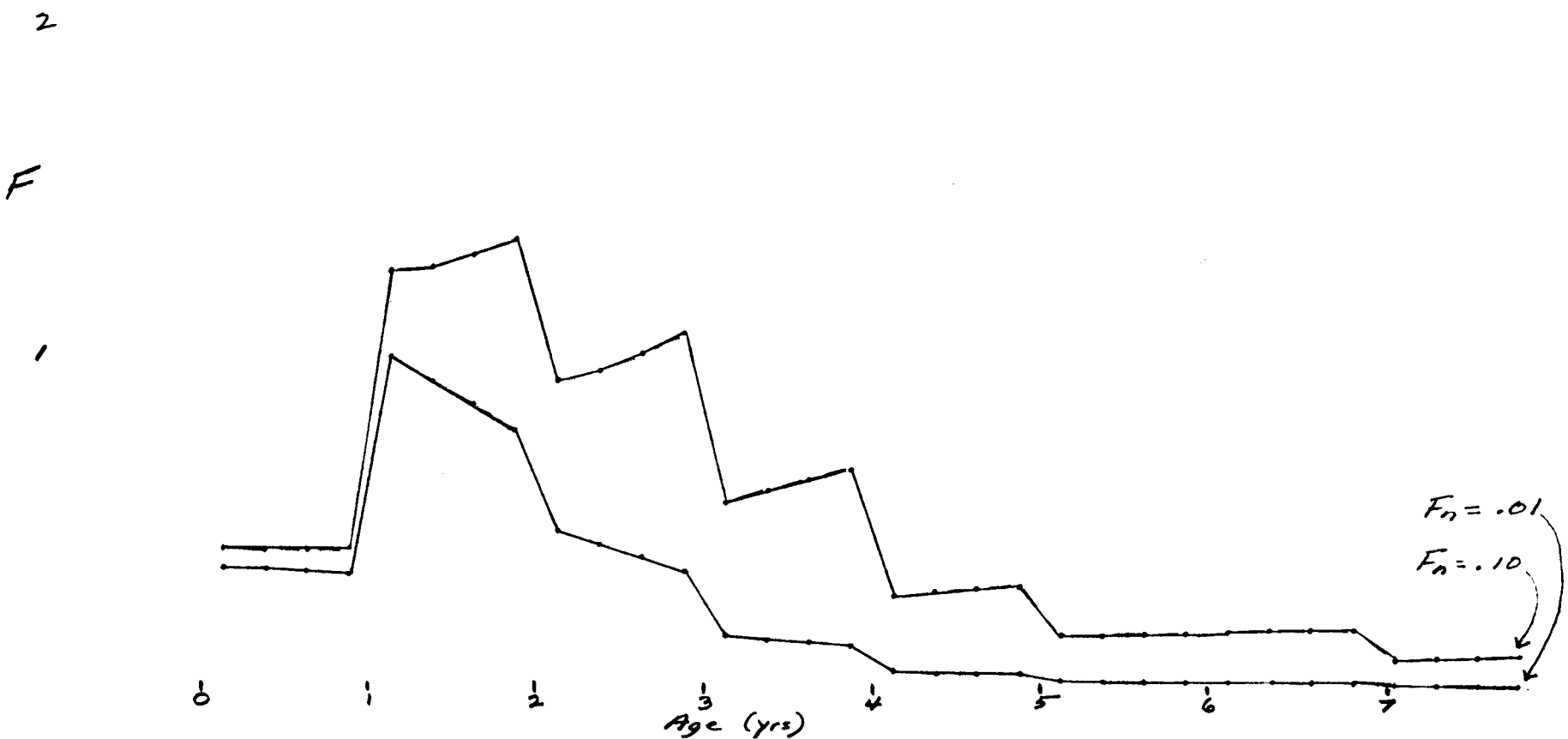


Figure 4b. Cohort analysis estimates of F_i, annually, for D1 - YC10

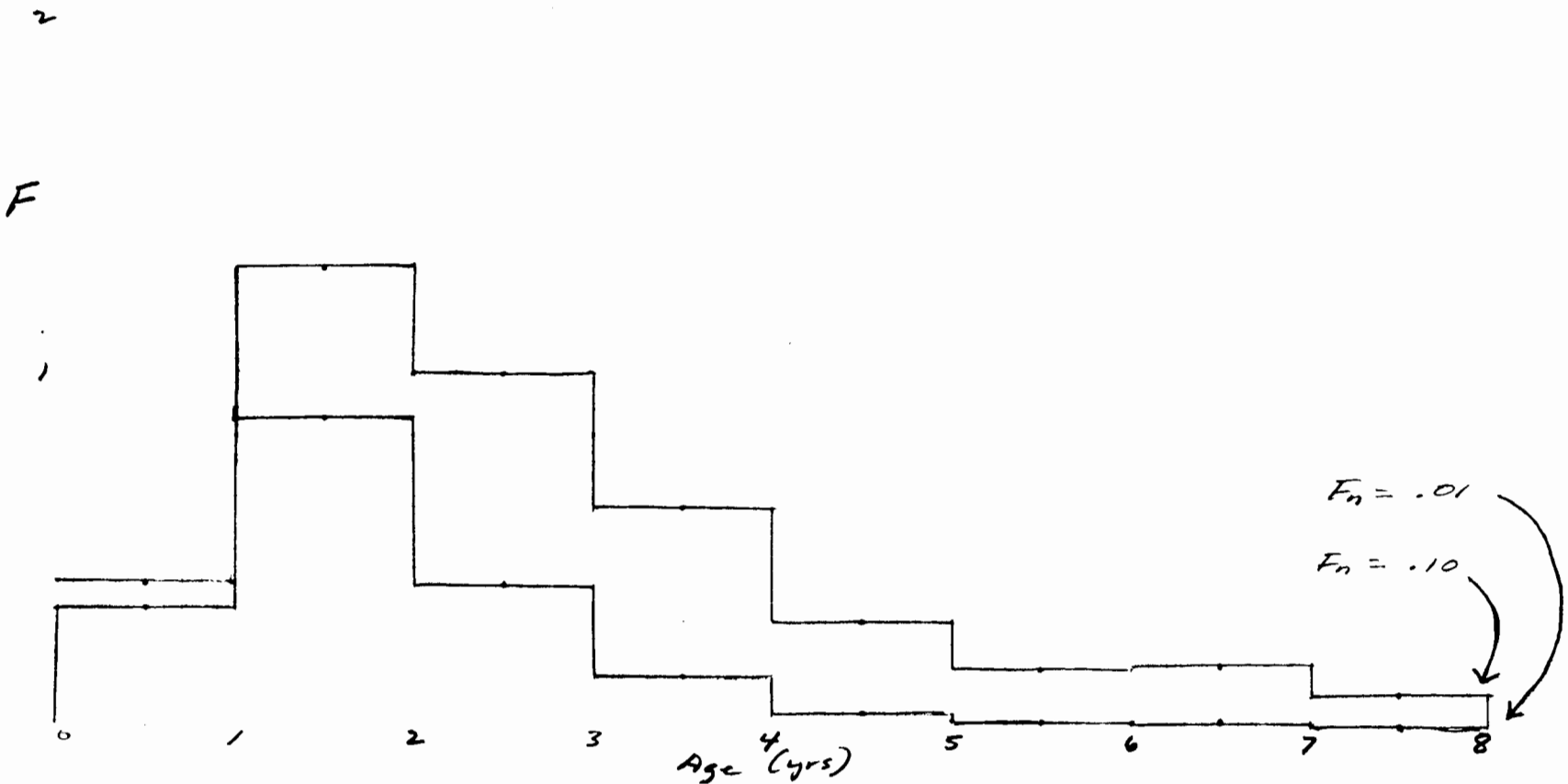


Figure 5a. Cohort analysis estimates of F_i, quarterly, for D2-YC20.

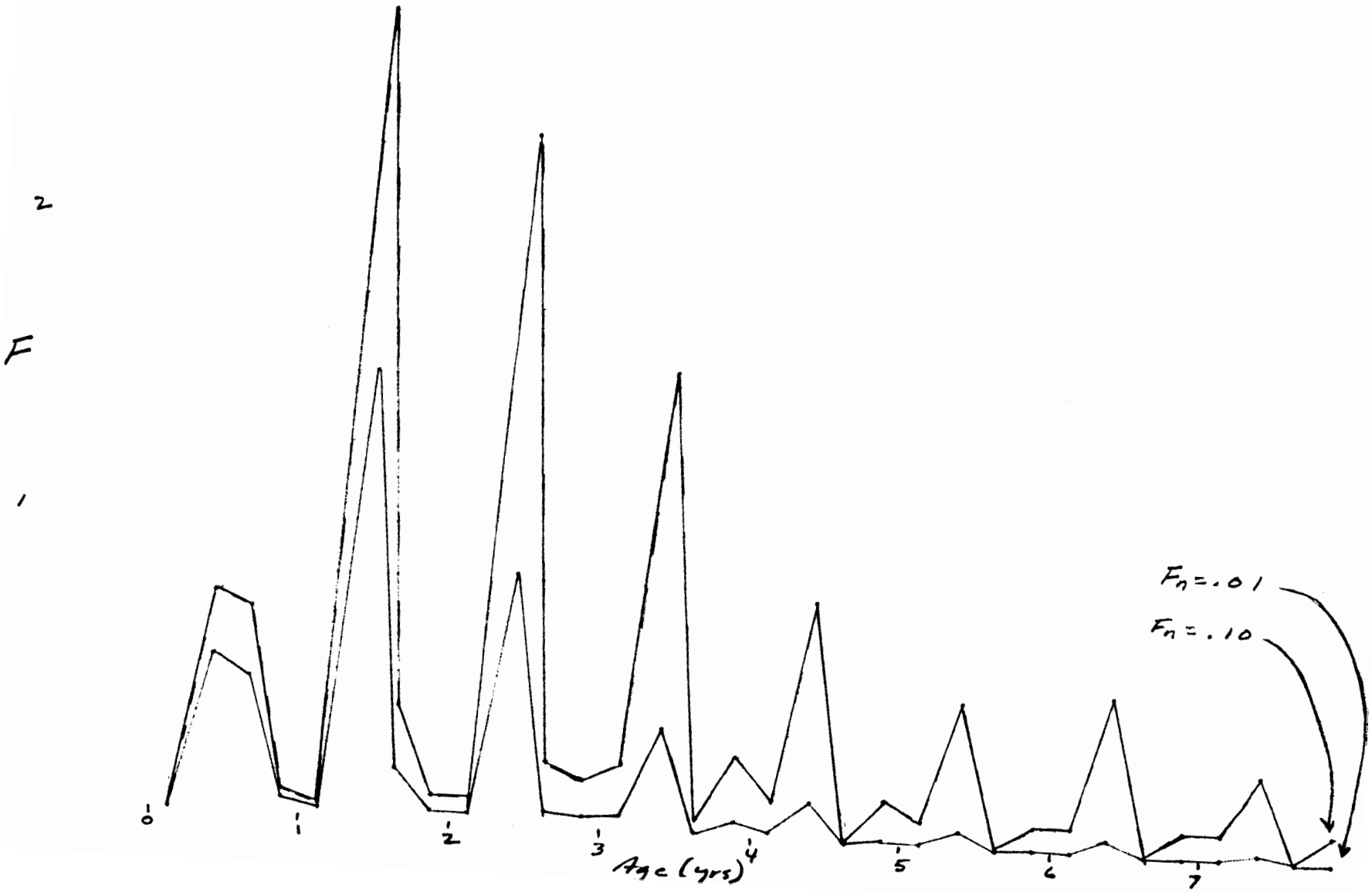


Figure 5b. Cohort analysis estimates of F_i, annually, for D2-YC20.

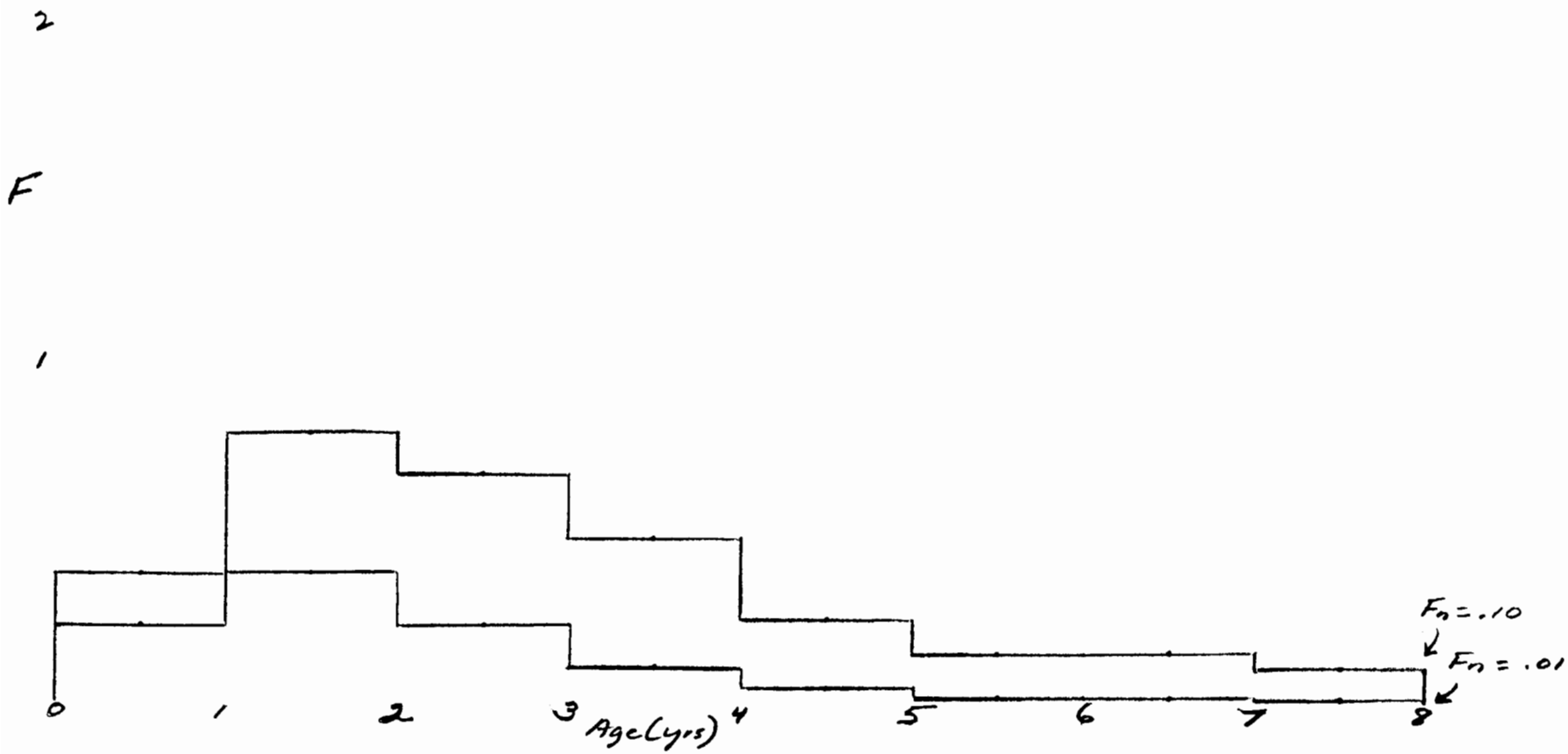


Figure 6. Actual data and fitted regression model, D1-YC10, quarterly.

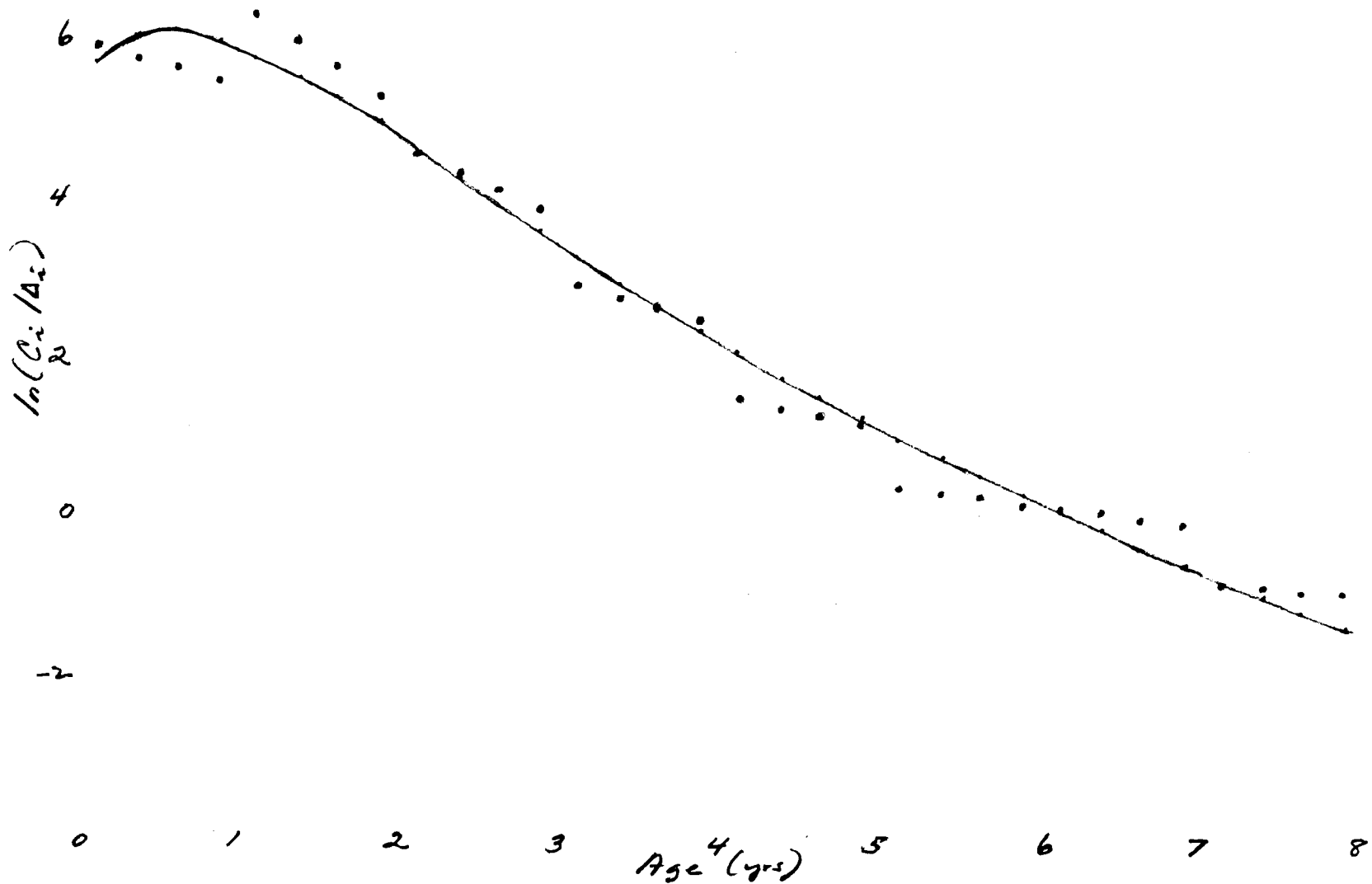


Figure 7. Actual data and fitted regression model, D1-YC10, annually.

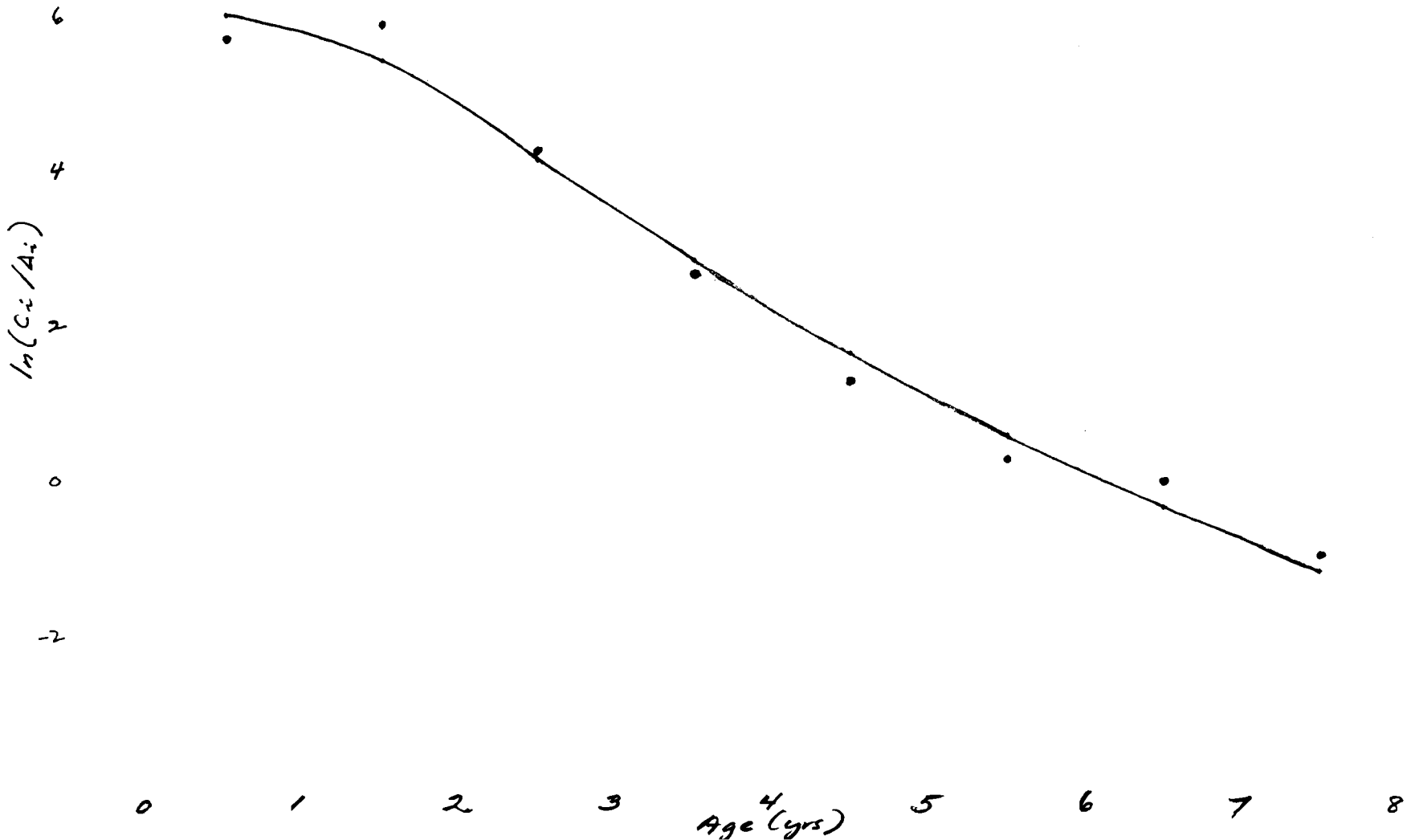


Figure 8. Actual data and fitted regression model, D2 – YC20, quarterly.

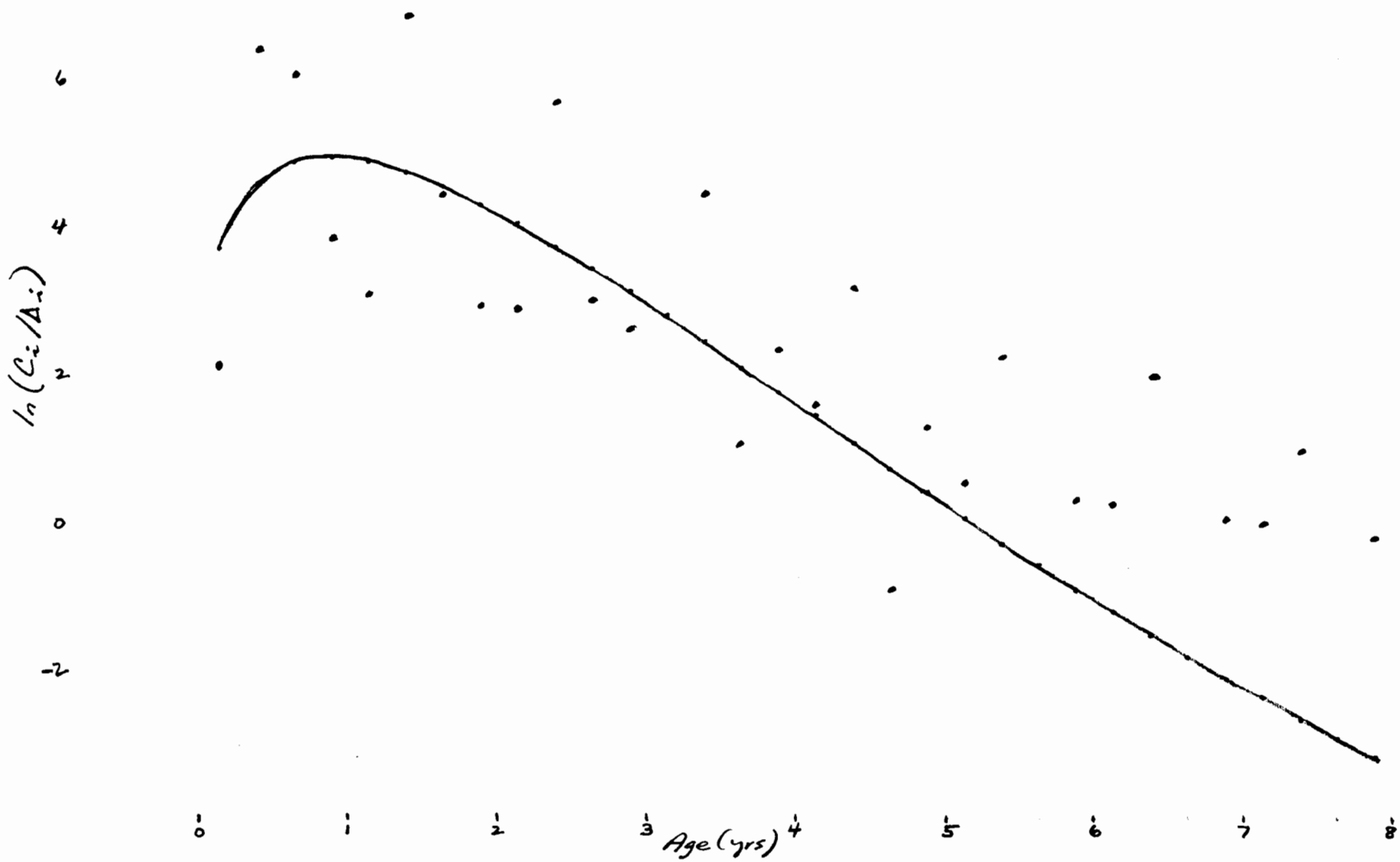
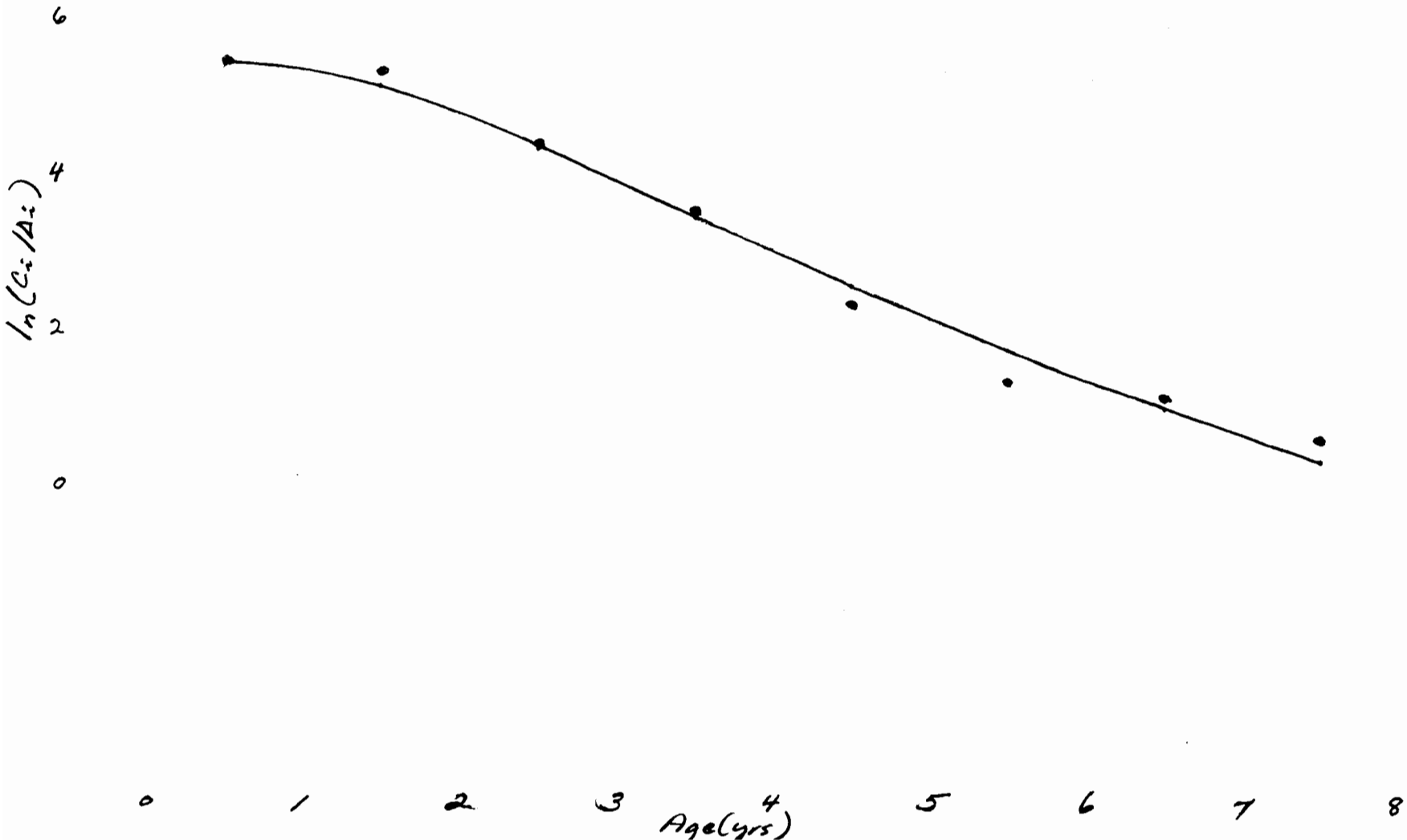


Figure 9. Actual data and fitted regression model, D2-YC20, annually.



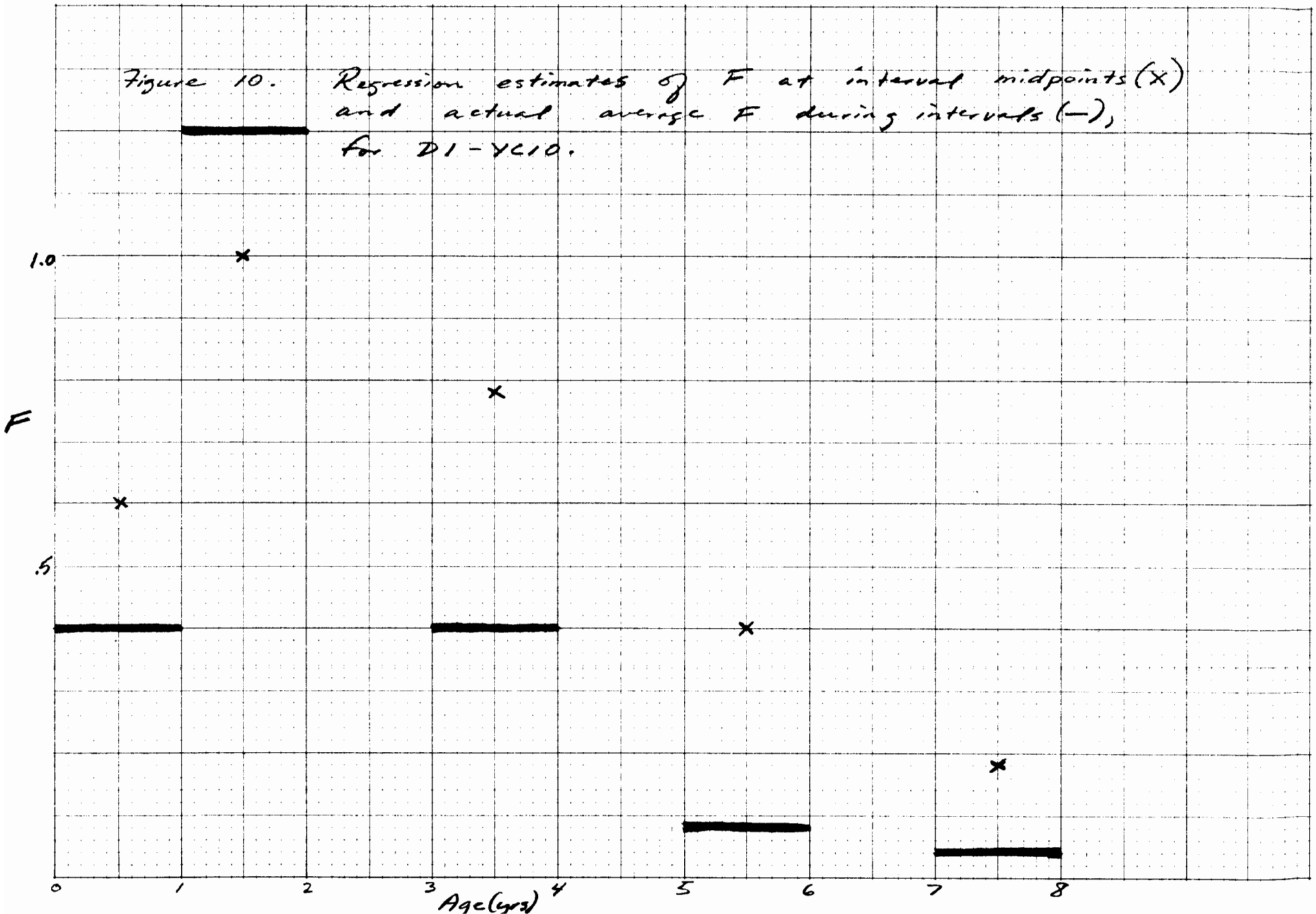


Figure 10. Regression estimates of F at interval midpoints (X) and actual average F during intervals (—), for D1-YC10.

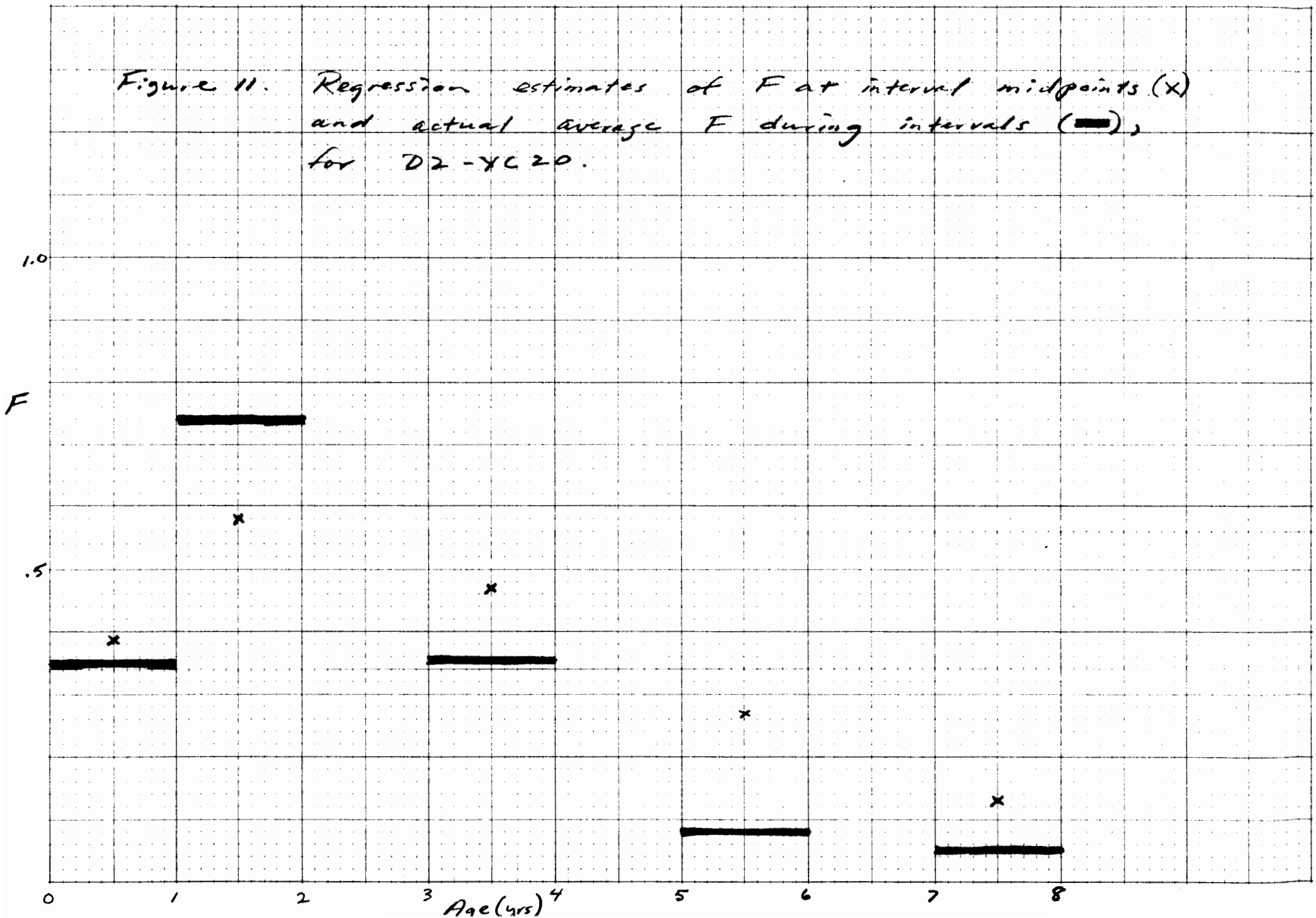


Figure 11. Regression estimates of F at interval midpoints (x) and actual average F during intervals (▬), for D2-YC20.

Figure 12a. Cohort analysis estimates of F_i, quarterly, albacore year-class 1961.

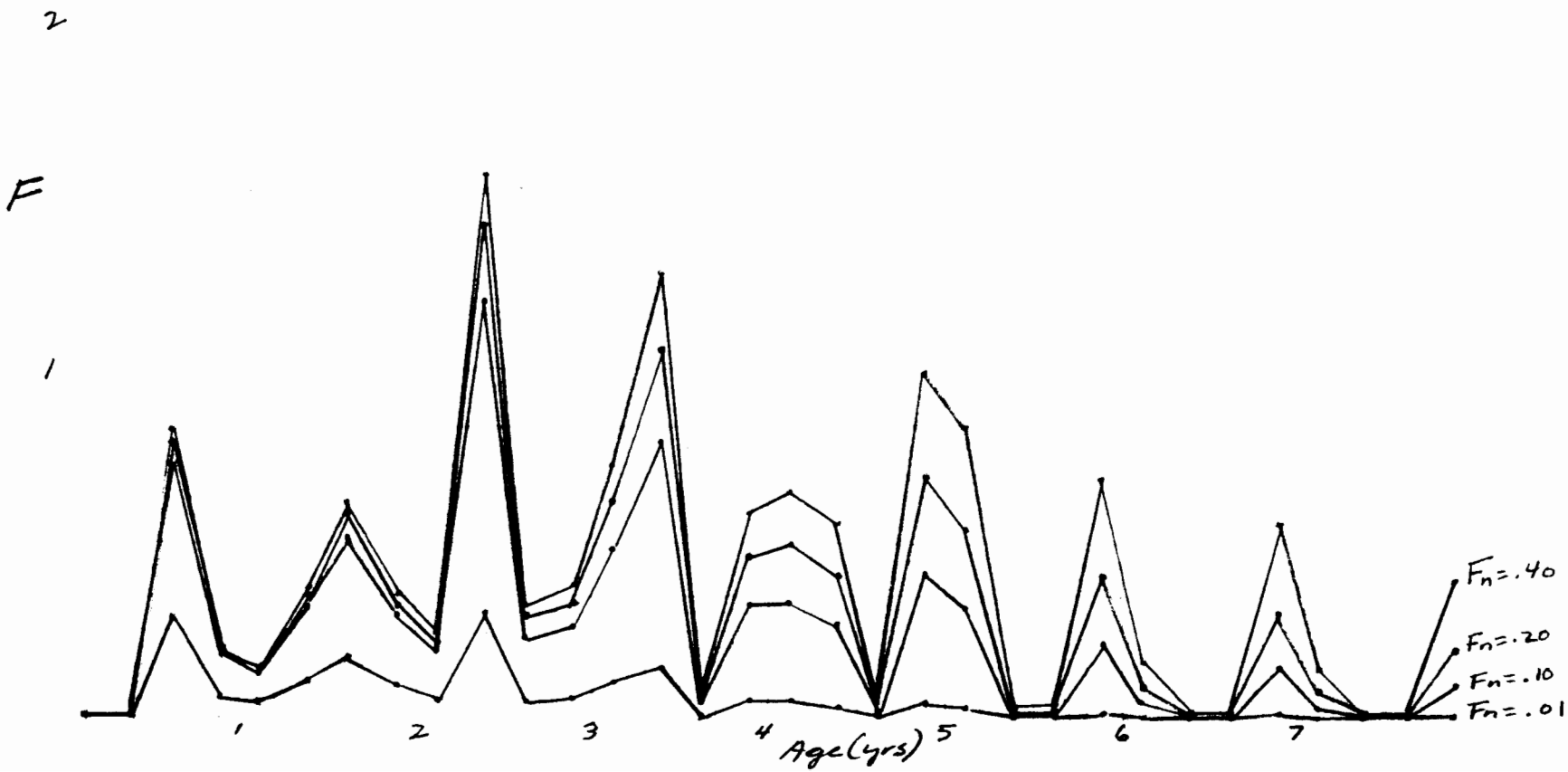


Figure 12 b. Cohort analysis estimates of F_i, annually, for albacore year-class 1961.

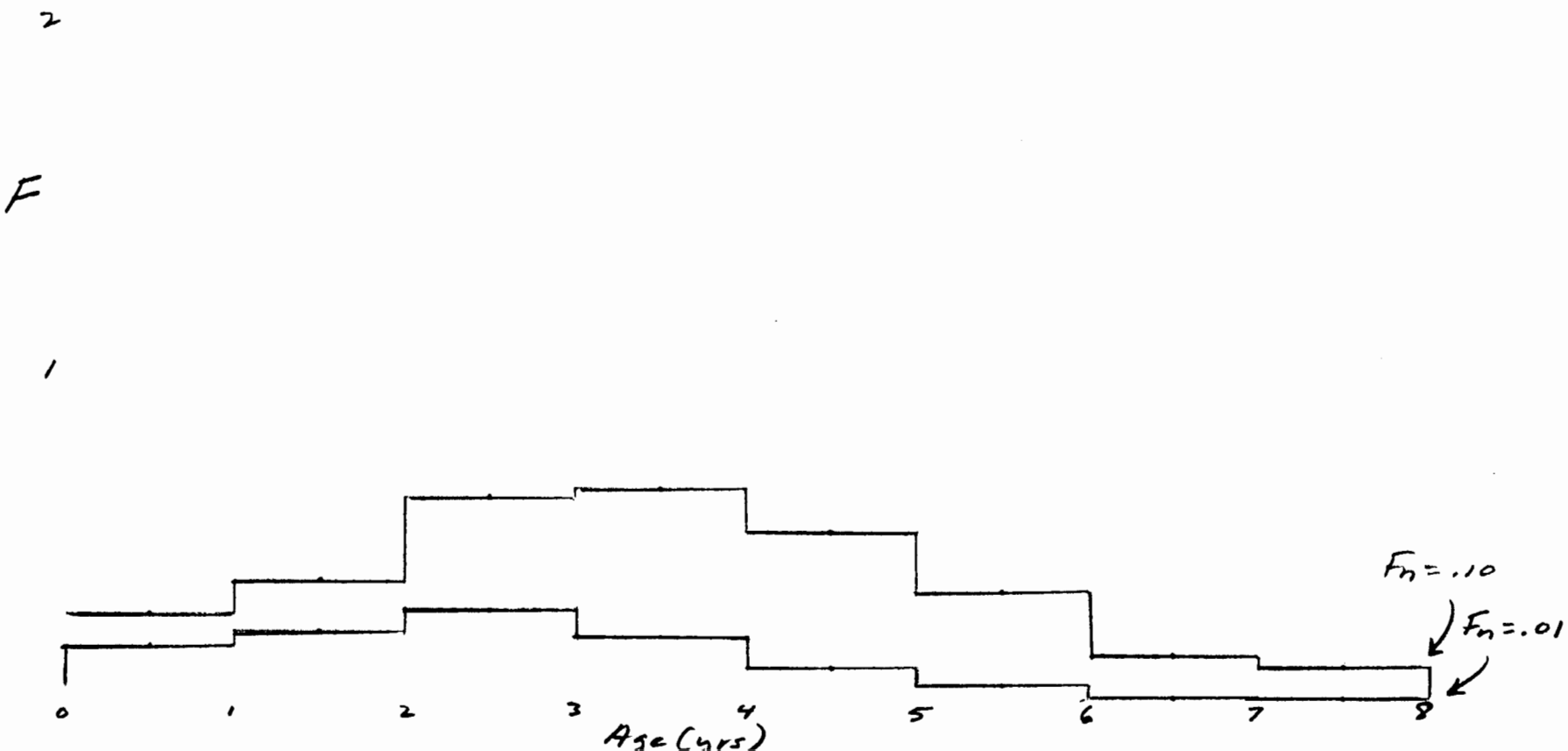


Figure 13a. Cohort analysis estimates of F_i, quarterly, for albacore year-classes 1957-61.

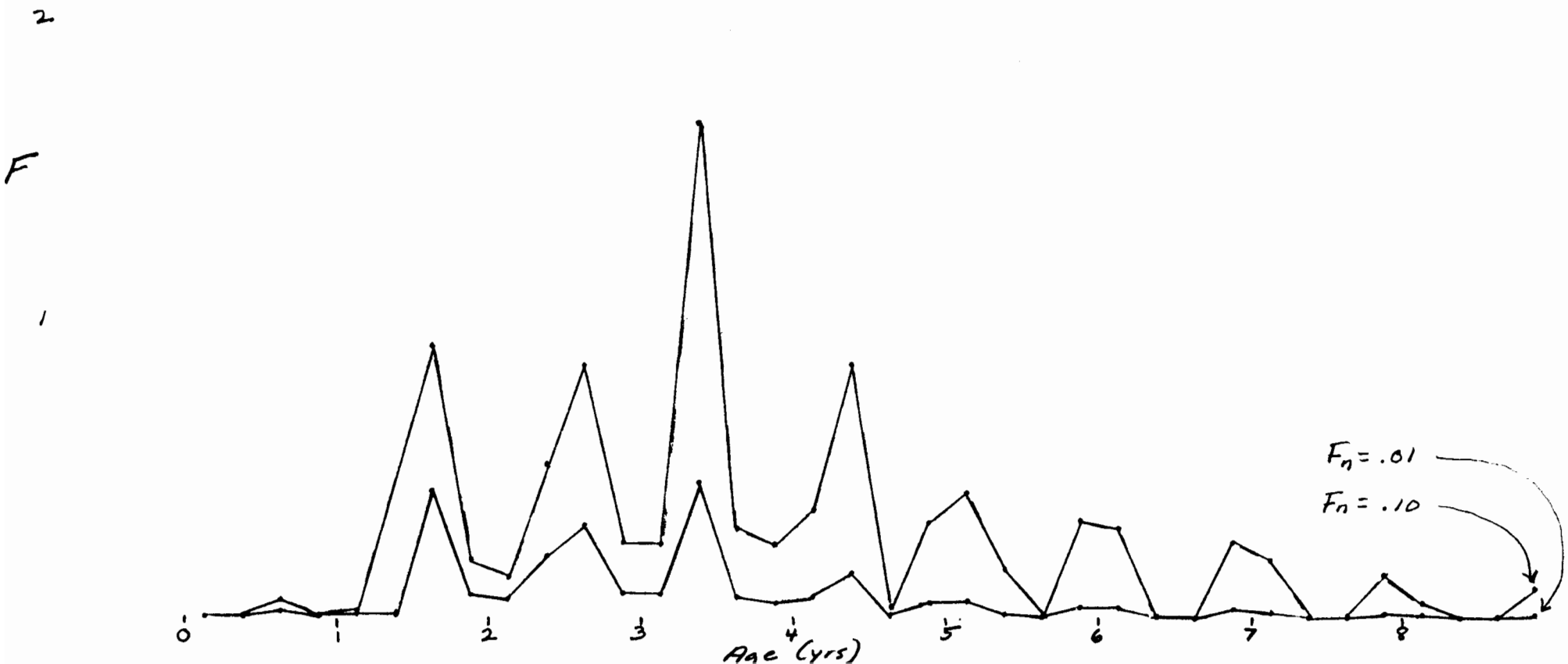


Figure 13b. Cohort analysis estimates of F_i, annually, for combined albacore year-classes 1957-61.

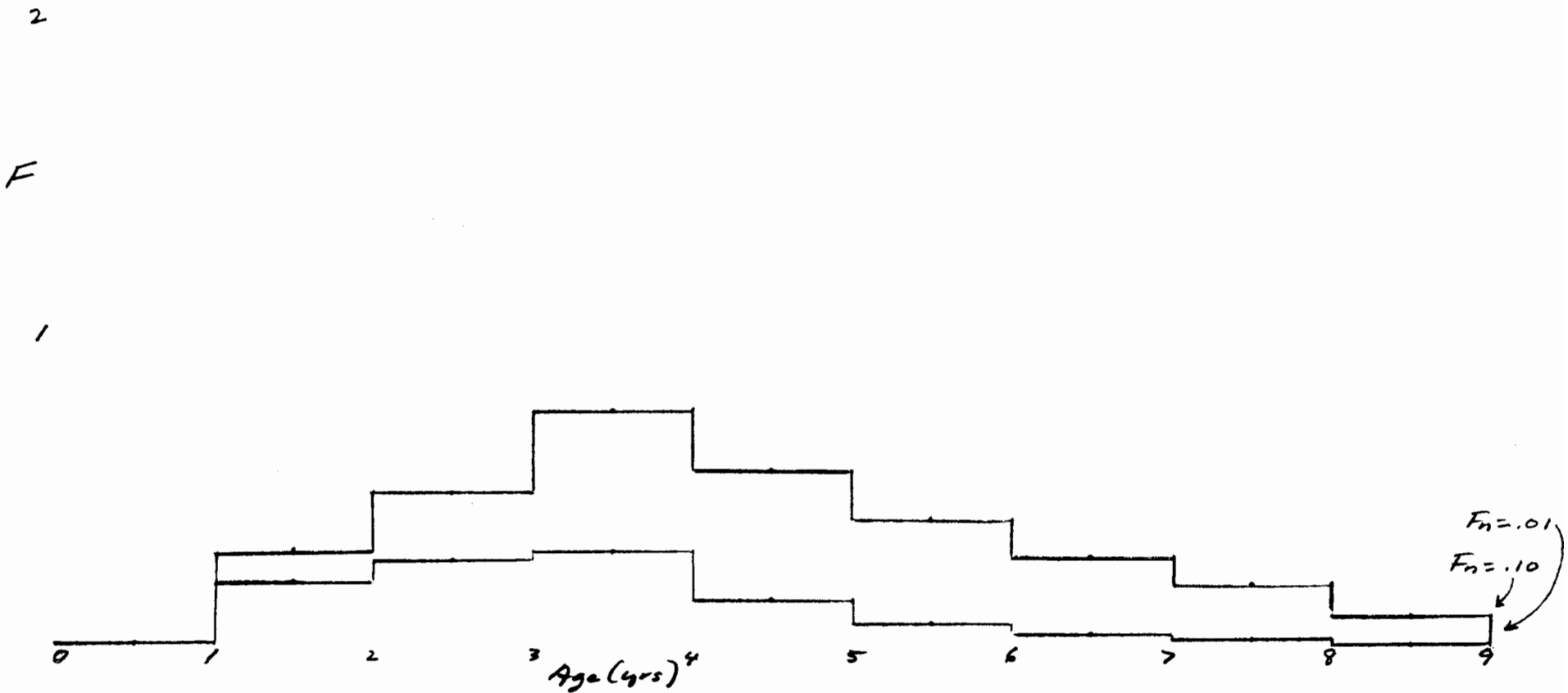


Figure 14. Actual data and fitted regression model, albacore year-class 1961, quarterly.

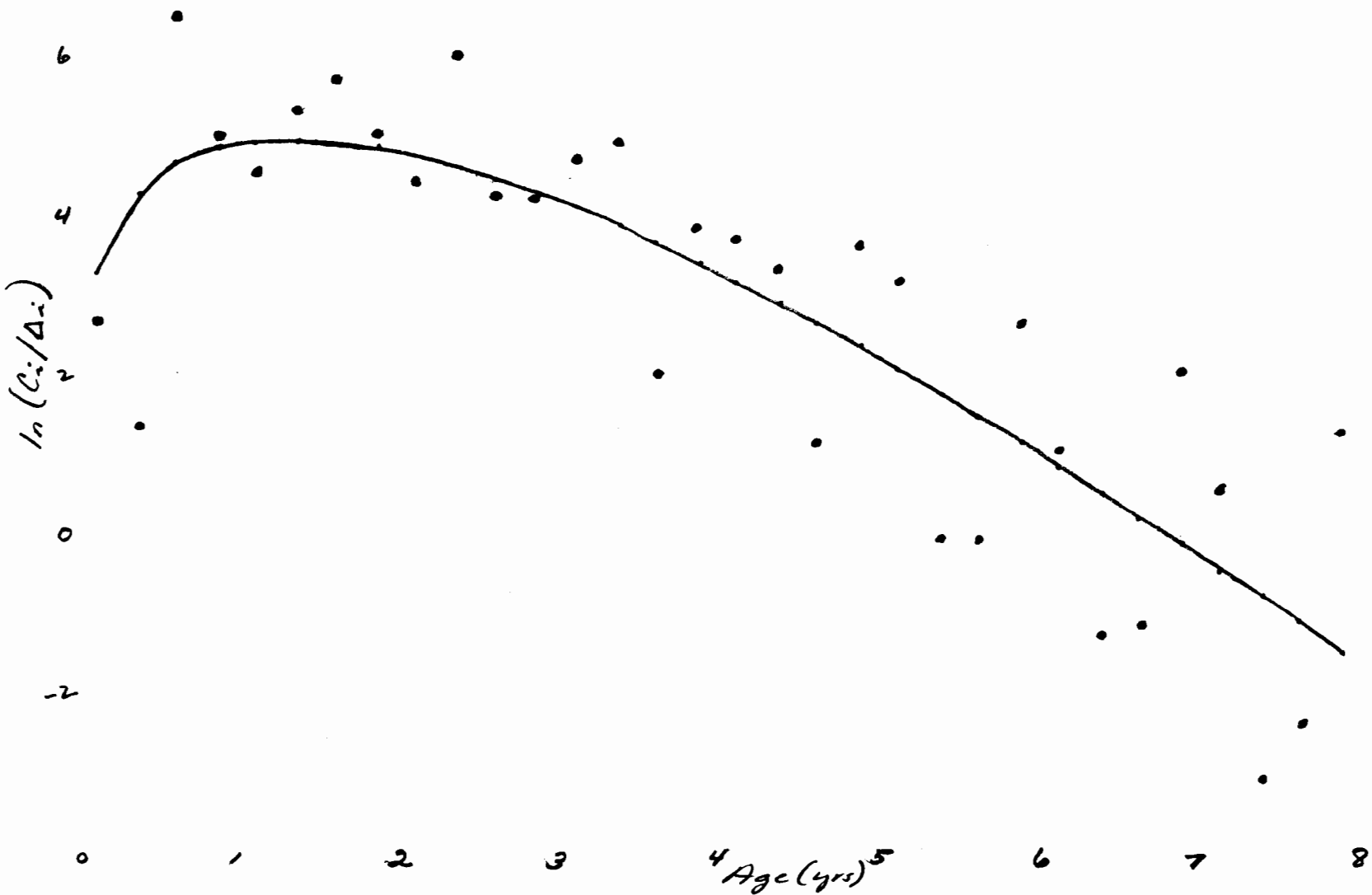


Figure 15. Actual data and fitted regression model, albacore year-class 1961, annually.

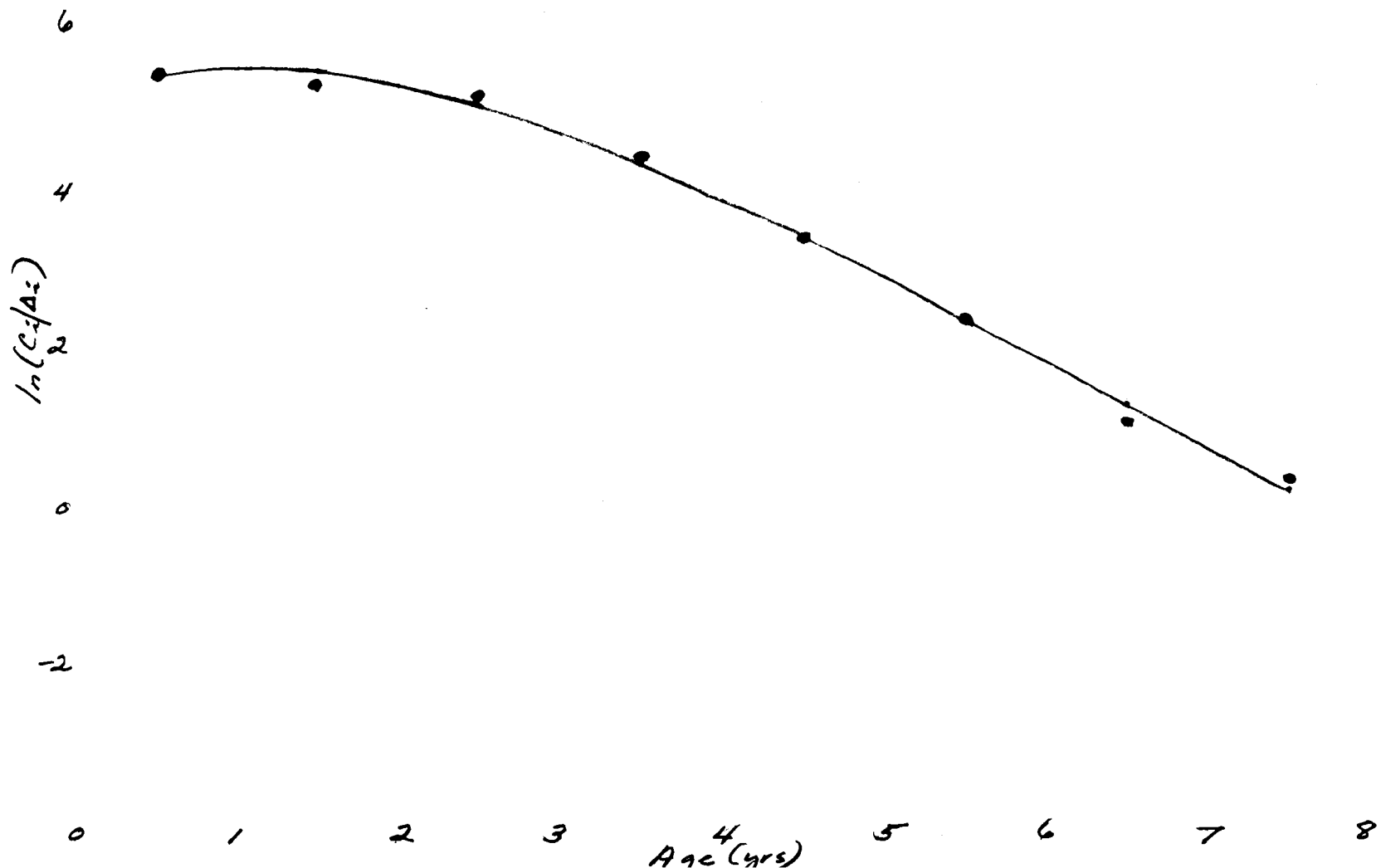


Figure 16. Actual data and fitted regression model, albacore year-classes 1957-61, quarterly

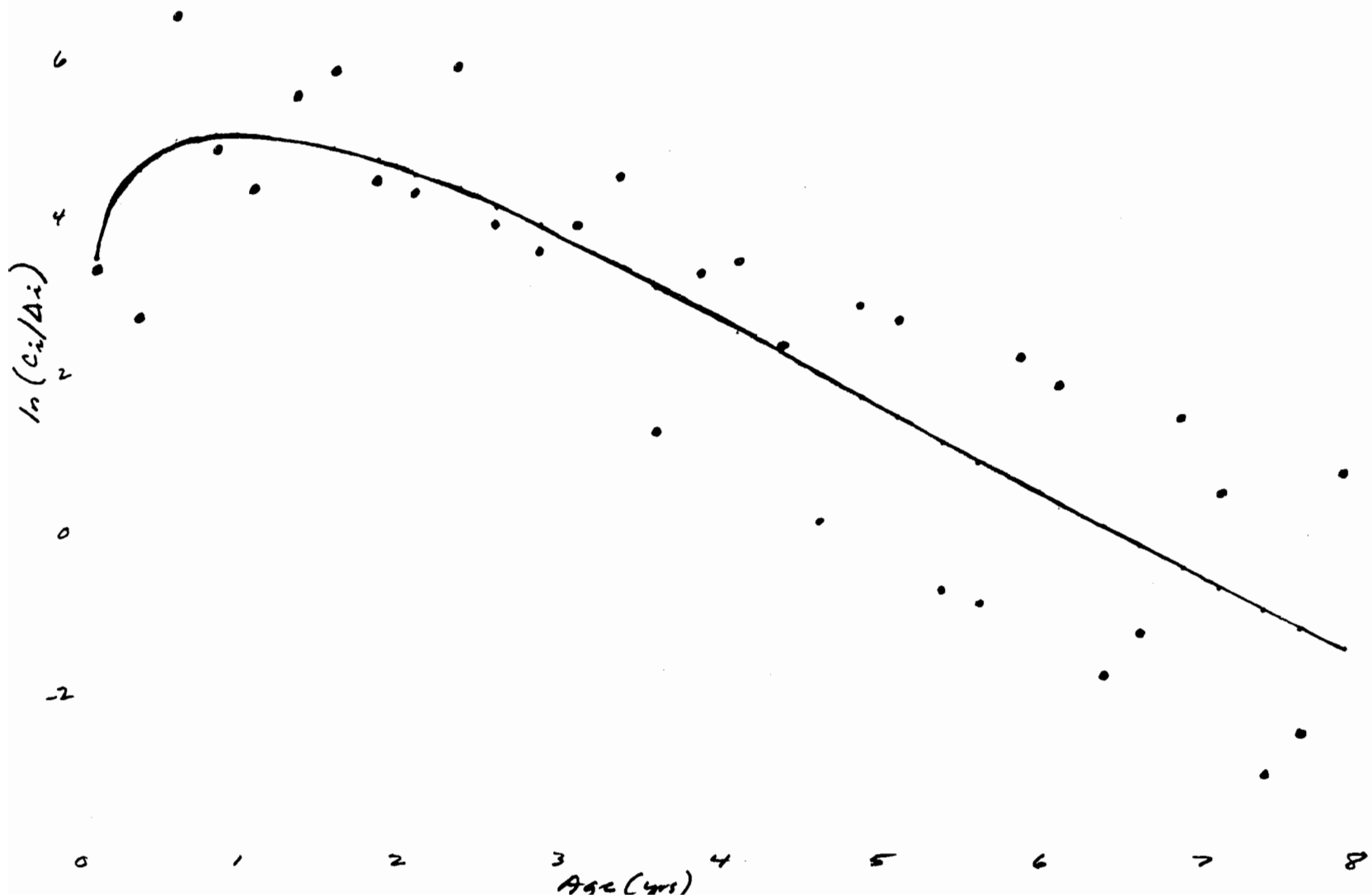
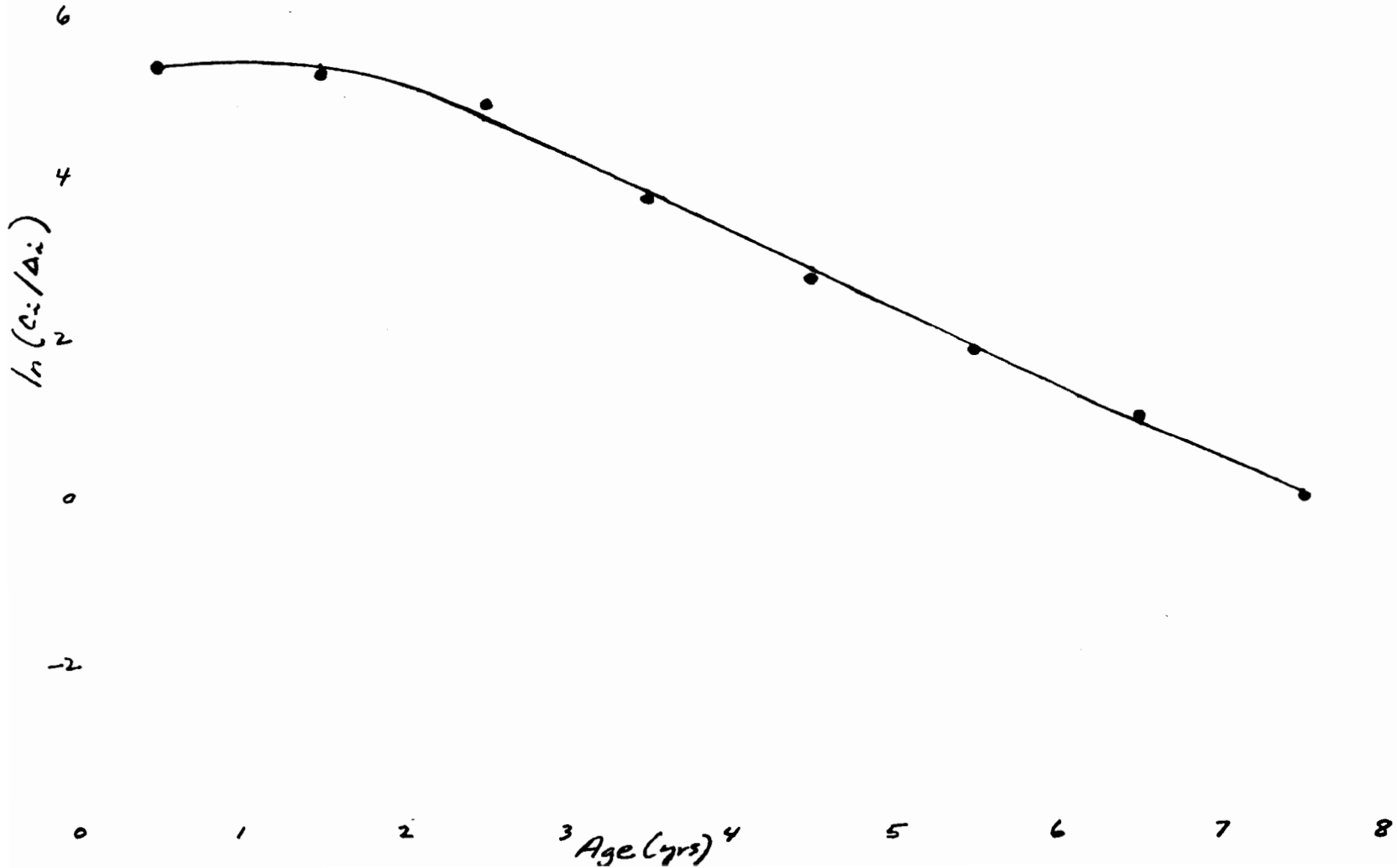



Figure 17. Actual data and fitted regression model, albacore year-classes 1957-61, annual.