

An Analysis of Growth and Maturation of the
4WX Herring Management Unit

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INTRODUCTION

An understanding of the controlling factors of growth and the age at maturity in exploited fish populations is of both fundamental and applied interest. The MSY models used in managing fish stocks assume that there are mechanisms by which the species adjust their population parameters in response to their abundance, i.e., "density-dependent" mechanisms. In this respect, "density dependent" changes in growth rates at various life history phases, and changes in age or length at maturity have been documented for several stocks. However, evidence for density-dependent growth and maturation in pelagic stocks is contradictory. The aim of this study is to analyze the accumulated data base on the 4WX herring management unit, with particular reference to growth and maturity. Since it is assumed that the juvenile distribution does not significantly overlap with the adults, the juveniles are considered separately from the adults in the analysis of density dependence. Given the proximity in the distribution of adults and juveniles of the 4WX stock during the summer months this assumption, however, may be questionable. Following the description of growth and maturation some implications on assessment methodology are addressed.

METHODS

The methods used to estimate mean lengths and weights at age for a given month and gear type, as well as for the estimation of lengths at 50% maturity, are described in Sinclair et al. (1980).

Population and cohort annual production were estimated from the yearly (July to July) increase in weight. Mean weights were calculated from 4Xa weir and purse seine mean weights weighted by numbers removed. Cohort production is

$$p_i = (w_i - w_{i-1}) \cdot N_i$$

where p_i = production by cohort at age i
 w_i = July weight at age i herring
 w_{i-1} = July weight of age $i-1$ herring
 N_i = cohort abundance at age i , January 1st.

Population annual production is

$$P = \sum_{i=3}^{10} p_i = \sum_{i=3}^{10} (w_i - w_{i-1}) \cdot N_i$$

Thus P includes growth from age 2 to 3, as well as that for the older ages.

The average biomass of a cohort (b_i) within the July to July period was estimated by the equation

$$b_i = \frac{w_i + w_{i-1}}{2} \cdot N_i$$

and the average population biomass (B) by

$$B = \sum_{i=3}^{10} b_i = \sum_{i=3}^{10} \frac{w_i + w_{i-1}}{2} \cdot N_i$$

Annual growth rate of a cohort at age i [$g_i = w^{-1}(dw/dt)$]

was estimated by $\Delta w/\bar{w}$ or

$$g_i = \frac{2(w_i - w_{i-1})}{w_i + w_{i-1}}$$

Ricker (1975) defines the above estimate as "relative growth rate".

Population growth rate (G) was estimated by P/B.

It is to be noted that only somatic growth is considered in the above definitions. Since there is no time series data on gonad weights for this stock (4WX herring), production of sexual products cannot be considered.

RESULTS

I. Juvenile Summer Growth

In Sinclair et al. (1980), it was observed that there was a marked change in the early 1970's in the relationship between summer increase in length (May to September) and initial length. In addition, there

was some indication that the summer length increment, when corrected for the length dependent bias (Iles 1967), was inversely related to juvenile population abundance, but unrelated to summer temperature. It is of interest, and consistent with the following treatment of adult growth, to consider the summer growth of two-year-olds in weight rather than length. The following equation was used:

$$\Delta W = aW^b e^{-cP} e^{dT}$$

where ΔW = summer growth increment (in grams)
 W = initial body weight in May (in grams)
 P = 'competing' population density
 T = summer temperature ($^{\circ}\text{C}$)

The equation assumes that the growth increment for a particular year-class is a function of initial body size, water temperature and year-class abundance. Since the two-year-old juveniles co-exist with a large part of the preceding three-year-old cohort (approximately one-third of the three-year-olds recruit to the adult population) and the frequency of good year classes have decreased with time (Sinclair et al. 1979), it was thought appropriate to consider the potentially competing population density (P_2 , abundance of two-year-olds plus two-thirds of three-year-olds) as well as the abundance of the year-class at age 2 (P_1). As mentioned above, appropriate mean weights by month for the early arriving two-year-olds are not available. The ΔW and W values were estimated from the length data using the following length-weight relationships:

$$W = 0.0042 L^{3.23} \quad (\text{May})$$

$$W = 0.00290 L^{3.30} \quad (\text{September})$$

The constants for the length-weight relationships are the means of the values estimated from the detailed biological samples from the New Brunswick weir fishery in 1977 and 1978. The complete data set used in the analysis is shown in Table 1.

The transformation for estimating the constants by linear regression is:

$$\ln(\Delta W) = \ln a + b(\ln W) + cP + dT$$

The correlation coefficients between summer growth (ΔW) and the independent variables (W , P_1 , P_2 , T), as well as the multiple regression statistics, are shown in Table 2. Although not significant at the 5% level, P_2 is better correlated (negatively) with summer growth than is P_1 (year class size). Temperature is not strongly correlated with summer growth, but the sign is in the expected direction. The multiple regression, in which P_2 is the population density variable, has an R^2 of only .269. The results of the analysis indicate that (when all years are considered) initial weight, population density and temperature do not explain a large part of the variance in summer growth. No doubt the change in the growth pattern that was observed in Sinclair et al (1980), which may be due to a change in the population composition in the juvenile weir fishery, complicates the analysis.

When a dummy variable is added to the regression analysis to account for the suggested discontinuous growth pattern in time, there is a considerable increase in the R^2 value from 26.9 to 76.8 (Table 2). In this analysis, the regression equation takes the form,

$$\ln(\Delta W) = \ln a + b(\ln W) + cP + dT + eD$$

where D is the dummy variable.

The dummy array was as follows:

65	66	67	68	69	70	71	72	73	74	75	76	77	78
0	0	1	0	0	0	1	1	1	1	1	1	1	1

Nevertheless, the analysis supports certain aspects of the previous approach in Sinclair, et al. (1980): suggestion of density dependence in juvenile growth, the lack of importance of temperature, and the effect of initial size on growth.

II. Annual Growth Rates at Age

Reliable data on mean length and mean weights at age are only available from 1968 to the present for herring caught on the Nova Scotia side of the Bay of Fundy. Mean lengths and weight for ages 2 to 10 from weirs and purse seines were weighted by removals at age to provide overall means (Table 3 and Figure 1). Since July was the month for which the

data is most complete, annual growth rates were calculated from July to July (see methods section). The estimates of biomass, production, and growth rate (P/B) are shown in Table 4.

The somatic growth rate declines rapidly with age, close to an order of magnitude between ages 2 and 6 (Figure 2). Also, the year-to-year variability in growth rate, in absolute terms, declines in a parallel fashion. Thus it appears that growth is more sensitive to environmental and population control during the juvenile phase.

Figure 3 shows a parallel distribution of population growth rate (P/B) and population biomass. This demonstrates that for non-steady state populations such as herring, population growth rate is directly related to population biomass. The greater the stock size, the higher the growth rate. This is clearly an age composition effect. The population biomass is at its largest when strong year classes are recruiting to the fishery. At such times, the population is dominated by younger fish with higher growth rates. For example, the growth rate of two-year-old herring is approximately 10 times that of six-year-olds (Figure 2). Because of this strong age composition effect on population growth rate, it is not a surprise that there is a significant relationship with population abundance (Figure 4a). The points for 1976-77 and 77-78 were not included in the calculation of R^2 because of the possible error in the estimation of population numbers obtained from the most recent years in the cohort analysis.

A plot of recruited population growth rate (5+) versus recruited population numbers (5+), which minimizes the age composition effect, also indicates a positive relationship (Figure 4b). To further investigate the importance of population abundance on growth rate, individual ages were considered (Figure 5). The analysis suggests that for intermediate ages, there is a dome-shaped relationship between growth rate and cohort size. The exceptionally large 1970 year class has a relatively depressed growth rate at intermediate ages. As this cohort decreases in abundance, by age 6 to 7, the relationship appears more asymptotic. Thus, overall, there is an unexpected positive relationship between somatic growth and population abundance.

III. Maturation

In Sinclair et al. (1980), a sharp decrease in length at 50% maturity was observed in the early 1970's. Also, there was evidence for a positive relationship between length at recruitment and length at 50% maturity. The relationship between length at recruitment and "population" size during juvenile growth (abundance of juveniles, age 2 plus 2/3 of age 3 cohorts, during the previous year) is complex (Figure 6). Over a broad range in population size, there is a decrease in length at recruitment with increasing cohort size suggesting density dependence. It is possible, however, that changes in the fishery pattern could have a similar effect. If there is a corresponding decrease in mean length at age 3 with increasing cohort size over the same population range, then the age at 50% maturity would be relatively constant. The results of the analysis of maturity by age (Figure 7) tend to support this, the herring in this stock being completely immature

at age 2 and almost completely mature by age 4. However, since the maturity ogives are based on two or, at most, three points, little confidence can be placed on the estimates of age of 50% maturity.

The two most recent year classes, 1974 and 1975, for which the maturing year classes were exceptionally small, recruited and matured at a relatively small length. Since the mean length at age 3 was small for these years, it is again indicated that the age at maturation did not shift downwards. The relationship between length at 50% maturity (ignoring the 1969 point) and juvenile population abundance supports the above arguments (Figure 8). The decrease in length at age 3, length at recruitment, and length at 50% maturity for the extremely small year classes is an unexpected result. It suggests that below some critical population level, the density dependent processes do not function.

IV. Biomass, Production and Catch

The temporal distributions of biomass, somatic production, and catch are shown in Figure 9. Production as well as catch are calculated from July to July. The catch is that taken in the 4WXa fishery plus 30% of the New Brunswick weir catch (to be consistent with the cohort analysis numbers at age estimates, which are used in calculation of production). The catch includes age 2+ fish from August to December and age 3+ from January to July. Two estimates of 3+ population biomass are indicated, that on January 1 and the remaining biomass of the same year classes on December 31. Thus, for the production and catch year 1968-69, the biomass estimates are for January 1, 1969 and December 31, 1969. The difference

between the January and December biomass estimates is due to the decrease in biomass from mortality (both fishing and natural) less the increase in biomass from production. The increase in biomass shown between December 31 of one year and January 1 of the next is the result of recruitment at age 3. Thus, it can be seen that at age 3, the 1970 year-class added 280,000 t to the population biomass.

Catch has exceeded production during two periods, from 1969-70 to 1971-72 and from 1977-78 to the present. In the former period, stock biomass was reduced sharply through a period of average recruitment. During this time period, the difference between January 1 and December 31 biomass was close to 150,000 t. The appearance of the strong 1970 year-class increased biomass and production, but not as high as the 1970 level. During this interval, production was greater than catch until 1976-77. Very poor recruitment in the two following years caused production to fall to 50,000 t, while the catch remained at 100,000 t. Biomass on January 1, 1978 was estimated to be 244,000 t and given that the 1978 catch was twice that of the estimated production, the December 31, 1978 biomass was likely to be in the region of 125,000 t, a critically and historically low level. However, current indications are that the 1976 year-class is large, and thus stock biomass will be on another upward swing.

It is possible that the relationship between production and catch for herring may be a useful criteria for management purposes. For example, when the $F_{0.1}$ catch exceeds production, this guideline could be replaced by a "surplus production" guideline.

SUMMARY OF RESULTS AND DISCUSSION

The following points summarize the results:

1. Juvenile summer growth (age 2) does not appear to be affected significantly by temperature but there is some evidence for density dependence in growth.
2. Length at maturity and at recruitment to the adult schools appears to be inversely related to the population density experienced during juvenile growth. However, at very low juvenile population size, growth appears to be inhibited. Maturity at age appears to be fixed within narrow limits.
3. Somatic growth rate and its year-to-year variability decreases by close to an order of magnitude with the onset of maturation. Because of this decrease with age and the radical shifts in age composition with time, population growth rate fluctuates markedly.
4. Since high population abundance parallels downwards shifts in age composition, there is a clear and expected positive relationship between population growth rate and population abundance.
5. There is a dome-shaped relationship between age specific somatic growth rate and cohort size at intermediate ages. This suggests that over a broad range in population size, adult growth rate is not density dependent. In contrast, it suggests that within limits, increasing population size enhances growth rate.

The growth and maturity results are of fundamental interest. There are contradictions in the literature concerning the existence of density dependent growth and maturation in both juvenile and adult herring. Iles (1967), Anthony (1971), Lett and Kohler (1976) and Hubold (1978) have shown evidence for density dependence in juvenile growth. Moores and Winters (1978) do not observe density dependent l_1 length for Gulf of St. Lawrence herring using the same data as Lett and Kohler (1976) and suggest that the latter study used faulty criteria in the interpretation of the raw data. Again, Lett and Kohler (1976) and Winters (1976) arrive at opposite conclusions concerning density dependent growth of adult herring in the southern Gulf of St. Lawrence. Lett and Kohler (1976) find no evidence, whereas Winters (1976) concludes there is density dependence. Lett (1978) argues correctly that Winters' (1976) conclusions are invalid since they are based on mean lengths and weights at age in relation to population biomass and not on growth rate. Iles (1971) shows some evidence for adult density dependent growth for North Sea herring but all the other studies on North Sea adult herring growth (Wood, 1965; Cushing and Burd, 1957; Hubold, 1978; Burd, 1978; Saville, 1978) do not directly address the problem of growth rate-at-age in relation to cohort size. Grosslein et al. (1978) concludes that there is no evidence for density dependent growth by Georges Bank adult herring. If anything, there appeared to be increased growth associated with larger year classes (Dornheim, 1976).

There is less information concerning shifts in maturation at length or at age for Atlantic herring. Winters (1976) indicates a downwards

shift in the age at 50% maturity for both spring and autumn spawners as the adult population biomass decreased (3.8 to 3.5 for spring and 5.9 to 5.2 for autumn). Hubold (1978) shows some evidence for similar shifts in maturity at age for North Sea herring. Parrish and Saville (1965) report the decrease in age of maturity for North Sea herring in the early 1950's. Lett (1978) found no evidence for shift in either length at maturity or age at maturity for mackerel in the Gulf of St. Lawrence and goes as far as to suggest that "the ability to shift their maturity ogive in relation to length is a basic difference between pelagic and demersal fish".

In summary, there appears to be some coherence in the observations on juvenile density dependent growth (with the exception of Moores and Winters, 1978) but contradictions in the literature on adult growth. This is partly due to the looseness in growth terminology. Changes in length or weight at age are frequently used in arguments concerning growth in relation to population density.

The results of this study tend to confirm the conclusions concerning juvenile growth but differ in the other two aspects (adult growth and maturation). Length at recruitment to the adult population and length at 50% maturity fluctuate in a density dependent fashion in response to the juvenile population size that was experienced. This results, however, in a relatively fixed maturity at age schedule in contrast to conclusions of Winters (1976) and Hubold (1978), but in partial agreement with Lett's hypothesis.

The unexpected result was the evidence for positive relationship between somatic growth rate of adults and cohort density, as was found by Dornheim (1976) for Georges Bank herring. For a schooling fish in a patchy environment, this may be interpreted in energetic terms. If the overall abundance of food for adult herring is non-limiting, but distributed in patches, and herring school size increases with cohort abundance, then it is possible that at increasing population density, the overall food abundance is more efficiently located (more patches of food per day are found when the schools are larger) (Mackay 1976). This interpretation of the observations assumes that there are behavioral mechanisms involved in schooling so that the information concerning the location of a food patch is passed between individuals and that the patch sizes are large enough so that the increased location of patches per day, for example, is not negated by the decrease in individual food consumption per day due to the increase in fish per school. Clearly, the interpretation is speculative but it is attractive in that it provides an energetic explanation for the evolutionary advantage of schooling.

The rapid decline in somatic growth rate of herring with age causes population production to decrease sharply when several recruiting year classes in a row are weak. This characteristic of herring populations may have serious implications on the use of the dynamic-pool models for this species. These models assume steady state conditions with resultant stable age composition. Following this assumption, annual population production is equal to the sum of the annual productions of a single cohort over its entire life. Annual MSY can then be estimated by analyzing the maximum yield that can be taken from a single cohort's production as it passes through the fishery.

When the stable age composition assumption is seriously in error (biased towards older ages), coupled with rapid decrease in somatic growth rate in the case of herring, the annual production of the population is no longer equal to the production of a single cohort throughout its life. In fact, it is much lower. Thus the F_{MSY} and even the more conservative $F_{0.1}$ generated TAC's may be inappropriate. This appears to be what we are seeing in Figure 9. The catches generated from $F_{0.1}$ TAC's can exceed population production when the age composition is biased towards older fish.

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Table 1. Weight, population abundance and temperature data used in the growth analysis

Year	Weight increment (gm)	Initial Weight (gm)	Abundance estimate $1(P_1)$ ($\times 10^{-9}$)	Abundance estimate $2(P_2)$ ($\times 10^{-9}$)	Tempsum ($^{\circ}\text{C}$)
1965	10.67	16.75	4.53	5.31	49.6
1966	15.99	12.69	2.76	4.43	50.6
1967	17.66	18.99	2.21	3.15	47.7
1968	9.11	15.97	4.71	5.51	54.0
1969	17.26	13.76	1.04	2.03	56.0
1970	14.98	14.17	1.46	1.79	58.1
1971	18.36	19.55	1.24	1.63	59.3
1972	16.79	31.32	5.50	5.91	54.9
1973	18.15	18.36	0.96	3.46	55.3
1974	25.88	18.40	1.83	2.25	54.8
1975	24.32	18.86	1.61	2.20	52.3
1976	19.25	23.55	0.22	0.85	64.0
1977	26.65	14.55	0.56	0.62	53.9
1978	27.33	16.17	5.11	5.27	56.2

Table 2. Correlation coefficients and multiple regression coefficients from the growth analysis

Correlations

	<u>Initial Weight (lnw)</u>	<u>Abundance Estimate 1 (P₁)</u>	<u>Abundance Estimate 2 (P₂)</u>	<u>Temperature (T)</u>
Weight Increment (lnΔw)	0.09	-0.39	-0.49	0.20

Multiple Regression

dependent variable - lnΔw
independent variable - lnw, P, T

<u>Variable</u>	<u>Coefficient</u>	<u>Standard Error</u>	<u>T-value</u>	<u>Variation</u>
lnw	0.272	0.404	0.67	2.6
P ₂	-0.100	0.056	-1.77	23.5
T	-0.00843	0.253	0.33	0.8
Intercept =	2.882			
R ² (%) =	26.9			

dependent variable - lnΔw
independent variable - lnw, P, T, dummy

lnw	-0.781	0.339	-2.30	21.2
P ₂	-0.013	0.039	-0.35	1.4
T	0.007	0.016	0.48	0.6
Dummy	0.675	0.154	4.39	53.6
Intercept =	4.32			
R ² (%) =	76.8			

Table 3. Estimated mean weights and lengths
at age in July for the 4XW stock

WEIGHT (GM)											21/11/79
	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
2	32.7	37.2	31.7	36.1	44.3	28.8	47.7	20.8	32.7	65.2	28.3
3	33.0	105.5	119.2	142.6	137.6	105.7	110.2	94.3	114.1	113.8	112.1
4	143.0	162.3	168.7	199.1	192.2	143.3	175.4	179.0	169.1	174.2	130.3
5	184.6	207.2	210.6	230.1	224.5	224.6	206.6	215.6	233.4	213.7	228.6
6	244.4	241.8	256.8	253.6	262.0	251.5	239.9	239.6	249.4	274.2	258.6
7	275.7	282.0	292.2	292.7	291.5	279.1	277.2	267.5	277.2	293.0	302.1
8	299.0	305.9	332.0	328.8	321.7	331.2	322.1	333.2	317.3	325.3	330.2
9	337.8	333.7	368.6	362.0	345.0	359.9	342.4	357.8	382.4	328.1	351.0
10	409.5	390.4	389.3	387.7	380.4	388.9	352.0	379.0	404.2	415.7	397.1

LENGTH (CM)											21/11/79
	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
2	15.7	17.6	16.6	22.8	18.4	16.3	19.0	14.8	16.9	19.9	15.6
3	22.2	24.2	25.2	26.7	26.3	24.2	24.5	23.2	24.8	24.2	23.9
4	26.9	27.7	28.1	29.5	29.2	27.0	28.4	28.6	28.0	27.5	27.9
5	28.8	29.9	30.0	30.9	30.7	30.7	29.9	30.3	31.0	29.4	30.0
6	31.5	31.3	32.0	32.3	32.2	31.8	31.3	31.3	31.7	31.9	31.2
7	32.7	32.8	33.3	33.3	33.3	32.8	30.9	32.3	32.7	32.6	32.7
8	33.5	33.7	34.7	34.5	34.3	34.6	34.3	34.7	34.2	33.8	33.7
9	34.3	34.7	35.8	35.6	35.0	35.5	35.0	35.5	35.2	33.6	34.6
10	39.6	35.9	36.4	36.3	36.1	36.3	35.2	36.1	36.8	36.6	35.6

Table 4. Biomass, production and growth rate estimates
for the 4WX stock

PRODUCTION (T)										
21/11/79										
	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
3	108312	39899	54610	31078	229638	51516	41372	89099	6923	11376
4	60934	44834	26082	14933	4785	173456	29890	40763	35700	2119
5	42932	24431	19547	4283	3510	14256	59138	15216	14521	16314
6	29970	22062	12330	5003	1810	380	5064	28826	6339	7582
7	10956	16378	9129	3390	1020	813	919	2980	21553	2124
8	3302	9013	6007	3557	2176	1346	1038	930	2275	10013
9	1450	4516	3300	1439	2141	324	743	590	109	973
10	671	1579	756	1046	2152	221	503	641	216	417
TOT	258628	162711	141762	64728	247232	242369	139166	179046	87737	50923

BIOMASS (T)										
21/11/79										
	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
3	102907	38050	50774	67497	280503	43985	63341	64413	6091	21503
4	94322	97258	51951	50312	61173	349774	63527	72392	85627	5119
5	128947	94311	63479	35715	22653	43827	287501	56498	62317	60399
6	111705	103191	55159	38536	15958	13365	34236	198283	39434	39876
7	76692	86766	69869	33724	16135	8360	8448	20482	134687	21933
8	33047	55339	50964	37631	17064	9407	5655	5413	14251	83875
9	13223	24246	38173	29916	19100	9737	7073	4291	3407	9400
10	4646	10267	14977	21100	17991	9039	4655	5259	2534	2139
TOT	555390	509428	395346	314531	450573	483393	474837	427036	348393	244296

GROWTH RATE (P/E)										
21/11/79										
	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
3	1.0535	1.0485	1.2725	0.4604	0.8187	1.1712	0.6611	1.3832	1.1366	0.5290
4	0.6466	0.4610	0.5020	0.2963	0.0782	0.4959	0.4705	0.5621	0.4169	0.4109
5	0.3333	0.2591	0.3079	0.1199	0.1550	0.3253	0.3056	0.2693	0.2330	0.2701
6	0.2683	0.2133	0.2235	0.1296	0.1134	0.0659	0.1473	0.1454	0.1608	0.1901
7	0.1429	0.1888	0.1307	0.1005	0.0632	0.0972	0.1033	0.1455	0.1602	0.0963
8	0.0099	0.1629	0.1179	0.0944	0.1275	0.1430	0.1635	0.1719	0.1597	0.1194
9	0.1007	0.1862	0.0865	0.0431	0.1121	0.0333	0.1050	0.1375	0.0319	0.1040
10	0.1445	0.1538	0.0505	0.0496	0.1196	0.0222	0.1015	0.1218	0.0834	0.1903
TOT	0.4674	0.3194	0.3586	0.2056	0.5497	0.4963	0.2031	0.4193	0.2512	0.2034

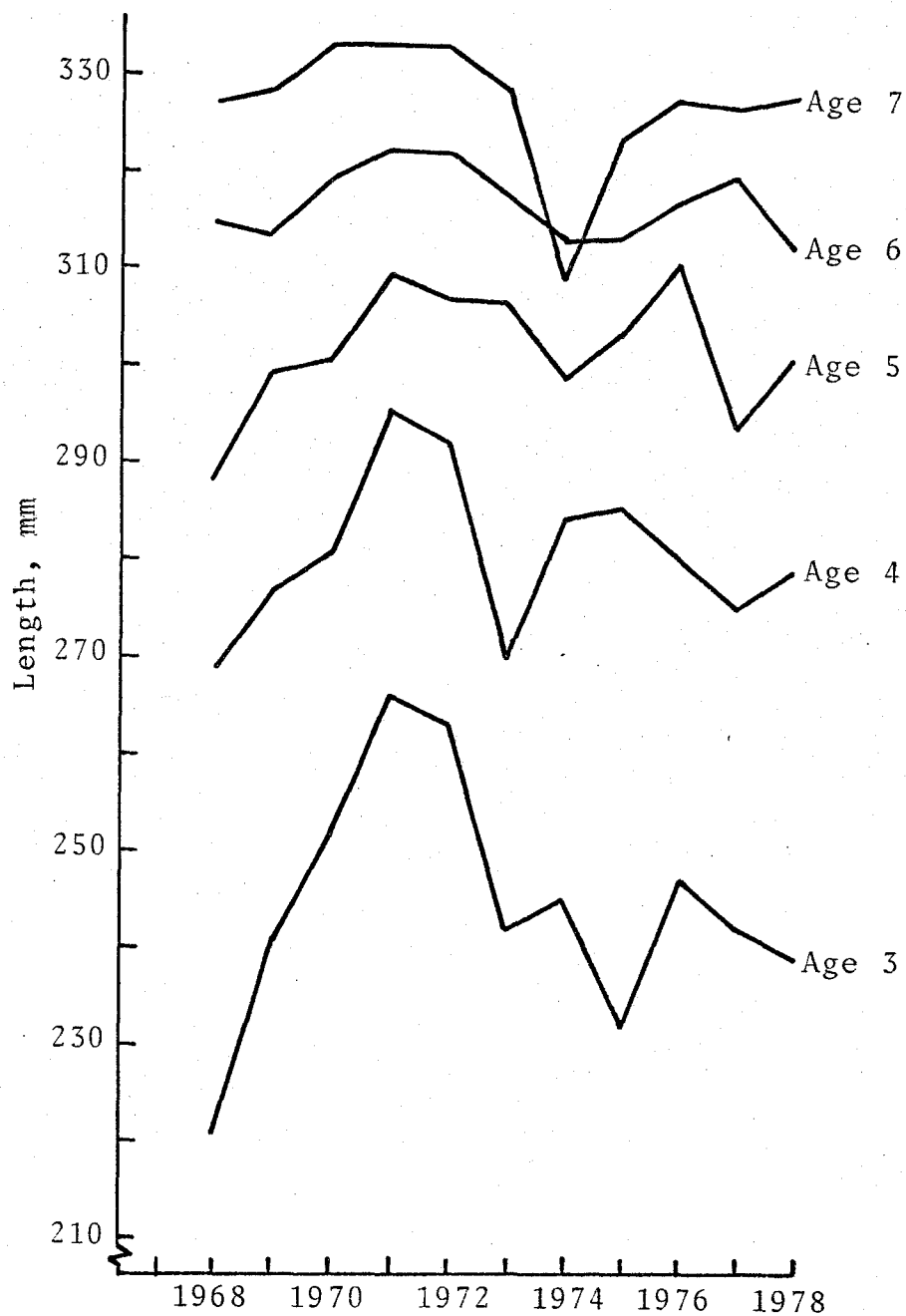


Figure 1. Trends in July mean length at age for the 4XW herring stock.

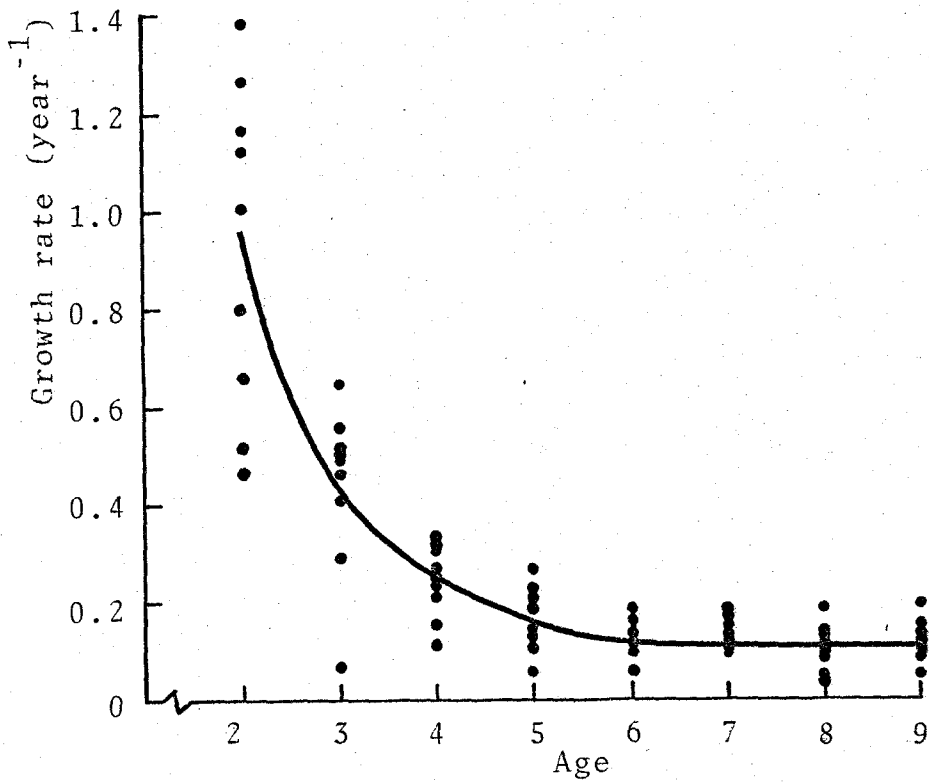


Figure 2. The decrease of somatic growth rate and range of growth rate with age in the 4XW herring stock.

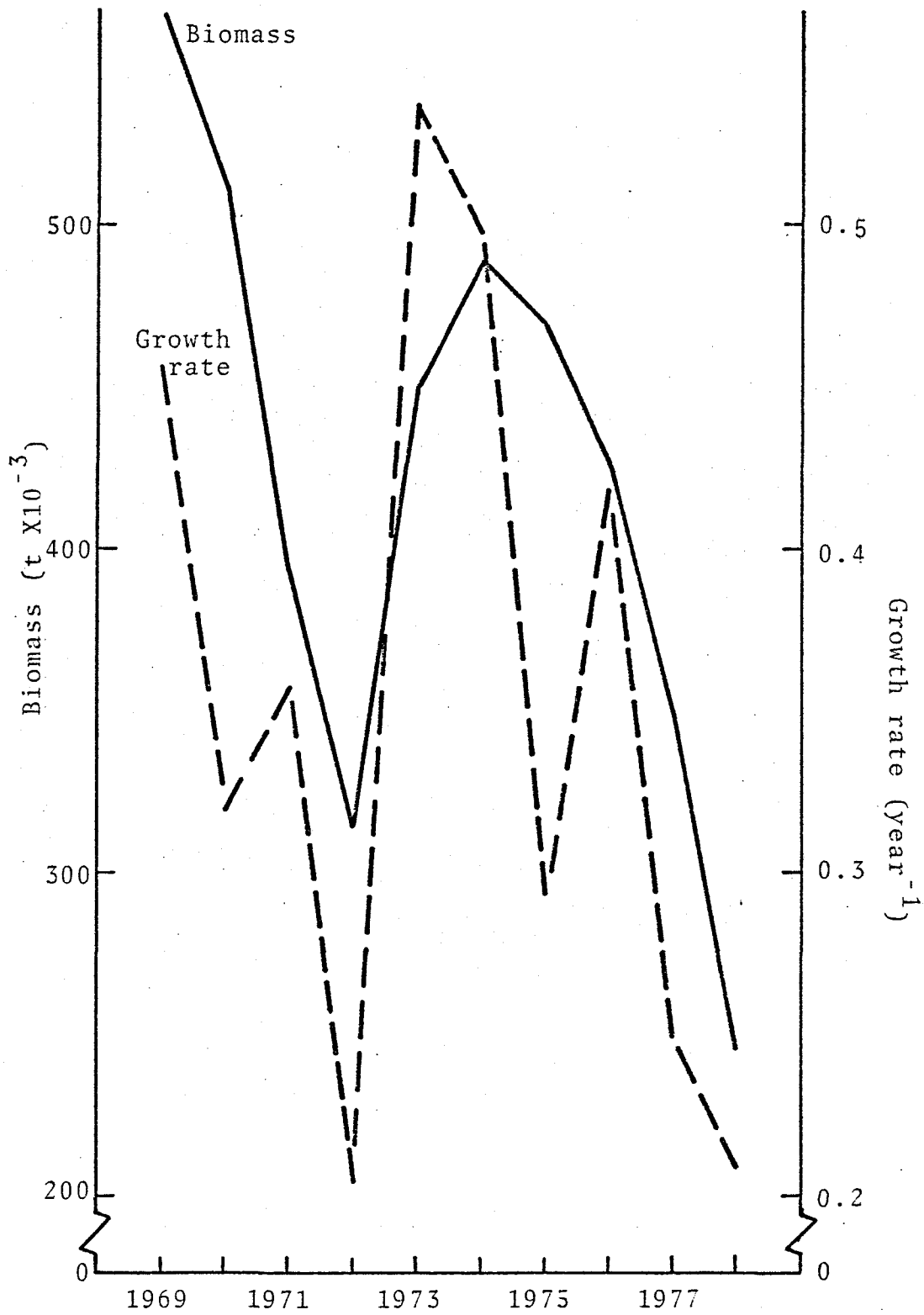


Figure 3. A comparison of population growth rate and biomass of the 4XW stock.

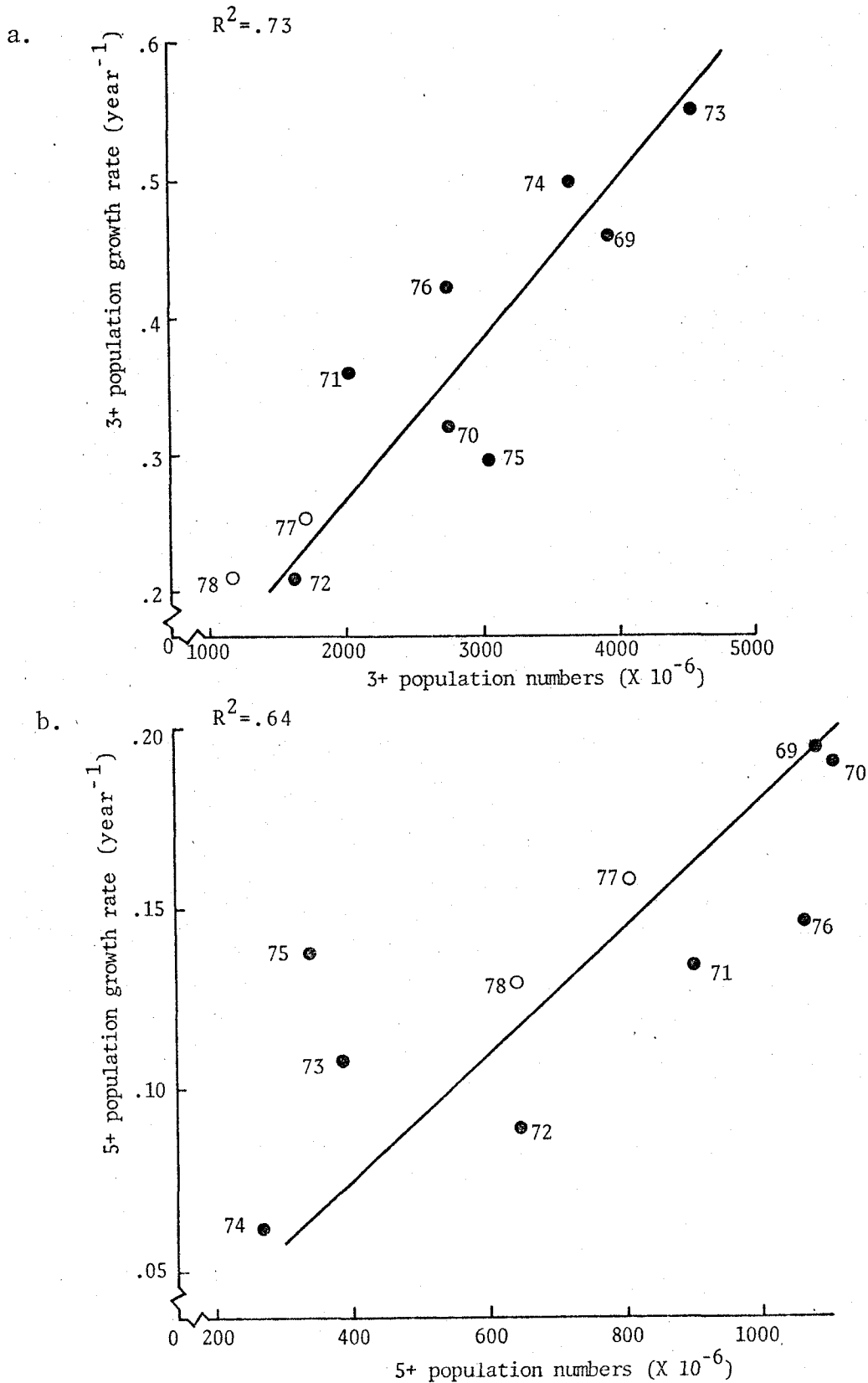


Figure 4. a) Relationship of population growth rate and population numbers of the 4XW stock.
 b) Relationship of recruited population size suggesting a reverse density dependence.

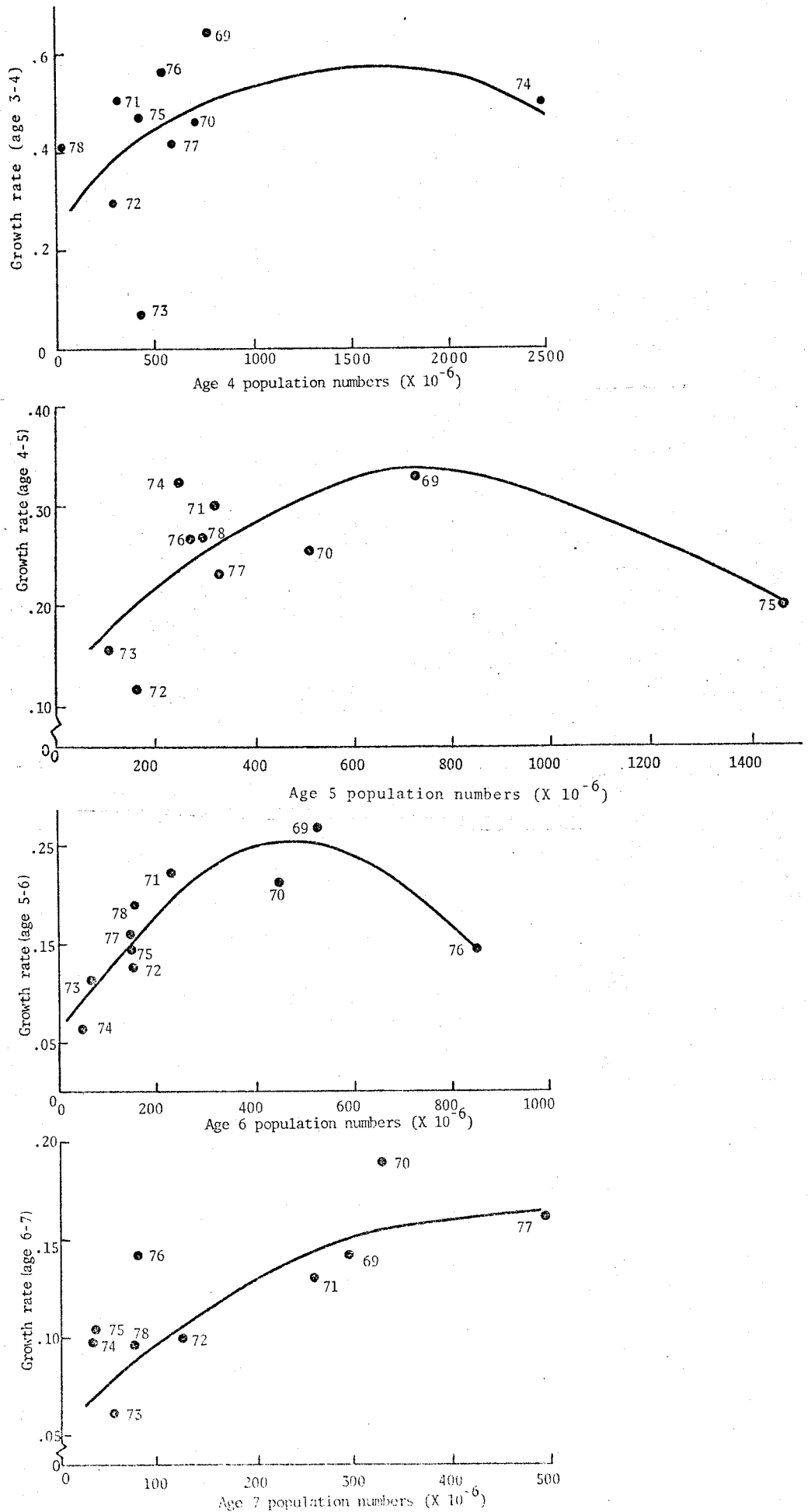


Figure 5. Cohort growth rate vs. cohort size (year rather than year-class indicated)

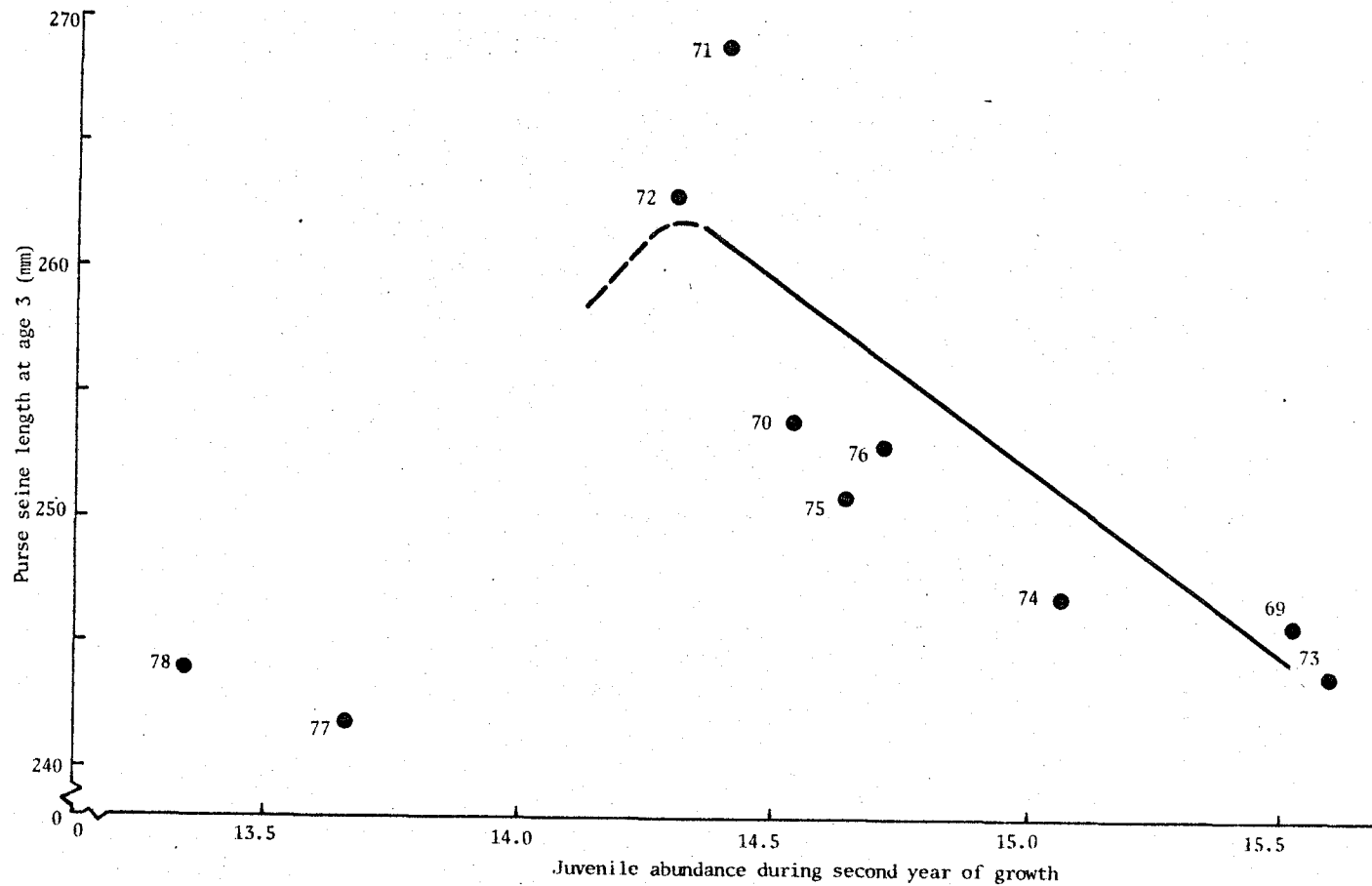


Figure 6. Relationship between age 3 mean length in the 4Xa purse seine fishery and juvenile abundance ($\ln(\text{age } 2 + 2/3 \text{ age } 3^{\#} \times 10^{-3})$) in the previous year.

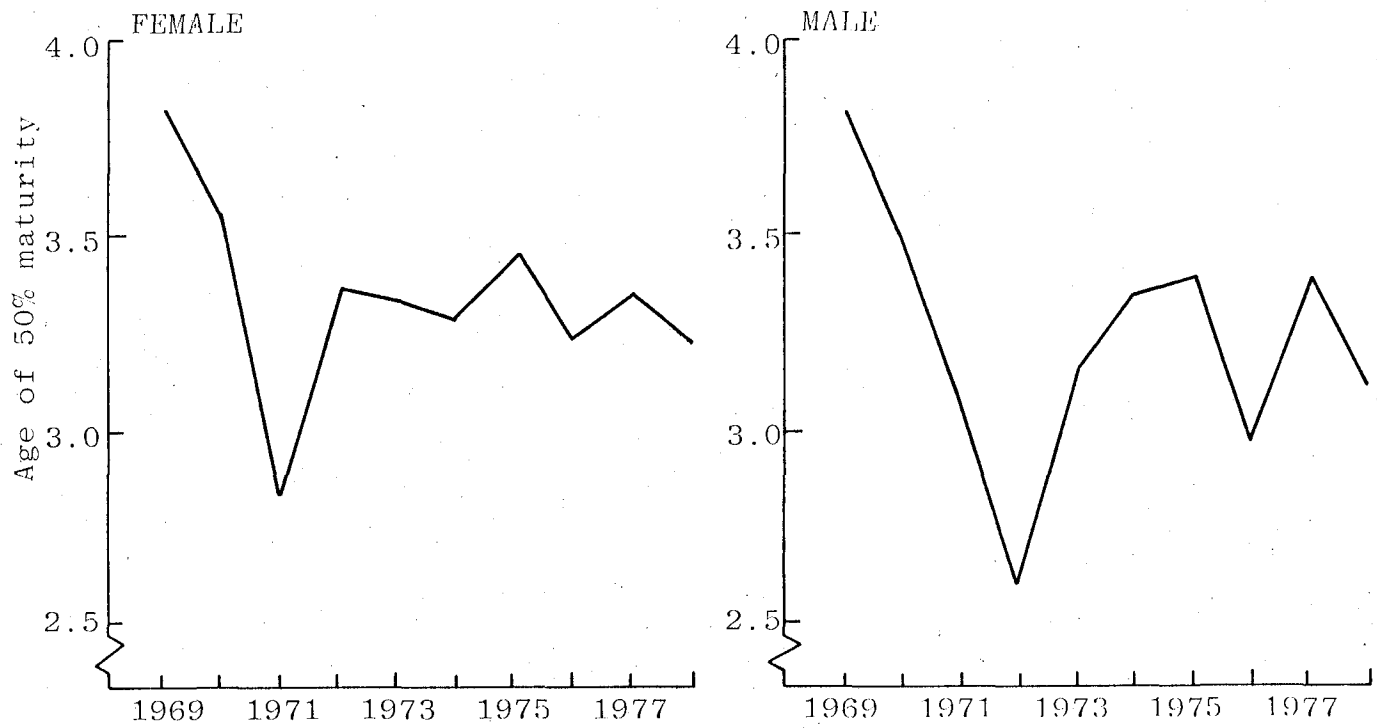


Figure 7. Changes in male and female age at 50% maturity of 4WX herring

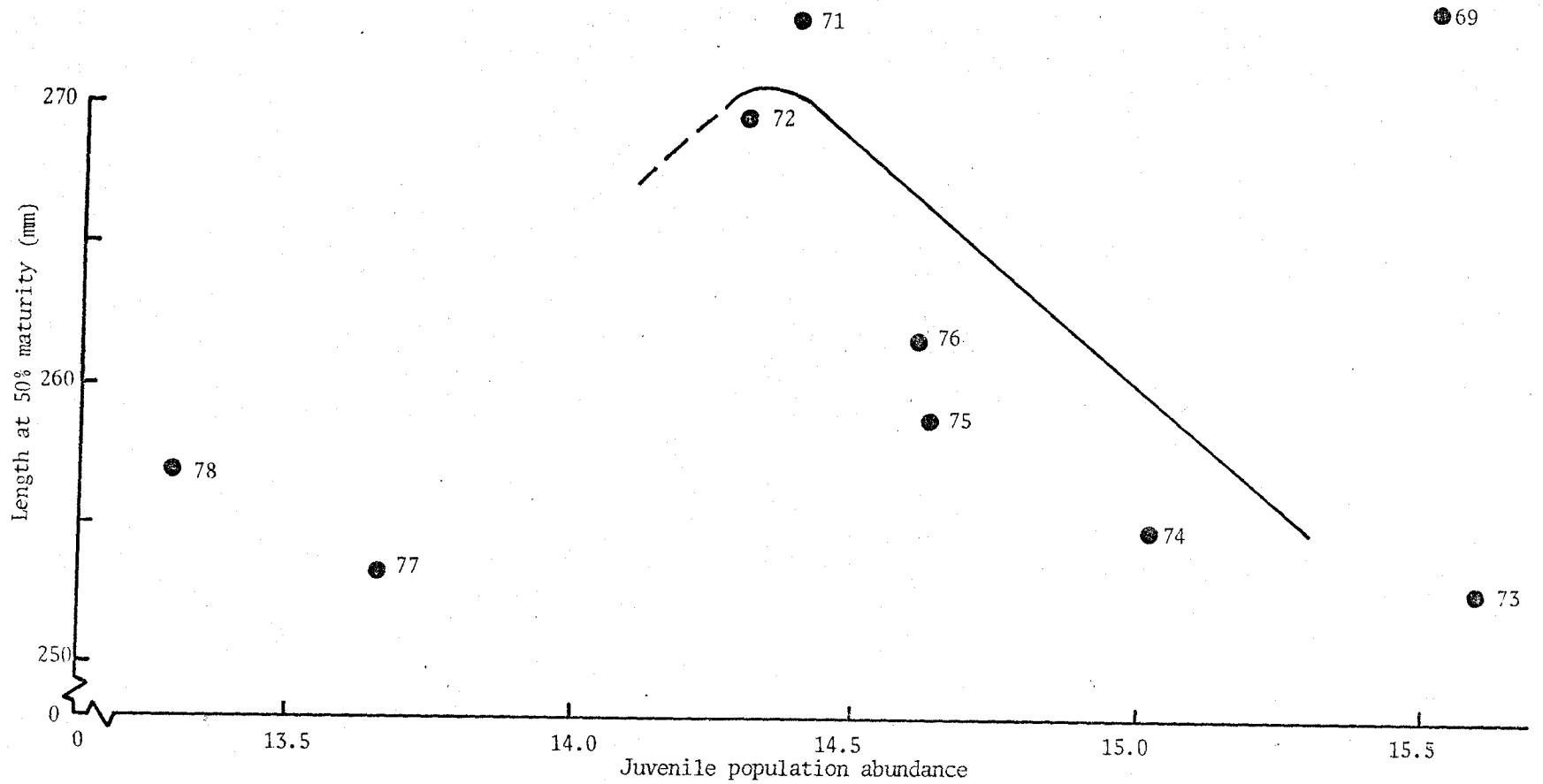


Figure 8. Relationship between mean length at 50% maturity and juvenile abundance in the previous year.

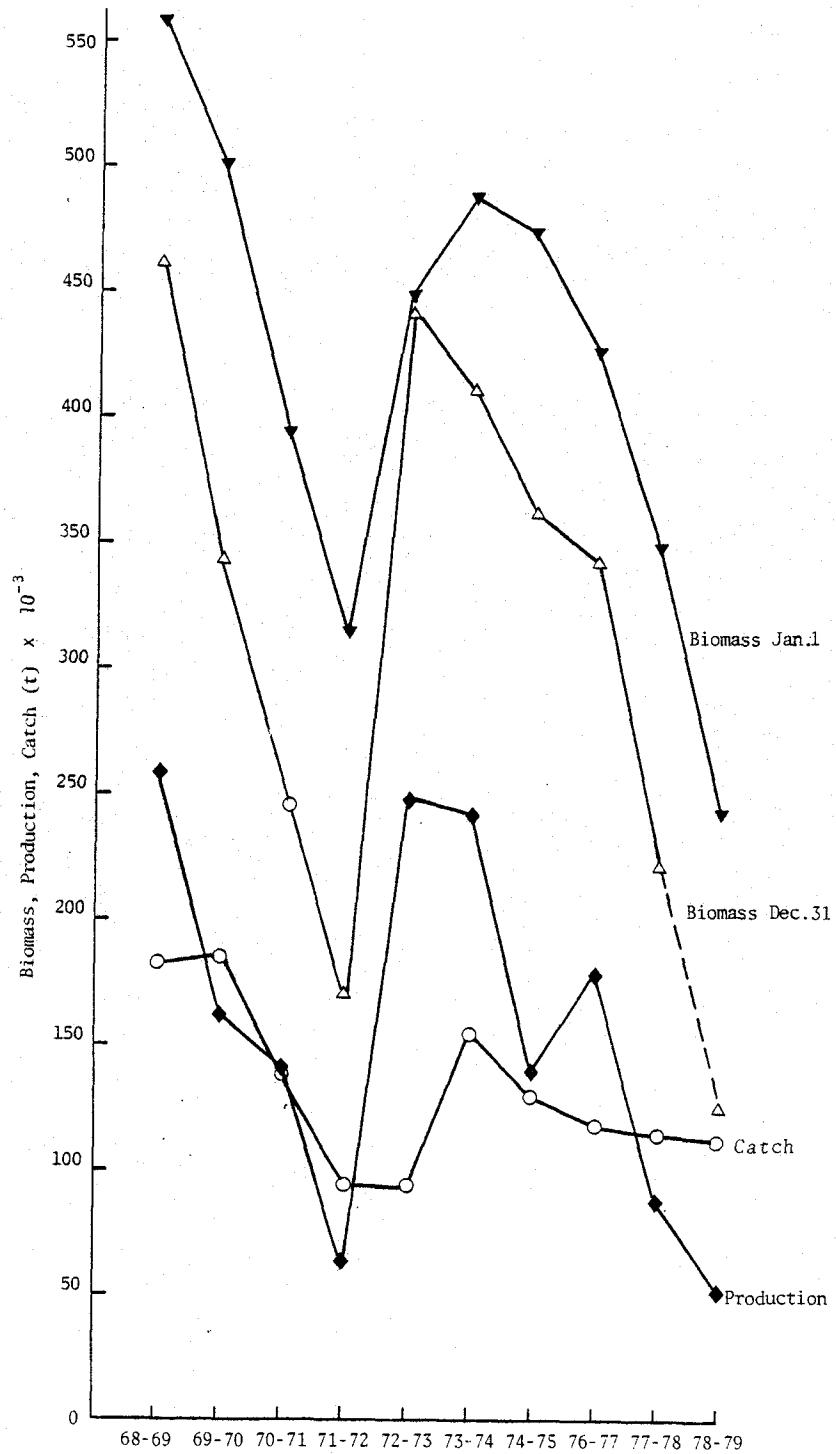


Figure 9. Trends in biomass, production and catch of the 4XW herring stock