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An analysis of some factors affecting the growth rates of Gulf of St. Lawrence cod from 1949 to 1973

by

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Abstract

Stepwise multiple linear regression analysis was used to analyze data on the growth of Gulf of St. Lawrence cod up to age 11 during the period 1949 to 1973. Temperature, stock size and the size of a fish were found to be significantly correlated with growth rate; temperature was positively correlated while stock size and the size of a fish were negatively correlated with growth rate. The importance of each variable changed with time and is probably ultimately attributable to changes in the fishery in the Gulf of St. Lawrence. Predictions of length-at-age in the regression equations showed generally good correspondence with empirical measurements.

Introduction

Many of the population attributes that fishermen and fishery biologists are concerned with are dependent upon the growth rates of fishes. The size composition of a fish stock is of major importance since mortality rates (Gulland 1965; Ponomarenko 1965, 1973), fecundity, maturity and quality of eggs (Dementyeva and Mankevich 1965; Hempel 1965; Iles 1965; Woodhead and Woodhead 1965; Bagnel 1973; Nikolsky *et al.* 1973; Schopka and Hempel 1973), and the degree of interspecific and intraspecific competition have been shown to a greater, or lesser, extent to be size-dependent.

It is known that growth rates, often used synonymously with length-at-age or the rate (K) of approaching von Bertalanffy's L_{∞} vary greatly both between and within populations of a given species (Taylor 1958; May *et al.* 1965; May 1966; Wiles and May 1968; Pinhorn 1969; Schopka and Hempel 1973). Fleming (1960), Kohler (1964), Postolaky (1967), Paloheimo and Kohler (1968), and Halliday (1972), to list a few, have reported substantial year to year variation in growth rates. For comparison with other estimates, we have calculated K , L_{∞} and t for the 4T cod stock by sampling year (Table 1), and by year class (Table 2). It is clear that values of K and L_{∞} for the 4T cod stock span the range of values calculated by other authors for different cod stocks, with the possible exception of 2 very large values of L_{∞} calculated by Taylor (1958) using Saemundsson's (1923 data; cited by Taylor). May *et al.* (1965) rejected the latter 2 values on the grounds of the method of calculation and the limited age data used. While we question the usefulness of the von Bertalanffy equation in characterizing growth it is useful in demonstrating that length-at-age is highly variable.

There are many abiotic and biotic factors which can potentially affect growth. The two which have been investigated most often, partly because of the relative ease of measurement, and partly because of some a priori knowledge of their effect in the laboratory, are temperature (Fleming 1960; Dementyeva and Mankevich 1965; Hermann and Hansen 1965; Jonsson 1965; May *et al.* 1965; Mankowski 1965; Ponomarenko 1965, 1973; Postolaky 1967; Wiles and May 1968) and stock density (Kohler 1964; Dementyeva and Mankevich 1965; Sonina 1965; May 1966; Meyer 1967; Postolaky 1967; Wiles and May 1968; Paloheimo and Kohler 1968; Halliday 1972). However, there has been much speculation (in the absence of quantitative information) and controversy concerning the importance of particular variables in field situations.

The year-to-year variability in these two factors, particularly temperature is such that many years of data are usually required to determine if a variable is statistically significant. As the

relative contribution of a variable to the variance of the parameter in question decreases the number of degrees of freedom must increase if we are to state with a given level of confidence that the effect of the variable is statistically significant. For example, if temperature truly accounts for 50% (i.e. $r=0.7$) of the observed variability in growth rates then we need at least 8 observations to confirm at the 5% level of significance that growth rate is significantly correlated with growth. On the other hand, if the contribution of temperature is only 25% then at least 16 observations are necessary for the same significance level. Considering the large number of potential factors involved it is reasonable to expect that a large data set is required.

Further, throughout the field of biology we observe thresholds of and non-linear responses to stimuli. These reduce the probability of identifying, by simple correlation or linear regression analysis, a variable as an important factor in a particular data set especially, where the data are few.

Fortunately, there exists for the southwestern Gulf of St. Lawrence (4T) cod stock an exceptional data set of natural growth rates. Studies by Kohler (1964) and later Paloheimo and Kohler (1968) were concerned with the period from 1949-65, while Halliday (1972) has examined the more recent period, from 1960-72, during which the fishing intensity increased markedly.

Kohler (1964) performed laboratory feeding experiments with cod in an attempt to interpret field observations on the changing length-at-age. He concluded that temperature increased appetite and food consumption, and hence, finally growth in an unlimited feeding situation. However, apparently due to the indirect affect of temperature and, the small number of experimental animals used, he was unable to demonstrate a significant correlation between temperature and growth. Thus, he dismissed the possibility that variations in water temperature in the Gulf of St. Lawrence can significantly effect the growth rate of 4T cod. In fact, he concluded that "much greater fluctuations in water temperatures (than those observed by Lauzier) would be required to produce growth variations of the magnitude" observed.

Kohler (1964) also compared growth rates with catch/effort statistics from the commercial fishery. He concluded that stock density as a whole and the proportion of cod over 70 cm had an inverse effect on the growth rates of these larger fish presumably because of changing competition for food. The increased availability of food, resulting from an epidemic herring mortality, was postulated as being the major factor producing a marked increase in the growth rates of large cod in the mid-1950's.

Paloheimo and Kohler (1968) analyzed the effect of stock density on the growth rate up to age 6 and, from 6 to 10 years of age. The former correlation was found to be significant at the 5% level while the latter was not. Halliday (1972) also attributed changes in specific growth rates of 6-7 and 7-8 year-olds to changes in stock density as estimated from catch/effort statistics and cohort analysis (Pope 1972).

The purpose of this preliminary communication is to examine changes in growth rates of fish up to age 11, and to determine whether these changes are correlated with the abundance of individual age classes and water temperature over the period from 1949-73.

Methods

Length at age data for 4 to 10 year olds for 1949-1959 were derived from May-October commercial otter trawl data (Kohler 1964: Table 2; and Paloheimo and Kohler 1968: Table 8). A length-weight relationship¹ for each year was calculated by using Kohler's length data, and Paloheimo and Kohler's weight data for age-classes in common. The lengths-at-age for other age groups were then calculated from these equations and Paloheimo and Kohler's weight data.

The length-at-age estimates for 1960-72 were taken from annual summary statistics and for 1972-73 from September survey cruise statistics compiled and kindly provided by Dr. R.G. Halliday.

Large numbers of 4 and 5 year olds were discarded up to and including 1964 (Paloheimo and Kohler 1968; Halliday 1972). Thus, it was deemed necessary to adjust the lengths-at-age measurements for these age classes from 1949-1964. The following assumptions were made: (1) that the size frequency of a particular age class follows a normal distribution (Fig. 1); and (2) that the landed fish in these age classes represents the largest members. The shaded area under the curve in Fig. 1 represents the fraction (L/C) of those fish caught (C) which are actually landed (L). The mean length (\bar{x}) of landed fish will lie at the point which divides this area into 2 equal parts. The area to the left of \bar{x} is equal the area to the left of $\mu + \infty$ in a normal distribution. Hence $\bar{x} = \mu + \infty$. If we know σ (or have an unbiased estimate s) and $(1 - \frac{L}{C} \times 2)^{\infty}$ can be looked up in a table for a cumulative

¹Length data for 1954 were obtained from the mean length weight relationship from 1953 and 1955 and Paloheimo and Kohler's (1968) weight data which they report was based on inadequate sampling.

normal distribution. Then μ can be calculated according to $\mu = \bar{X} - \alpha\sigma$. An estimate, s , of σ was obtained for 1964-72 and 1965-72 for 4 and 5 year olds respectively from Halliday's annual summary statistics. These adjusted lengths were used in all subsequent analyses.

Abundance estimates of each age-class for 1949-73 were made using cohort analysis (Pope 1972). Estimates for 1960-73 were provided by Dr. R.G. Halliday, while those for 1949-59 were calculated by multiplying Paloheimo and Kohler's (1968) catch/effort data (their Table 2) by the units of effort ("Total all years"; their Table 3). An initial $F = 0.50$ for 16+ year-old fish and $M = 0.19$ were assumed.

Grande-Rivière monthly mean temperature (denoted, for example, by T_6 for the mean June temperature in any particular year) data for 1938-1970 are summarized by Boudreault *et al.* (1972); data for 1971-72 were kindly provided by the Quebec government.

Since length-at-age statistics were from May-October samples in 1949-59, from annual summary data in 1960-72, and September survey cruise data in 1972-73 we assumed that these data represented the length for the next age-class at the beginning of the next growing season. Thus, for example, the adjusted sample estimate of the length-at-age 4 in 1949 represents the length of a 4 year-old at the end of the 1949 growing season, which is assumed to be equal to the size of a 5 year-old in June 1950.

The specific growth rate for each age class (5-10) in each year was calculated according to the formula

$$g = \frac{\ln\left(\frac{L_{t_2}}{L_{t_1}}\right)}{t_2 - t_1}$$

where \ln is the natural logarithm. Since length-at-age data for 3 year-olds and younger were not available, the length of a 4 year-old at the end of the first 5 growing seasons (i.e. L_4) was used as a starting point for the calculation of specific growth rates.

Estimates of the number of 3 year-olds (S_3) to 9 year-olds (S_9) and for fish 10 years or older (S_{10+}) were used for the analyses involving specific growth rates and, S_4 to S_{8+} for the analysis of L_4 .

The 4T cod stock has a peak spawning time towards the end of June (Powles 1958; Templeman 1962). This is followed by a feeding period which Wiles and May (1968) found lasts for about 4 months in the northeastern Gulf of St. Lawrence cod stock. Kohler (1964) found that otoliths with opaque edges predominated in the months of June to September, suggesting that the growing season of 4T cod also lasts about 4 months. Hence, June to September mean monthly Grande-Rivière surface temperatures were used as an indicator of the temperature conditions experienced by 4T cod 5 years and older during the feeding season. May temperatures were included for younger fish since they presumably commence feeding earlier (Stanek 1974).

We note in many length-at-age plots that there is a tendency towards an asymptote. Whether this is caused by "aging", or is a function of the maximum size of available food (Kerr 1971) etc. is not known. In any event, it has been widely accepted that the specific growth rate is a function of body size (Parker and Larkin 1959). For this reason, the length of the fish at the beginning of the growing season (L_1) was also considered in the analysis.

Beginning with the 1949 data, we conducted a stepwise multiple linear regression of L_4 against the mean monthly temperature over the 5 preceding growing (i.e. 1949 T_5 temperature was an average July temperature over 1945-1949) seasons for the months of May to September, and against S_4 to S_{8+} . For all other ages $S_3 - S_{10+}$, $T_6 - T_9$, and L_1 were used as independent variables in the analysis of g .

Recognizing the inherent problems discussed by Ricker (1958) and Gulland (1965) concerning correlation analysis involving a large number of independent variables, we adopted the following selection criteria. First, variables were only accepted if they significantly reduced the residual sum of squares about the regression. Second, only the first three variables entering the equation are included. While there is no firm statistical basis for this latter procedure, it seems justified, since it reduces the chance of introducing spurious correlations with independent variables which may pick up some of the residual 'noise'. Analyses affected by this second criterion are identified in Table 3.

¹The maximum adjustment was 5cm for L_4 and 1cm for L_5 .

The introduction of otter trawling had marked effects on the 4T cod stock especially in the late 1950's. The most outstanding effects are the reduction in the proportion of large cod, and the decrease in the biomass of fish 4 years and older. In the late 1960's the stock biomass was about half the level calculated for the early 1950's. For this reason we performed the analysis on the combined data for the 1950-1973 growing seasons, and also separately for the 1950-61 and the 1962-73 periods.

Results

Multiple linear regression equations for the length at the end of the 5th growing season, L_4 , for the 1949-72, 1949-60, and 1961-72 periods, and for the specific growth rates (g_5 to g_{10}) of 5 to 10 year-olds in the 1950-73, 1950-61, and 1962-73 periods are presented in Table 3. The multiple-R values and the degrees of freedom are given for each equation

For comparison, the observed and predicted L_4 (using Equation 1a) are given in Fig. 2. The lengths of 5 thru 10 year-olds at the end of each year have been predicted in 2 ways. First, the observed length at the beginning of the year together with the predicted specific growth rates were used to calculate the length at the end of the growing season; these predicted values are joined by the broken lines in Fig. 3-8. Second, lengths-at-age were predicted using only the predicted L_4 and the predicted $g_5 - g_{10}$ from equations 1a-7a (dashed lines Fig. 3-8). That is, empirical length-at-age data beyond L_4 were not used to predict successive lengths-at-age. In both cases virtual population estimates of stock size and Grande-Rivière monthly mean surface water temperatures were used as independent variables in the model.

Discussion

Correlations between growth rates, temperature and stock abundance have been found for several populations. However, it is probably safe to say that there are as many or more examples of a lack of such correlations. Thus, the objectives of this study were two fold. Firstly, we wished to determine whether or not such correlations do exist for the 4T cod stock. Secondly, we wished to identify the relative importance of temperature and stock density, before and after the introduction of otter trawling.

In this preliminary communication we will not attempt to explain the derived equations in detail. Moreover, while we acknowledge that none of the correlations discussed here are beyond question, we feel that a reasonable biological explanation can be given for the majority of variables which enter the equations.

Of the regression equations (1a-7a) describing the period from 1949-1973, 4 were found to be highly significant, while 2 were almost significant at the 5% level. The R-value for the remaining equation (2a) was non-significant.

It is instructive to compare the equation describing the entire 24 year period with those describing the first 12 and last 12 years. First, perhaps we can generalize by saying that from 1950-61 temperature, and more specifically mean July temperature, appears to be the most important factor determining the growth rate of 5 to 10 year-olds.² In the most recent period, however, the stock density becomes a more important factor for 5 to 8 year-olds, while the initial size of 9 and 10 year-olds becomes the single most important variable. The increased significance of stock size and length of a fish is perhaps attributable to effects of the fishery not only on the size structure of the 4T cod population, but also on other fish populations such as herring which are of major importance in the diet of large cod (Powles 1958; Kohler and Fitzgerald 1969; among others).

A comparison between the empirical length-at-age data and the predicted values joined by the dashed line in Fig. 2 and the broken lines in Fig. 3-8 shows few serious discrepancies. The possible exception to this is for L_9 from 1954 to 1957.

A similar comparison between the empirical length-at-age data and the predicted values joined by the broken lines in Fig. 3-8 indicates generally good correspondence except from 1955-58. This disparity may be due to the mass herring mortality discussed by Kohler (1964). In any event, considering the large number of potential sources of variation in growth and sources of error in our measurements, the good fit for 10 year-olds is encouraging since older age-classes undergo greater fluctuations in length than younger ones.

²The absence of a temperature effect in equations 1b and 1c for L_4 is perhaps due to the averaging over 5 years; some weighting for different growing seasons might have been desirable to emphasize the importance of the first couple of years of growth.

Summary

1) Temperature, stock density and the size of a fish have been shown to be correlated with growth rate. Further, these factors can change in their importance due perhaps to such things as a change in the intensity and selection of the fishery.

2) Lengths-at-age for 4 through 10 year-old cod were predicted in two ways. First, the empirical length at time t was used in conjunction with predicted specific growth rates to predict the length a year later ($t + 1$). Second, predicted lengths at the end of the fifth growing season (L_4) and predicted specific growth rates were used to calculate subsequent lengths-at-age.

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Table 1 - Von Bertalanffy growth parameters by sampling year for the 4T cod stock. Parameters computed on 4 to 10 year-olds.

Sampling Year	K	L_{∞}	t_0
1949	0.07	130	-2.45
1950	0.08	102	-3.73
1951	0.10	103	-1.88
1952	0.19	82	-0.42
1953	0.29	80	1.24
1954	0.28	74	0.85
1955	0.06	159	-2.58
1956	0.12	119	-0.06
1957	0.07	152	-1.30
1958	0.09	123	-0.95
1959	0.11	106	-0.56
1960	0.14	98	-0.01
1961	0.07	153	-0.58
1962	0.06	154	-0.42
1963	0.06	153	-0.25
1964	0.06	156	-0.60
1965	0.05	135	-3.78
1966	0.05	139	-3.71
1967	0.06	134	-3.11
1968	0.07	133	-1.65
1969	0.05	153	-3.45
1970	0.06	158	-0.54
1971	0.06	156	-1.13
1972	0.06	160	-0.87
Min	0.05	74	
Max	0.29	160	

Table 2 - Von Bertalanffy growth parameters by year-class for the 4T cod stock. Parameters computed on 4 to 10 year-olds.

Year Class	K	L_{∞}	t_0
1945	0.05	154	-2.75
1946	0.06	166	-1.15
1947	0.07	164	-0.77
1948	0.15	107	0.43
1949	0.42	77	2.29
1950	0.34	77	1.47
1951	0.05	143	-4.90
1952	0.05	154	-2.49
1953	0.05	152	-2.70
1954	0.05	156	-1.49
1955	0.05	135	-4.36
1956	0.05	139	-2.91
1957	0.08	143	-1.80
1958	0.07	147	-0.23
1959	0.06	136	-1.54
1960	0.07	158	-0.43
1961	0.06	156	-1.22
1962	0.06	160	-1.35
Min	0.05	77	
Max	0.42	166	

Table 3 - Multiple linear regression equations for the length at the end of the 5th growing season (L_5) and the specific growth rates of 5 to 10 year-olds (g_5 to g_{10}). The independent variables are listed in the order of importance.

Y	Years Used	Equation $Y =$	d.f.	R	Equation Number
L_5 end	1949-72	$26.5495 - 6.153*10^{-5}S_6 + 1.364 T_7 + 4.501*10^{-5}S_{6a}$	20	** 0.730	1a
	1949-60 ^b	$55.56 - 5.246*10^{-5}S_4 - 1.129*10^{-6}S_6 - 7.951*10^{-5}S_{6a}$	8	** 0.913	1b
	1961-72	$43.35 - 8.934*10^{-5}S_7 - 1.869*10^{-5}S_5$	9	0.896	1c
g_5	1950-73	$0.0411 - 1.675*10^{-6}S_8 + 6.889*10^{-3}T_8$	21	0.384	2a
	1950-61 ^b	$- 0.0093 + 1.024*10^{-2}T_7 + 1.737*10^{-6}S_7 - 2.954*10^{-7}S_4$	8	0.577	2b
	1962-73	$0.0599 - 1.552*10^{-6}S_7 + 7.667*10^{-3}T_8 - 5.217*10^{-7}S_4$	8	0.727	2c
g_6	1950-73 ^b	$- 0.1209 + 8.965*10^{-3}T_8 + 1.277*10^{-2}T_6 - 7.752*10^{-7}S_7$	20	** 0.547	3a
	1950-61	$- 0.2442 + 1.627*10^{-2}T_7 + 3.051*10^{-6}S_8 + 1.239*10^{-2}T_6$	8	0.823	3b
	1962-73 ^b	$0.2574 - 1.256*10^{-6}S_7 - 4.043*10^{-6}S_9 - 8.287*10^{-3}T_7$	8	** 0.751	3c
g_7	1950-73	$- 0.1185 + 6.121*10^{-3}T_7 - 1.442*10^{-6}S_7 + 1.657*10^{-2}T_6$	20	** 0.543	4a
	1950-61 ^b	$- 0.0018 + 2.890*10^{-2}T_7 - 2.354*10^{-2}T_9 - 5.930*10^{-7}S_5$	8	0.822	4b
	1962-73	$- 0.2703 - 2.439*10^{-6}S_7 + 3.791*10^{-2}T_9$	9	** 0.903	4c
g_8	1950-73	$0.2432 - 9.620*10^{-6}S_9 - 8.408*10^{-7}S_4 - 9.961*10^{-7}S_6$	20	** 0.660	5a
	1950-61 ^b	$0.0153 + 1.690*10^{-2}T_7 - 4.986*10^{-2}T_9 + 2.865*10^{-2}T_8$	8	** 0.764	5b
	1962-73	$0.1635 - 5.295*10^{-6}S_8$	10	0.678	5c
g_9	1950-73	$0.5898 - 7.761*10^{-3}L_1 - 3.256*10^{-6}S_9$	21	** 0.631	6a
	1950-61	$- 0.2115 + 2.105*10^{-2}T_7$	10	** 0.461	6b
	1962-73 ^b	$0.9580 - 1.322*10^{-2}L_1 - 1.374*10^{-5}S_9 + 8.549*10^{-7}S_6$	8	** 0.936	6c
g_{10}	1950-73	$0.5909 - 7.561*10^{-3}L_1 - 2.225*10^{-6}S_{10a} + 2.536*10^{-6}S_8$	20	** 0.673	7a
	1950-61	$- 0.2999 + 2.679*10^{-2}T_7$	10	0.650	7b
	1962-73	$0.7908 - 5.676*10^{-3}L_1 - 2.861*10^{-2}T_9$	9	0.501	7c

* significant at the 5% level

** significant at the 1% level

∞ almost significant at the 5% level

b only the first 3 variables were entered into the equation

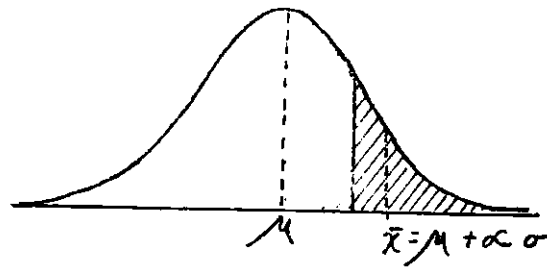


Fig. 1. Normal population size frequency distribution. The shaded area represents the size frequency of landed fish (L) with mean $\bar{x} = \mu + \alpha \sigma$ where μ is the mean size of fish caught (C).

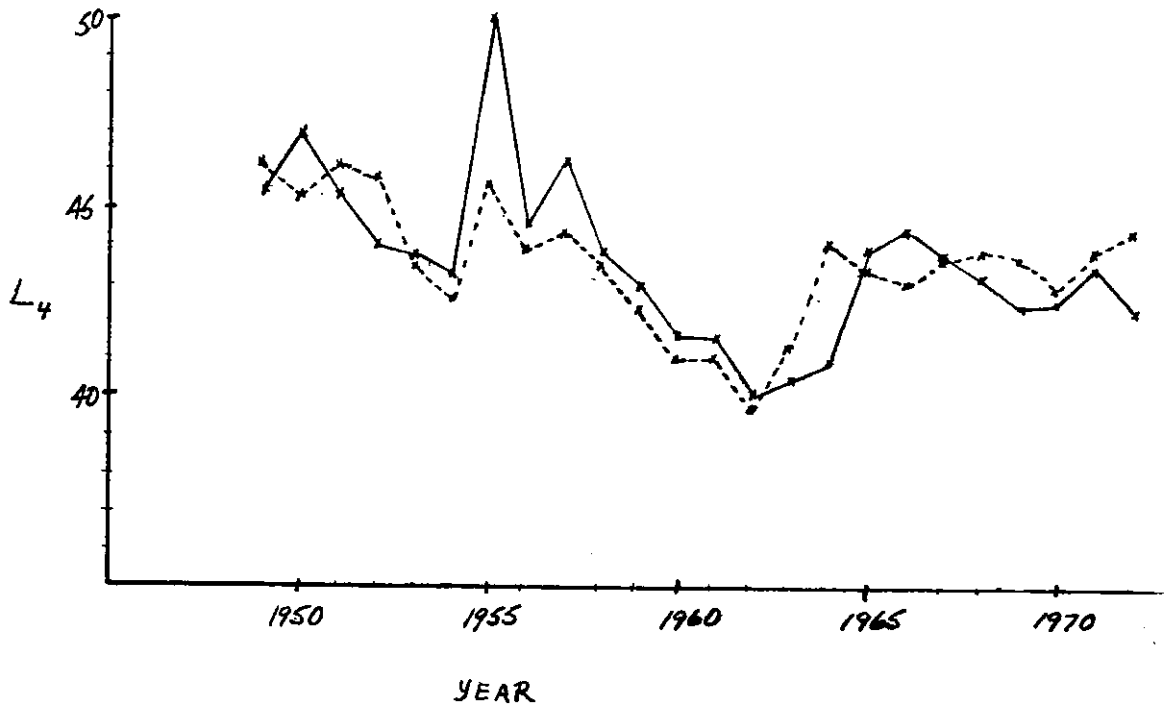


Fig. 2. A comparison of observed L_4 (solid line) and L_4 predicted from equation 1a (dashed line).

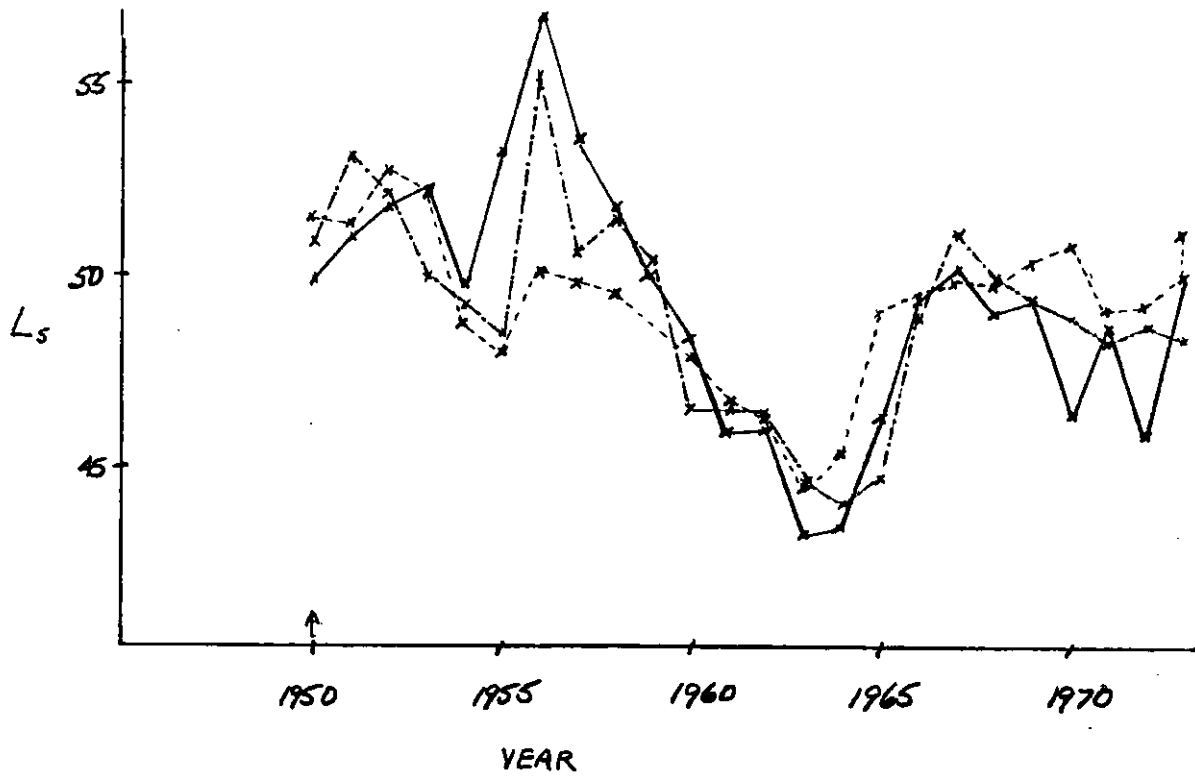


Fig. 3. A comparison of observed L_5 (solid line), L_5 predicted from equation 2a and the observed L_4 (broken line), and L_5 predicted from equation 2a and the predicted L_4 (dashed line) in Fig. 2.

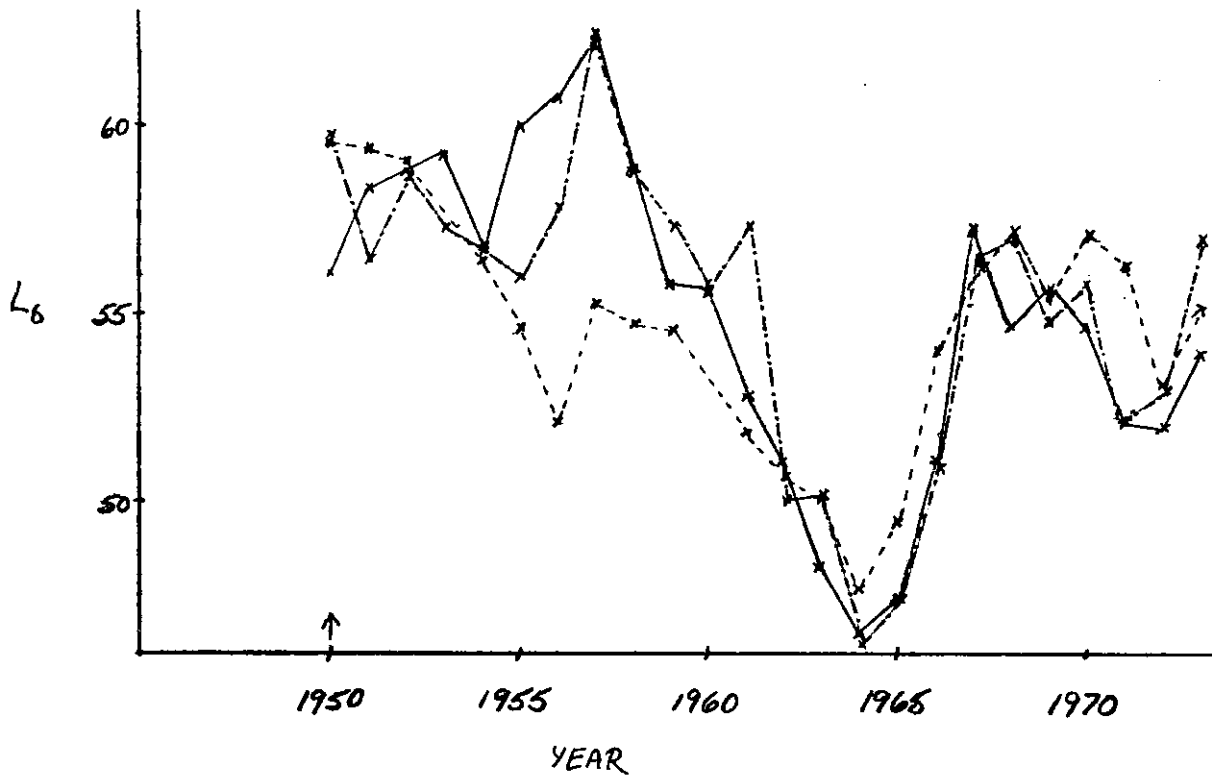


Fig. 4. A comparison of observed L_6 (solid line), L_6 predicted from equation 3a and the observed L_5 (broken line), and L_6 predicted from equation 3a and the predicted L_5 (dashed line) in Fig. 3.

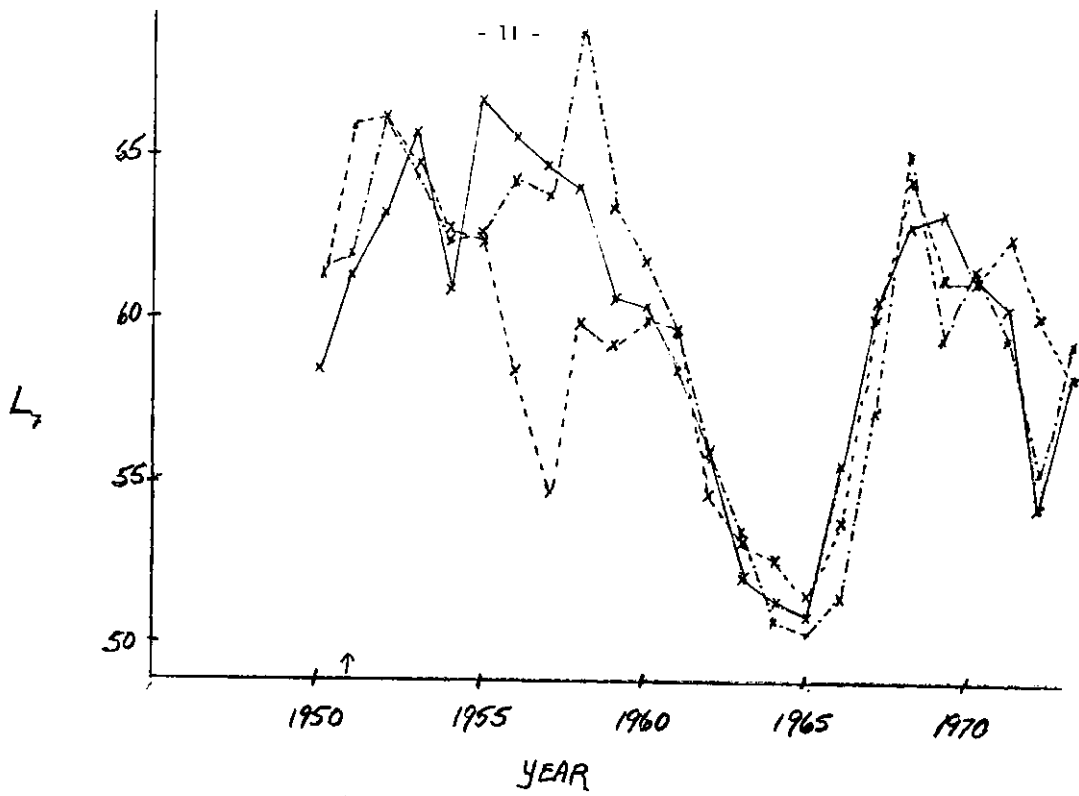


Fig. 5. A comparison of observed L_7 (solid line), L_7 predicted from equation 4a and the observed L_6 (broken line), and L_7 predicted from equation 4a and the predicted L_6 (dashed line) in Fig. 4.

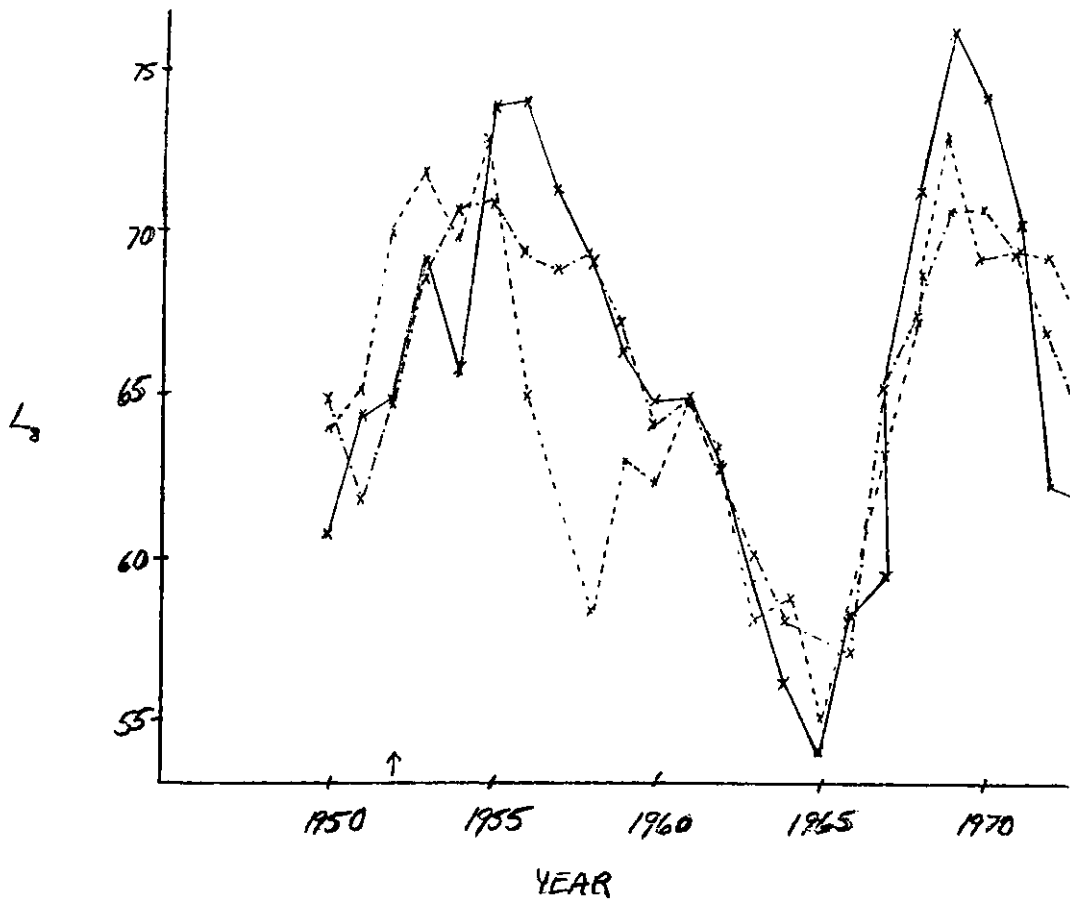


Fig. 6. A comparison of observed L_8 (solid line), L_8 predicted from equation 5a and the observed L_7 (broken line), and L_8 predicted from equation 5a and the predicted L_7 (dashed line) in Fig. 5.

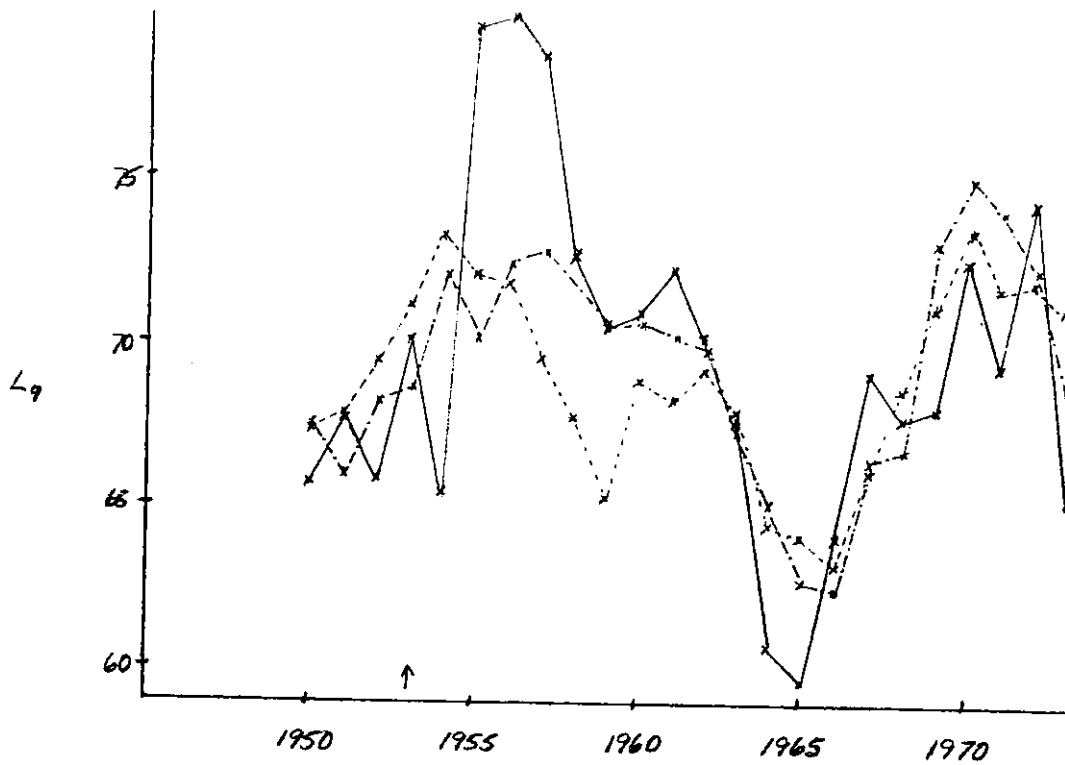


Fig. 7. A comparison of observed L_9 (solid line), L_9 predicted from equation 6a and the observed L_8 (broken line), and L_8 predicted from equation 6a and the predicted L_8 (dashed line) in Fig. 6.

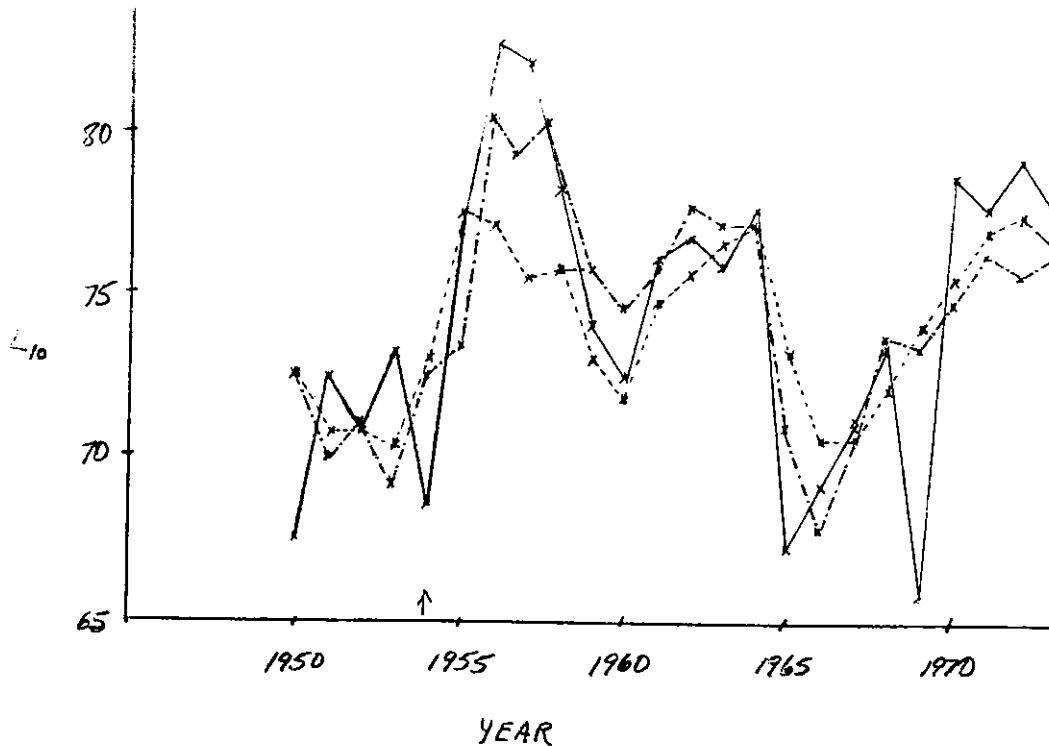


Fig. 8. A comparison of observed L_{10} (solid line), L_{10} predicted from equation 7a and the observed L_9 (broken line), and L_9 predicted from equation 7a and the predicted L_9 (dashed line) in Fig. 7.