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RELATION BETWEEN FISH CONDITION AND POPULATION SIZE IN THE SARDINE (*Sardinops caerulea*)

By JOHN S. MacGREGOR

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ABSTRACT

Data are presented for 15 fishing seasons between 1941 and 1957 showing the year-to-year trends of mean condition factor and mean length of the Pacific sardine (*Sardinops caerulea*) at San Pedro, and the trend of relative population size of the sardine as measured by the California catch. The data for condition factor and length are based on the four major months of the fishing season, October through January.

There is a high degree of inverse correlation between condition factor and catch, and between length and catch, and a high positive correlation between length and condition factor for the 15 seasons. The correlation between condition factor and catch remains high when the condition factor data are analyzed by restricted length groups, but there is no significant within-season correlation between length and condition factor when the data for each of the 15 seasons are analyzed separately. The high inverse correlation between condition factor and population size is interpreted as a cause and effect relation. While population size may also affect length growth, the primary factor causing the high inverse correlation between average length and population size is probably that both length composition and size of the population are affected by the size of the year-class of sardines just entering the population of sardines exploited by the fishery. The positive between-season correlation between condition factor and length is also considered to be a parallel correlation rather than cause and effect.

RELATION BETWEEN FISH CONDITION AND POPULATION SIZE IN THE SARDINE, *SARDINOPS CAERULEA*

By **JOHN S. MacGREGOR**, ***Fishery Research Biologist***, **BUREAU OF COMMERCIAL FISHERIES**

Stunted growth of some species of fresh-water fishes in densely populated lakes and ponds is a well-known phenomenon to fishery biologists. Hile (1936) reviews in part the less voluminous literature concerning the relation between density of population and rate of growth of marine fishes. I wish to describe the inverse correlation existing between condition factor and population size in a pelagic marine fish, the Pacific sardine (*Sardinops caerulea*), a situation apparently paralleling that of the stunting of fish under conditions of high population density. Stunting reflects growth conditions over a considerable period of time and especially during preadult life. Condition factor reflects recent feeding conditions. Both stunting and low condition factor may be caused by a meager food supply which, in turn, may result from a large population of fish.

This study is a byproduct of fecundity studies (MacGregor 1957) conducted as part of the broader studies of the California Cooperative Oceanic Fisheries Investigations. The California Cooperative Oceanic Fisheries Investigations are carried out under the sponsorship of the California Marine Research Committee by the California Academy of Sciences, the California Department of Fish and Game, the Hopkins Marine Station of Stanford University, the Scripps Institution of Oceanography of the University of California, and the South Pacific Fishery Investigations of the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. The number of eggs spawned by a sardine appears to be more closely related to the weight of the fish than to its length or age. A sardine having a higher condition factor will generally develop a greater number of eggs than one having a lower condition factor, when the two fish are of similar length and age. However, the increased relative fecundity of a small population having high condition factors does not compensate for the much larger absolute number of eggs that are developed by a large population having lower condition factors and a lower relative fecundity. There is no apparent correlation between year-class size (either absolute or relative to the parent population) and the condition factor of the population that produced that year-class. Relative fecundity as related to condition factor, which in turn is related to population size, may be one component of a complex of factors that tend to retard population fluctuations, preventing unlimited expansion on the one hand and extinction on the other.

I wish to thank the California Department of Fish and Game for the sampling records, the staff of the South Pacific Fishery Investigations, Bureau of Commercial Fisheries, for helpful criticisms and suggestions, and A. H. Vrooman for preparing the illustrations.

METHODS

Condition-factor data were derived from sampling records compiled by the California Department of Fish and Game. In making age and length determinations of the commercial catch of sardines, a number of samples of 50 sardines each were obtained from the commercial catch each season. Among the data obtained for each sample were the standard lengths of the individual fish in millimeters and the total weight of the sample of fish in kilograms. From these were obtained the mean lengths and the mean weights of the 50-fish samples.

Condition factor may be defined as $K=\frac{W\times 10^7}{L^3}$, in which K=condition factor, W=mean weight of fish in grams and L^3=cube of the mean stand-

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NOTE.—Approved for publication Sept. 26, 1958. Fishery Bulletin 166.

ard length of fish in millimeters. Multiplying W by 10^7 changed K from a 7-place decimal to a more easily handled 3-digit whole number.

Although the condition factor derived from the mean length and mean weight of sardines in a 50-fish sample will differ from the mean of the individual condition factors of the sardines in the sample, the difference is negligible. The fish within any one sample tend to be approximately the same size and have fairly similar condition factors. Condition factors based on the mean weight and mean length of fish in a sample were compared with the mean condition factors based on the average of the 50 condition factors for the individual fish for several samples in which individual fish weights were known. In no case did the K value computed from the mean length and mean weight differ from the mean K value by as much as 1 percent. For example, in one composite 50-fish sample consisting of ten different 5-fish samples taken over a 1-month period, individual condition factors ranged from 118 to 176 with a mean of 138; lengths ranged from 189 mm. to 256 mm. with a mean of 212 mm., and weights ranged from 92 grams to 198 grams with a mean of 132 grams. The condition factor based on mean length and mean weight was 139 or only one K unit higher than the mean condition factor. The condition factors used in this paper are based on samples that are probably all considerably more homogeneous as to length, weight and condition factor than the above composite sample.

The data used are from a period of 15 fishing seasons, 1941–42 through 1956–57 at San Pedro; for each season the observations cover the 4 principal months, October through January. No data are available for December 1953 and for the entire season of 1944–45.

Condition factors are used as a measure of the "fatness," although not necessarily the fat content, of fish. It is assumed that no appreciable change occurs in the specific gravity of the fish. K values may be compared not only among fish of the same length, but also, if it can be shown that there are no changes in body proportions peculiar to any length group within the size range studied, among fish of different lengths.

A second formula often used by fishery workers, and one related to the condition factor formula, is that for weight-length relation. This formula generally takes the form $W = CL^n$, in which W = weight, C = a constant determined by the data and L^n = length raised to an exponent determined by the data. This formula describes the weight-length relationship of a sample of fish. Hile (1936) discusses the uses of and the differences between the two formulas in considerable detail.

The formula $W = CL^n$ provides for the possibility that changes in body proportions take place at a constantly increasing or decreasing rate throughout the range of data. This is not necessarily true, especially if the range of data includes both immature and adult fish. Theoretically, if n is less than 3, condition factors should decrease with increase in length, and if n is greater than 3, condition factors should increase with increase in length. The value of n can be influenced by sampling irregularities, such as including in the sample fish from different environments or from different years or months when the length ranges of the fish are not comparable in the different sample components. These irregularities, as well as those caused by including immature and adult fish in the same sample, generally show up as high percentages of plus or minus deviations within one or more restricted length ranges within the total length range of the length-weight curve.

Clark (1928) determined the length-weight relation of the Pacific sardine from data based on fish from the commercial catch at San Pedro from January to April 1921, December 1924 to March 1925, November 1925 to March 1926, and December 1926 to May 1927. Also included were a series of fish of less than 150 mm. standard length (70 to 150 mm.; a size range not represented in the commercial catch) taken from January to December 1921. The length range of the fish taken in the commercial fishery samples is fairly well represented throughout each of the months and years during which sampling was conducted. Clark found that the value of n in the formula $W = CL^n$ was 3.15 for this combined sample of fish. She also concluded that sardines smaller than 200 mm. have a different seasonal weight cycle than sardines larger than 200 mm.

In a later paper Clark (1934) further demonstrated that immature sardines have a different seasonal fat cycle than adults. She also stated (1) that the 3.15 value of n was reduced to 3.07 if fish smaller than 150 mm. are omitted; (2) that there was no significant difference between the length-weight relationships of males and females; (3) that the value of n for San Pedro sardines (longer than 150 mm.) between May and October 1929 was 2.80 and (4) that the value of n for female sardines throughout an entire year, October 1928 to October 1929, was 2.94. These close approximations of n to the cube indicate that condition factors of sardines of different lengths are comparable, at least within certain limits.

A second and more direct method of determining the comparability of condition factors of fish of different lengths is to determine the trend of K when plotted against fish length in a representative sample. Clark (1928) has done this for each of the months January, February, and March. Each monthly sample consisted of fish taken in four different years, but all lengths were represented fairly well in each of the years. Her data indicated an increase in K from a fish length of about 155 mm. to 195 mm., no change in K between 195 mm. and 250 mm. and a slight decrease in K between 250 and 280 mm.

I have used no sardine samples having mean lengths of less than 190 mm., nor samples having mean lengths greater than 240 mm. K values of sardines within this length range are comparable.

Measures of population size used in this paper are (1) the California commercial catch in tons, (2) the California catch in numbers of fish (3) accumulated age estimates (numbers of fish) Felin and Phillips, 1948; Mosher et al., 1949; Felin et al., 1949, 1950, 1951, 1952, 1953, 1954, 1955 (in press); Wolf et al. (in press); Clark and Marr, 1955. The latter measure is a minimal population estimate based on the Pacific coast commercial catch. Data for additional years have been included with that of Clark and Marr (1955) for accumulated age estimates. The commercial catch is believed to be a good relative measure of population size off the California coast over the 15 seasons covered by the data because the fishery has been intensive over this period. The catch has fluctuated from almost 600,000 tons to about 3,000 tons during this period. The general trend in catch has been downward since the late 1930's with temporary increases in catch following the entries of the relatively large 1946, 1947, 1948, and and 1952 year-classes into the fishery. The use of catch data as a relative measure of the size of the sardine population is discussed at some length by Clark and Marr (1955).

TABLE 1.—*Basic data for San Pedro commercial sardine fishery, 1941–42 through 1956–57 seasons*

Season	Mean condition factor					Mean length					Number of 50-fish samples				
	Oct.	Nov.	Dec.	Jan.	4-month mean [1]	Oct.	Nov.	Dec.	Jan.	4-month mean [1]	Oct.	Nov.	Dec.	Jan.	Total
1941–42	126	123	121	117	122	195	197	196	196	196	70	48	38	46	202
1942–43	126	122	119	118	121	203	203	201	199	202	82	77	76	48	283
1943–44	127	125	123	122	124	201	200	202	200	201	84	53	59	47	243
1944–45	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
1945–46	131	130	128	126	129	203	203	202	208	204	25	14	13	20	72
1946–47	135	130	130	128	131	201	203	206	210	205	25	16	22	14	77
1947–48	138	135	134	132	135	210	217	221	221	217	20	18	14	9	61
1948–49	134	129	128	128	130	201	200	200	200	200	18	15	15	12	60
1949–50	128	124	123	124	125	200	199	201	205	201	20	11	17	13	61
1950–51	132	131	129	127	130	205	207	213	214	210	35	40	25	30	130
1951–52	129	128	125	129	128	208	211	212	217	212	40	28	20	21	109
1952–53	137	137	135	137	137	232	235	233	232	233	12	15	9	5	41
1953–54	144	140	------	134	139	215	234	------	222	224	16	14	0	3	33
1954–55	137	133	127	132	132	205	206	207	209	207	17	28	20	3	68
1955–56	136	133	132	136	134	214	213	215	215	214	33	25	25	11	94
1956–57	140	137	135	134	137	223	226	228	227	226	34	15	5	7	61

[1] Unweighted average.

CONDITION FACTOR TRENDS

The trends of condition factors of sardines taken at San Pedro from October to January in each of 15 fishing seasons are shown in figure 1. Since the sardine fishermen locate the sardine schools primarily by bioluminescence, the fishery is carried on at night during the dark of the moon. Because of this, the monthly trends are somewhat in error; sardines from portions of two fishing periods are often included in 1 month, and fishing periods are often divided between 2 months. Comparison of fishing periods would also contain an error since they do not occur at the same time each year.

Nevertheless, the month-to-month trends and the year-to-year changes in condition factors are well marked. It is apparent that condition factors generally decrease as the fishing season progresses, although there is often an increase from December

Table 2.—*California sardine catch data and estimated population (by accumulated age) for the fishing seasons 1941–42 through 1956–57*

Season	California catch [1]		Estimated population [2]
	Thousands of tons	Billions of fish	Billions of fish
1941–42	585	5.34	11.5
1942–43	502	3.96	9.1
1943–44	475	3.48	7.0
1944–45	551	3.81	5.8
1945–46	399	2.81	3.6
1946–47	228	1.86	1.7
1947–48	110	0.93	1.4
1948–49	160	1.50	2.7
1949–50	334	2.75	4.3
1950–51	351	2.59	3.7
1951–52	127	0.96	1.2
1952–53	5	.02	0.4
1953–54	3	.02	0.7
1954–55	67	.53	1.2
1955–56	73	.52	0.8
1956–57	33	.19	----------

[1] Felin and Phillips, 1948; Mosher et al., 1949; Felin et al., 1949, 1950, 1951, 1952, 1953, 1954, 1955 (in press); Wolf et al. (in press).

[2] Clark and Marr, 1955; (1950–51, 1951–52 and 1952–53 seasons corrected and 1953–54, 1954–55 and 1955–56 seasons added on basis of more recent data).

to January. At the beginning of the fishing season (October), the highest condition factor is 144 (1953); the lowest, 126 (1941 and 1942). At the end of the fishing season (January), the highest condition factor is 137 (1953); the lowest 117 (1942).

Over the range of K values observed, the relative measurement, K, equals the absolute measurement, weight in grams, of a 215½ mm. sardine. That is, from $K=\frac{W\times10^7}{L^3}$ it follows that $L^3=\frac{W}{K}\times10^7$, and when $W=K$, $L^3=10^7$, and $L=215\frac{1}{2}$. A 215½ mm. sardine is near the midpoint of the range of sardine lengths (190–240) in the samples used.

Some condition factor data are available for sardines landed at Monterey for 8 of the 16 seasons considered. These are compared with San Pedro sardine condition factors for the corresponding months (fig. 2). The number of 50-fish samples is given in parentheses for Monterey condition factors whenever they are based on less than 10 samples. The January, 1947–48, San Pedro sample is based on nine 50-fish samples; all other San Pedro condition factors are based on 10 or more. Not only are the Monterey data meager, but also their relative abundance is greatest during periods when the sardine population was highest and condition factors lowest. It may be seen (fig. 2) that the Monterey condition factor trend generally follows that at San Pedro, but is higher in value at the beginning of the season and about the same toward the end of the season.

The least squares regression of Monterey on San Pedro condition factors for each of the four months are shown in figure 3 and regression statistics and other data in table 3. Although these correlations are based on small samples (numbers of pairs of data), the probabilities (P) that such high correlations would occur by chance alone are relatively low.

Table 3.—*Correlation between Monterey and San Pedro condition factors*

Month	a	b	Number of samples	Observed r	r when P[1]=.05–.02	r when P[1]=.02–.01	r when P[1]=.01–.001
October	−104.32	1.8794	7	.891	----------	----------	.875–.951
November	1.043	1.0435	6	.885	----------	.882–.917	----------
December	5.354	.9798	6	.911	----------	.882–.917	----------
January	25.112	.8062	5	.917	.878–.934	----------	----------

[1] Fisher and Yates, table VI, page 54.

The Monterey data for one point (1948) on the October correlation of figure 3 are not included in figure 2. This is a single 50-fish sample with a mean K of 149 (mean length=196 mm.). That this K value is not aberrantly high is indicated by the K values of the two samples in the 180–189 mm. length group taken at Monterey at the same time. One had a K value of 151 (mean length 186 mm.) and the other, 141 (mean length 185 mm.).

Although the K trend appears to drop more sharply from October to January, and although K values are noticeably higher at the beginning of the season in Monterey, the San Pedro K values do bear a relative relation to those of Monterey. Therefore, it is logical to examine the relationship between San Pedro K values (for which the longest series of data are available) with the total California catch (which should be the best measure available of the total sardine population off the coast of California).

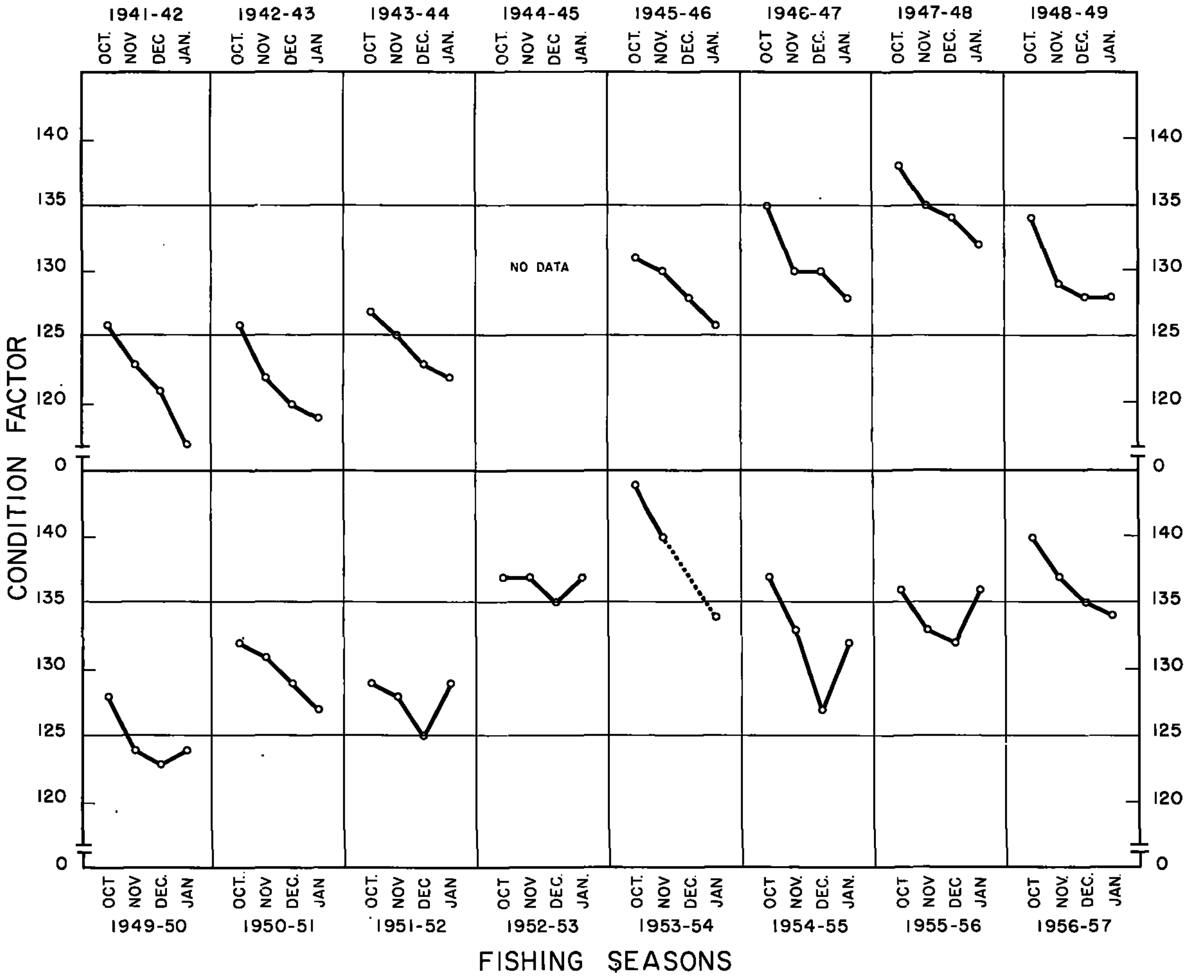

FIGURE 1.—Condition factor trends for San Pedro sardines.

CATCH, LENGTH, AND CONDITION FACTOR RELATIONS

The year-to-year trend of the California sardine catch (thousands of tons) and the inverse trend of the 4-month means of length and condition factor for the 1941–42 through 1956–57 fishing seasons are shown in figure 4. The trends of catch or estimated population in billions of fish and the inverse trends of length and condition factors for any of the 4 months considered separately parallel those in this figure.

Figures 5, 6, and 7 show the least-squares regressions of length and condition factor on each of the three relative measurements of population, and figure 8 shows that of condition factor on length. The regression statistics and other data are given in table 4. All seven associations are significant, but the three relationships involving condition factor and population have higher correlation coefficients than the three involving length and population.

TABLE 4.—*Regression statistics and other data for the regressions of length and condition factor on each of three relative population measurements and of condition factor on length*

[*Ct*=California catch in thousands of tons; *Cb*=California catch in billions of fish: *EP*=estimated population in billions of fish; *L*=length; *K*=Condition factor.]

X	*Y*	*N*	*a*	*b*	*r*	*P*
Ct	*L*	15	220.165	−.04359	−.788	<.001
Ct	*K*	15	136.188	−.02573	−.903	<.001
Cb	*L*	15	219.952	−5.36347	−.797	<.001
Cb	*K*	15	136.005	−3.13440	−.905	<.001
EP	*L*	14	216.244	−2.05723	−.685	<.01
EP	*K*	14	134.641	−1.37874	−.865	<.001
L	*K*	15	37.667	0.44067	.856	<.001

The regressions involving length are more accurately described by curves than by straight

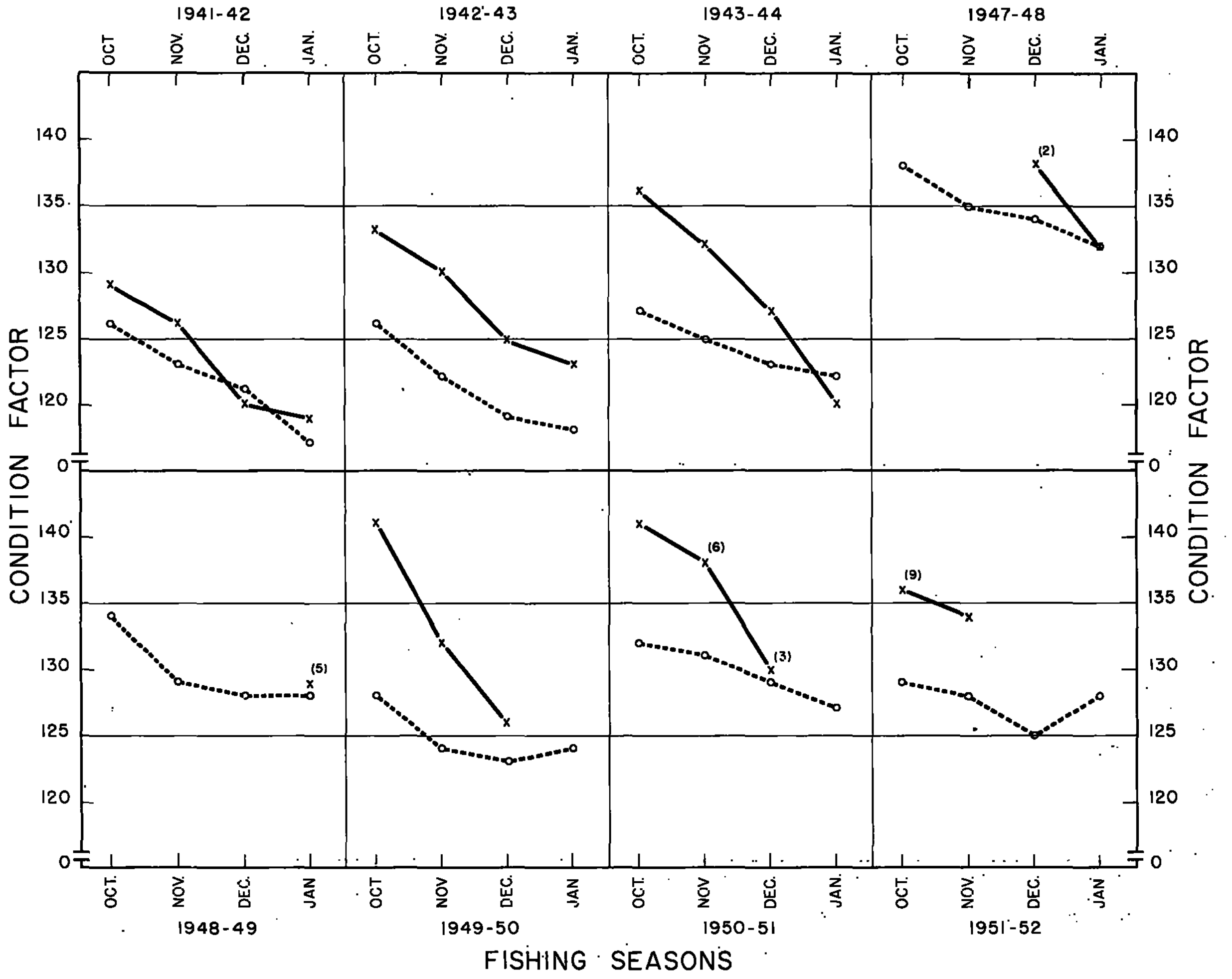

Figure 2.—Comparison of San Pedro and Monterey condition factor trends.

lines, even apart from the fact that the lower length limit was arbitrarily taken at 190 mm. For example, in figure 9, the curvilinear regression $Y=193.11+35.08\left(\frac{1}{X+1}\right)$ fits the plots of length (Y) on catch in billions of fish (X) better than the rectilinear regression $Y=219.95-5.363X$ and the coefficient of correlation is increased from 0.797 to 0.907. However, the rectilinear regression demonstrates the existence of a significant correlation, which is sufficient for the present purposes.

The length and condition factor data taken for each month separately also show high degrees of correlation with one another and with the three relative population measurements.

It now remains to be determined which of the above groups of correlations may represent cause and effect and which are probably parallel or accompanying phenomena.

DISCUSSION

One result of intensive fishing of a stock of marine fishes is often decreased catch accompanied by decreased fish size (length). In the sardine data, decreases in catch under intensive fishing are accompanied by increases in average fish length, and increases in catch are accompanied by decreases in average fish length. The reasons for this appear to result from the interaction of two factors: (1) any year-class of sardines contributes by far the greatest tonnage to the fishery in its third and fourth years of life (i.e., fish whose scales show, respectively, 2 and 3 annual growth rings), and (2) strength of year-classes fluctuates greatly

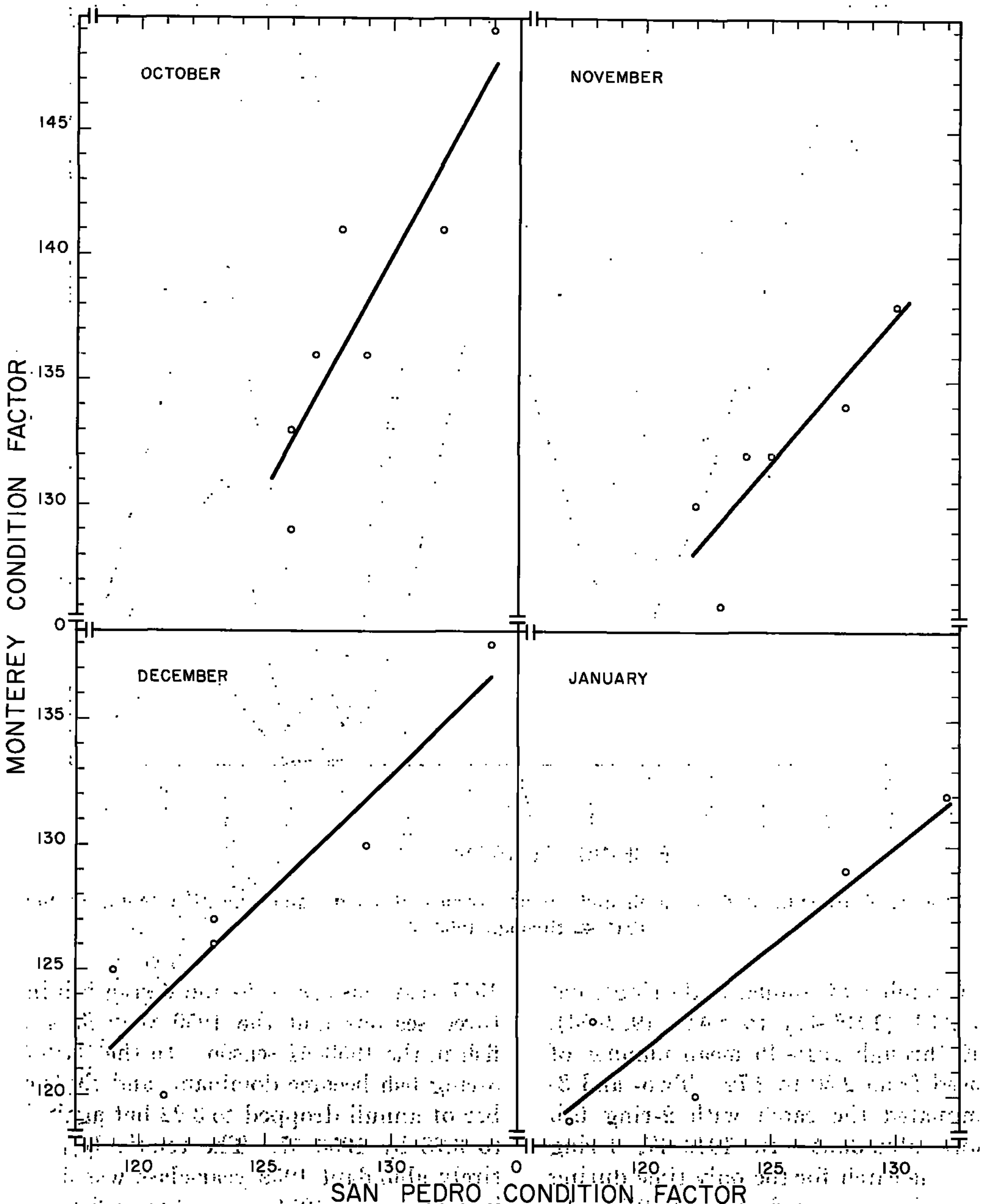

FIGURE 3.—Regressions of Monterey on San Pedro condition factors by months.

from year to year. Thus, the large catches are associated with large year-classes of fish in their third and fourth years of life. These fish are relatively small. On the other hand, small catches are associated with small year-classes in their third and fourth years, together with relatively high percentages of larger, older fish from some former large year-class. According to data presented by Clark and Marr (1955), which covers the period 1932–33 through 1952–53, the size of the year-class entering the fishery (as 2-ring fish) has averaged 91 percent of the adult population size to which it has been added, and has ranged from 10 percent (1949 year-class in the 1951–52 season) to 286 percent (1946 year-class in the 1948–49 season).

In the 16-season period (1941–42) through 1956–57) the sardine age at San Pedro, as meas-

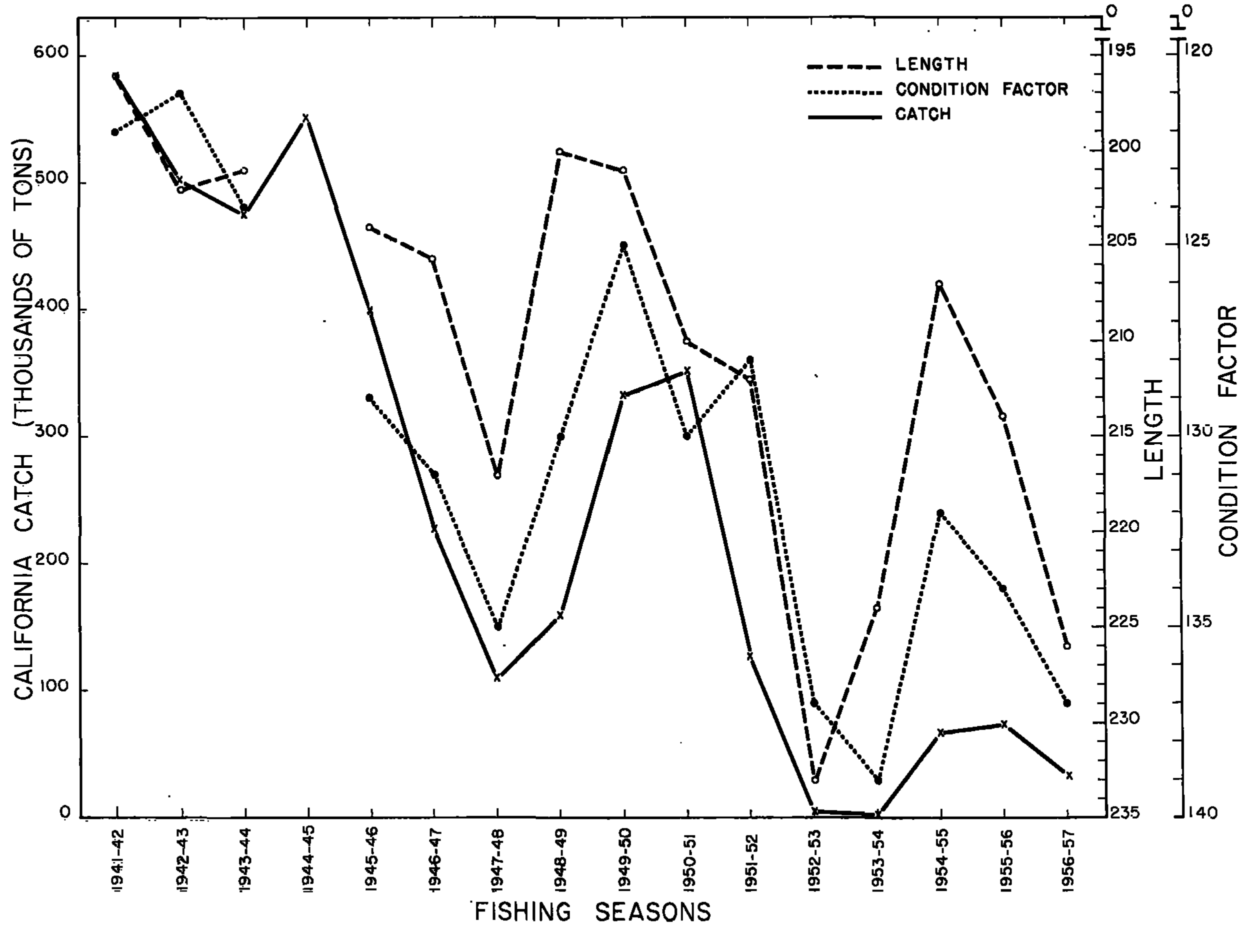

Figure 4.—Trend of California sardine catch and inverse trends of length and condition factor at San Pedro 1941–42 through 1956–57.

ured by mean number of annual scale rings, has ranged from 2.01 (1946–47) to 4.41 (1952–53). From 1941–42 through 1945–46 mean number of annuli increased from 2.30 to 2.72. Two- and 3-ring fish dominated the catch with 2-ring fish generally more abundant. In 1946–47, 1-ring fish dominated the catch for the only time during the 16 seasons and mean age dropped to 2.01. In the following four seasons it again increased to 2.73, and during this time 2-ring fish again dominated the catch. From 1950–51 through 1952–53 the mean number of annuli increased from 2.73 to 4.41 and dropped slightly to 4.21 in the 1953–54 season. During these four seasons the 1948 year-class dominated the catch as 2-, 3-, 4-, and 5-ring fish, respectively. This was caused by the almost complete failure of the 1949, 1950 and 1951 year-classes.

Of secondary importance were sardines in the 1947 year-class as 4-, 5- and 6-ring fish in the first three seasons and the 1950 year-class as 3-ring fish in the 1953–54 season. In the 1954–55 season 3-ring fish became dominant, and the mean number of annuli dropped to 3.22 but again increased to 3.78 by 1956–57. The relatively, but not entirely abundant 1952 year-class was of secondary importance in 1954–55 as 2-ring fish, and dominated the catch in the two following seasons as 3- and 4-ring fish, respectively. In the 1956–57 season the persistent 1948 year-class was fourth in abundance as 8-ring fish. During the first 10 seasons (1941–42 through 1950–51) of the 16-year period the California sardine catch averaged 2.90 billions of fish and ranged from 0.93 billions to 5.34 billions; the mean number of annuli averaged 2.46 and ranged from 2.01 to 2.73. During the next six seasons (1951–52) through 1956–57); the catch averaged 0.37 billions and ranged from 0.02

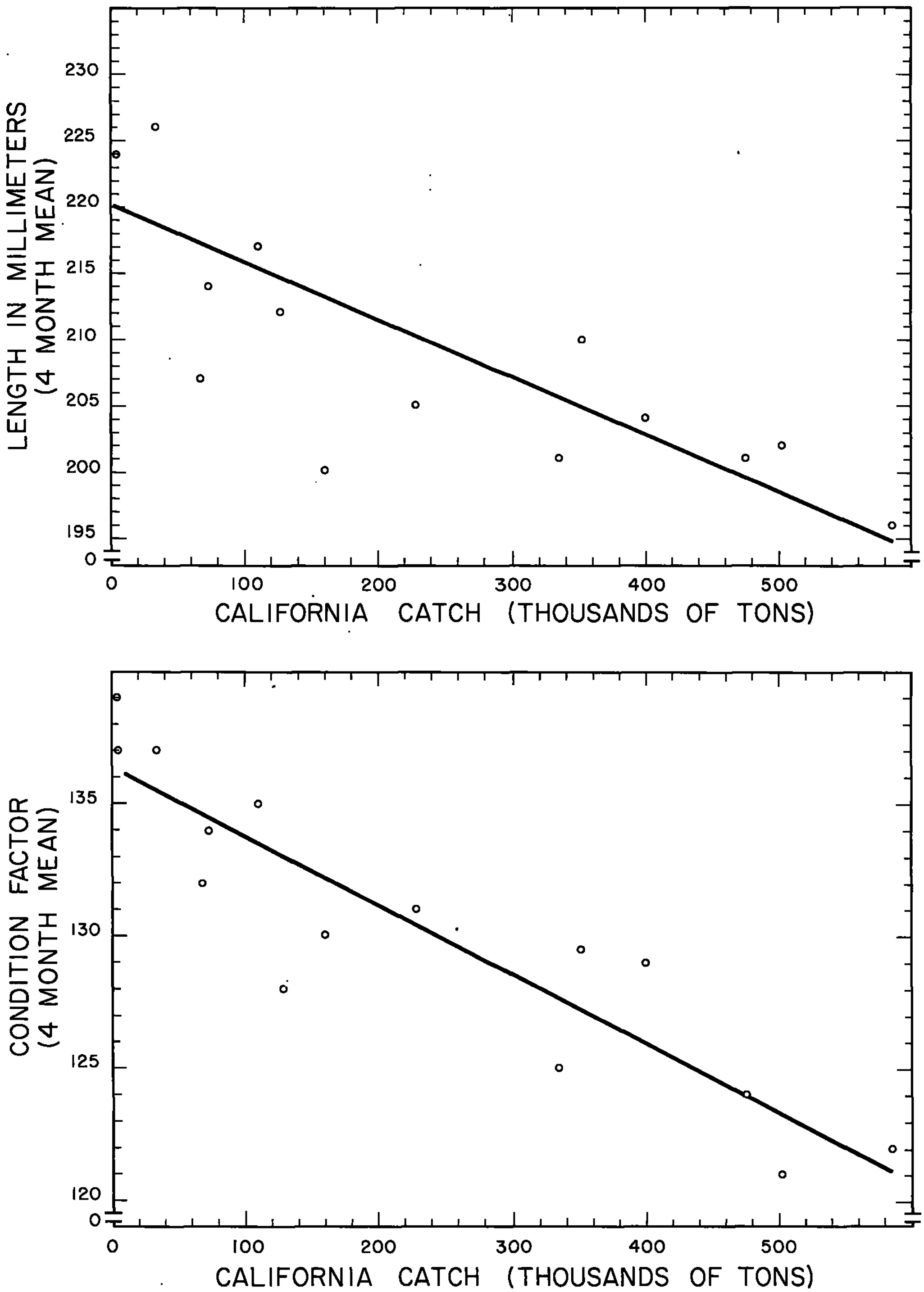

FIGURE 5.—Regressions of length and condition factor at San Pedro on California catch in thousands of tons.

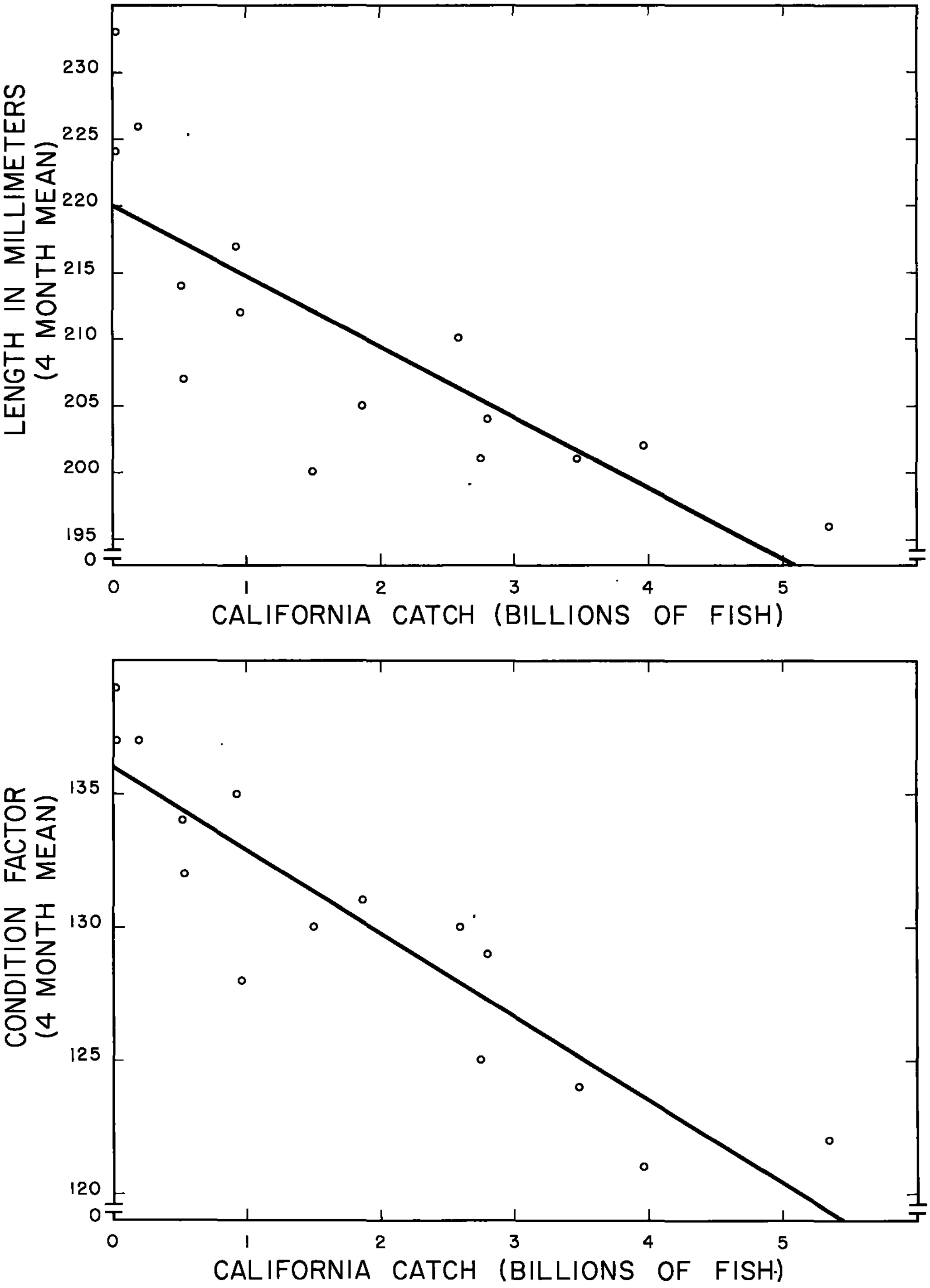

Figure 6.—Regressions of length and condition factor at San Pedro on California catch in billions of fish.

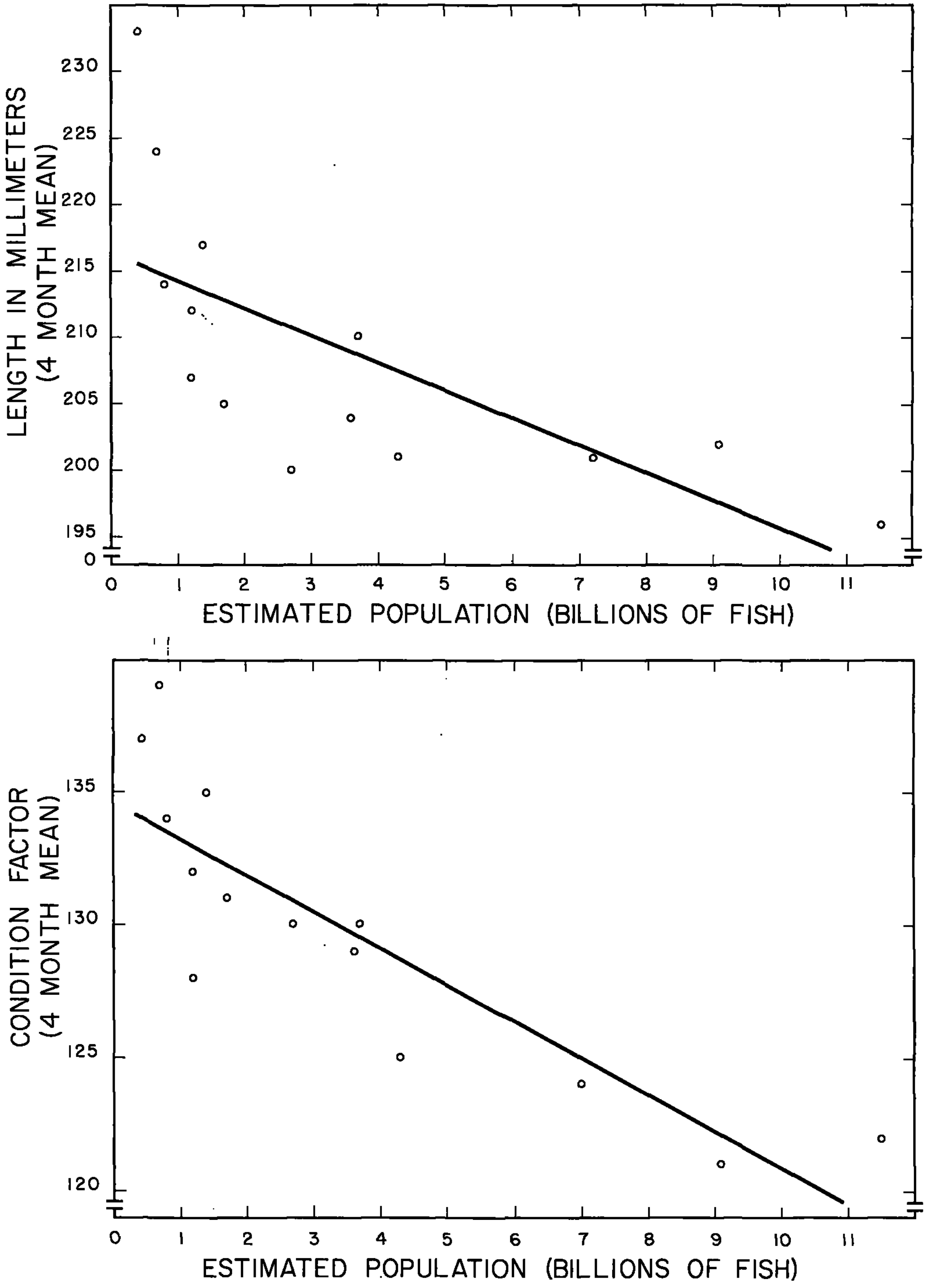

Figure 7.—Regressions of length and condition factor at San Pedro on estimated sardine population in billions of fish.

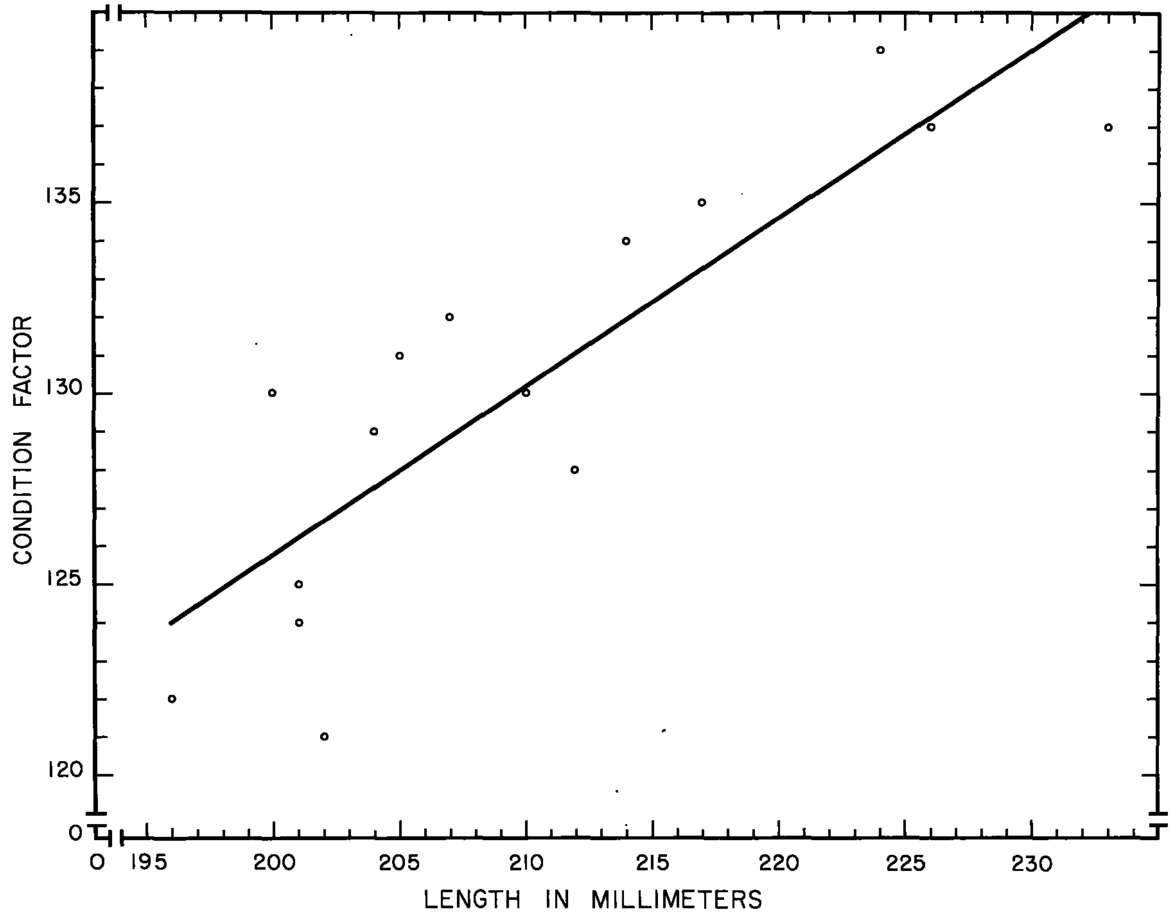

Figure 8.—Regression of condition factor on length (October through January means at San Pedro for seasons 1941–42 through 1956–57).

billions to 0.96 billions; mean number of annuli averaged 3.71 and ranged from 3.22 to 4.41.

The lack of direct correlation between condition factor and length is demonstrated by the data in table 5. When the means of *K* and length for January of each of the 15 years are correlated *r* is high and *P* is less than 0.001, but when *K* and length are correlated for the individual samples for January of each of the 15 years, *r* is generally low and *P* is high. By using the data for a single month, errors arising from the seasonal *K* trends are minimized. Data from any of the other 3 months gives similar results. The data for the years 1954 and 1955 are meaningless because *N* is too small and the length range is too restricted. *N* is also too small to have significance in the year 1953.

Table 5.—*Correlation of condition factor and length for each of 15 seasons (by individual samples) and seasons combined (mean values) for the month of January at San Pedro*

Season (January)	Length range		N	r	P
	Minimum	Maximum			
	mm.	*mm.*			
1942	190	210	46	−.217	>.1
1943	190	214	48	.183	>.1
1944	190	225	47	.321	.05>.02
1946	193	220	20	.292	>.1
1947	198	227	14	.000	>.1
1948	204	231	9	.394	>.1
1949	191	211	12	.050	>.1
1950	194	213	13	.675	.02>.01
1951	208	221	30	.173	>.1
1952	202	234	21	.134	>.1
1953	228	239	5	.278	>.1
1954	221	222	3	.316	>.1
1955	208	209	3	−.316	>.1
1956	210	220	11	.070	>.1
1957	221	232	9	.770	.02>.01
11 years	196	233	15 (means)	.858	<.001

The fact that 12 out of 15 of the correlation coefficients have a positive value might indicate that there is a slight tendency for *K* to increase with length, but this could also arise from other causes. For example, there appears to be a tend-

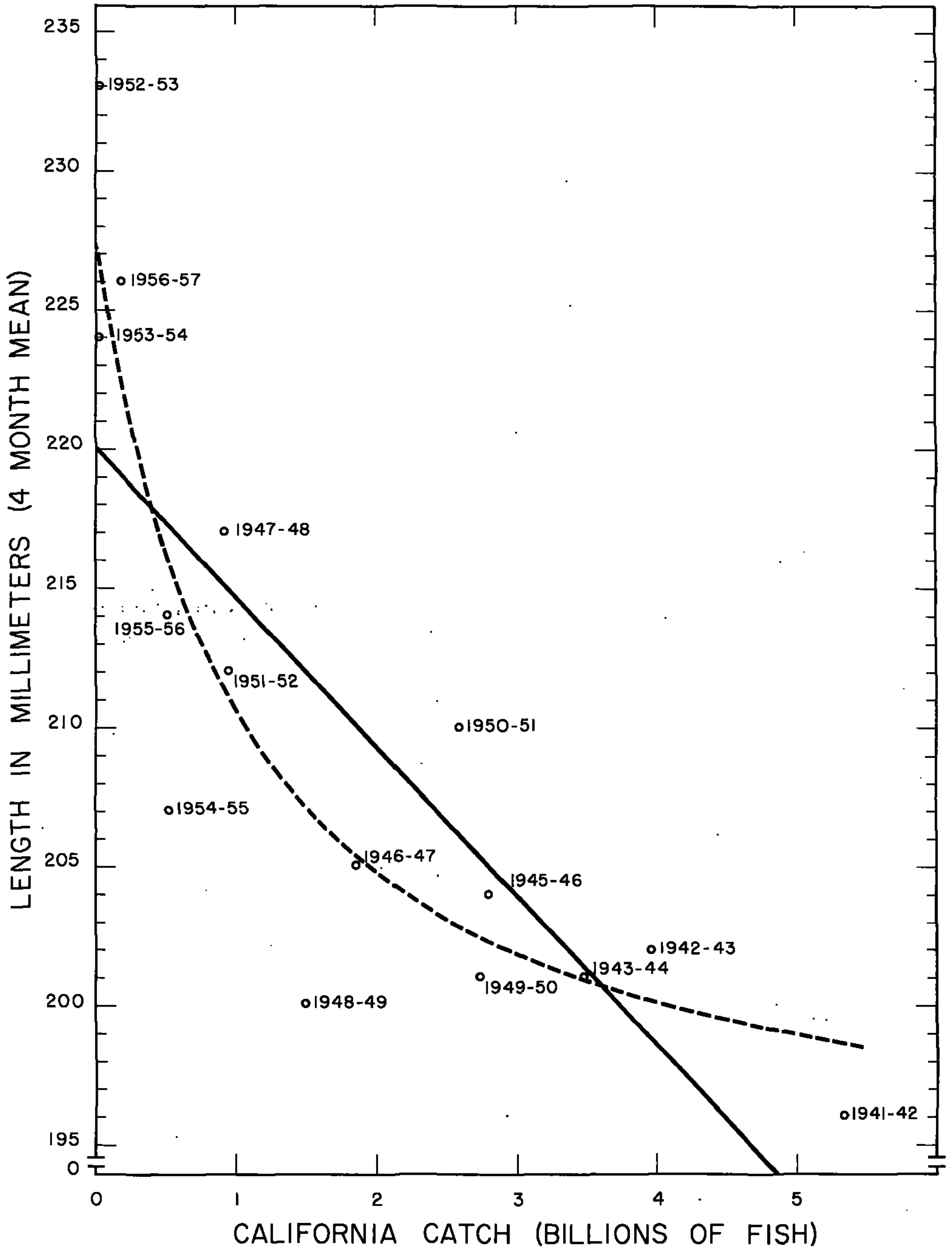

FIGURE 9.—Comparison of curvilinear and rectilinear regressions of mean length of San Pedro sardines on California catch in billions of fish. Solid line: $Y=219.95-5363X$, $r=.797$; dashed line: $Y=193.11+35.08\left(\frac{1}{X+1}\right)$, $r=.907$.

ency for the sardine population off the California coast to move southward during the course of the fishing season, and there is also a tendency for the more northern fish to be of larger size. However, this does not explain the highly significant correlation of K and the length for all years, or the general lack of significance for the individual years. Mean length is strongly influenced by the size of the last large year-class, which in turn determines in large measure the population size (as measured by catch). Also, condition factor is apparently determined to a considerable degree by population size, and hence, there has been, over the 15-year period, an apparent correlation between length and *K*. That this correlation is of a parallel nature rather than cause and effect is in agreement with Clark's (1928, 1934) findings that the weight-length relationships of the sardine closely approximate the cubic form.

Table 6 presents the data illustrating the correlation of California sardine catch and *K* for January at San Pedro for the years 1942 through 1947. The data include the means for all fish and for each of the five 10-mm. length groups observed during the period. The value of *r* is high in each of the six groups and *P* is greater than 0.001 only in those two in which *N* is very low. This constitutes additional evidence that changes in *K* are probably associated with population size, and not length.

It is probable that the growth rate in terms of length is also greater for the sardine in times of low population density than in times of high population density. Of the 15 year-classes 1939 through 1952, five averaged less than 200 mm. in length as 2-ring fish. The estimated size of these five year-classes (1939, 1940, 1941, 1946, and 1947) (Clark and Marr, 1955) ranged from 1.9 billion fish to 7.2 billion fish and averaged 3.34 billion fish. Ten-year-classes averaged 200 mm. or larger as 2-ring fish. Seven of these year-classes ranged in estimated size from 0.1 to 2.3 billion fish and averaged 1.04 billion fish. Data for the other three year-classes (1951, 1952, and 1953) are incomplete, but they were well within the range of the other seven and would not markedly affect the average.

There are several complicating factors in the apparent association between year-class size and length growth. The size of the remaining population is not taken into account. Also, length reflects cumulative growing conditions over the life of the fish, while the condition factor more closely reflects current conditions. A year-class originating primarily in Sebastian-Viscaino Bay off Baja California probably has a different growth pattern than one originating off southern California, and one originating from a peak March spawning probably has a different growth pattern than one originating from a peak June spawning.

Table 6.—*Correlation data for condition factor (by length groups) at San Pedro in January and California sardine catch (thousands of tons) for the years 1942–57*

Length group	[1] *N*	*r*	*P*
190–199	7	−.859	.02>.01
200–209	11	−.913	<.001
210–219	10	−.846	<.001
220–229	9	−.946	<.001
230–239	4	−.972	.05>.02
All lengths	15	−.954	<.001

[1] Each *K* value is a mean of all January samples for that year.

One possible explanation of the high degree of inverse correlation between population size, as measured by the California catch, and condition factor is that there is a southward shift of the entire population (possibly owing to hydrographic conditions) in years of small population and a northward shift during years of large population. The data of figure 2 shows that the condition factors at Monterey tend to run higher than at San Pedro. However, the high degree of inverse correlation between catch and condition factor for January, when Monterey and San Pedro condition factors tend to be most nearly the same, does not substantiate this hypothesis.

Although the range of the California sardine extends farther to the north in years of large population and contracts toward the south in years of small population, sardine schools are not uniformly distributed throughout their range. During good years the population density is much greater within the range, also seasonal concentrations of schools occur within the range. Although the range of the sardine is bounded by land only on the east, it is probable that it is also bounded on the other sides by oceanographic features, so that as population size increases, within-range density increases more rapidly than the total range. Therefore, the inverse correlation of *K* and population (as measured by catch) could result from less available food-per-fish in times of large population and vice versa if the total amount of food available within the area did not vary considerably from year to year. If this hypothesis is true, it implies that the adult sardines have little interspecific competition for food.

Other similar-sized schooling species whose ranges overlap that of the sardine in California waters are the anchovy (*Engraulis mordax*), the Pacific mackerel (*Pneumatophorus diego*) and the jack mackerel (*Trachurus symmetricus*).

Anchovies have been abundant during the past few years, while the sardine population has been small. To a certain extent anchovies tend to frequent areas where sardines are not present and vice versa, although they are sometimes found schooling together. The largest anchovy catch in the years 1916 through 1955 occurred in 1953, when 43 thousand tons were taken by the commercial fishery and 6,000 tons by the live-bait fishery (Miller 1956). The anchovy stock is not fished intensively.

Landings of jack mackerel reached a peak of 67,000 tons in 1950 (Fitch 1956a). The population is probably not being intensively exploited by the fishery. Both the anchovy and jack mackerel were not fished to any great degree until the decline of the sardine population caused these two species to be sought as substitutes for canning purposes.

The Pacific mackerel has been intensively fished off the California coast over the 1940–41 to 1956–57 period covered by the sardine data. The highest catch in this period was 54,000 tons in the 1940–41 season (Fitch 1956b), although higher tonnages were landed in two seasons in the previous decade. Large year-classes of Pacific mackerel seem to have a slight tendency to coincide with large year-classes of sardines.

The anchovy appears to be a filter-feeder, whereas the two mackerels are selective feeders. Fitch (1956a) found that jack mackerel feed to a large extent on small crustaceans and also at times on juvenile squid and anchovies. Fitch (1956b) also stated that examination of 228 Pacific mackerel stomachs revealed that they feed largely on larval and juvenile fish and small crustaceans.

Lewis (1929) stated that the sardine is a filter-feeder, but Radovich (1952) concluded that it is also a particulate feeder. He found one occurrence of sardines feeding on juvenile anchovies. Sardines kept in tanks or large aquaria have been observed feeding selectively on numerous occasions.

Nothing is known about interspecific food competition between the adult anchovy and sardine. There is probably competition between the mackerels and the sardine as, in fact, they are not infrequently found in mixed schools and, at times, apparently feeding on much the same types of organisms. However, very little information is available on food competition among these and other local marine species, and such relationships must remain a matter of conjecture for the present, at least. A second way in which population size might affect feeding and condition factor is by its effect on school size. Large populations could result in large schools and smaller populations in smaller schools. It seems logical that a small school could feed more efficiently per individual fish than a large school.

SUMMARY

Low population levels of the Pacific sardine (*Sardinops caerulea*) (as indicated by the California catch) are associated with higher condition factors and greater average lengths of these fish and, conversely, high population levels are associated with lower condition factors and smaller average lengths.

The high degree of inverse correlation between population size and condition factor is interpreted as a cause and effect relation; that is, high population levels result in less available food-per-fish and lower condition factors, while low population levels result in more available food-per-fish and higher condition factors.

The inverse correlation between population size and fish length appears to result from the entrance of large year-classes into the population. When this occurs, average size (and age) is reduced as population size is increased. When small year-classes enter the population, average size (and age) is increased (because of the relatively high proportion of large, old fish in the population) as population size is decreased.

The apparent positive correlation between condition factor and length over the 15 seasons is not of a cause and effect type, but rather a parallel phenomenon. In years when high condition factors prevailed, all fish had high condition factors regardless of size and, conversely, in years when condition factors were low, all fish had low condition factors regardless of size.

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