RELATION BETWEEN SPAWNING-STOCK SIZE AND YEAR-CLASS SIZE FOR THE PACIFIC SARDINE *SARDINOPS CAERULEA* (GIRARD)

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

ABSTRACT

A high degree of inverse correlation between spawning-stock size and year-class size (based on indices of total fish caught) was found for the Pacific sardine (*Sardinops caerulea*). Over the 26-year period for which data are available it appears that catch, on which the indices are based, was determined primarily by population size and secondarily by availability and effort. The data indicate that spawning-stock size influences year-class size and that this is not merely a secondary result of year classes occurring in cycles which generate similar cycles of spawning populations several years later.

The object of this paper is to explore the relationships between spawning-stock size and year-class size for the Pacific sardine, *Sardinops caerulea* (Girard). It also treats to a lesser extent some of the other related factors involved in the population dynamics of the sardine.

The introductory paragraphs of Clark and Marr (1955) sum up the considerations of the problems as follows:

At the present stage of our knowledge, there is rather universal agreement that the only way Man can affect a population of marine fishes is by fishing (and, perhaps, by pollution in special situations). That is, we cannot economically fertilize large areas of the sea, nor can we treat epidemics in fish populations, nor hope to stock the ocean by means of hatchery-reared fish. There is further agreement that Man can affect fish populations by varying the amount of fishing and by varying the method of fishing. There is, however, disagreement about the nature and magnitude of such effects.

According to one theory, big spawning populations produce bigger year-classes than do small spawning populations. Therefore, one might suppose that reducing the total catch would make the spawning population bigger and therefore result in the production of bigger year-classes. Although this assumption has been made many times, it has not been demonstrated for any marine fish. The possibility that this theory does not conform to the fact will be discussed below. Unfortunately, this assumption is perhaps more often made tacitly than explicitly. There must, of course, be a critical population size below which the population will not be able to perpetuate itself.

And further:

The death rates from fishing and from natural causes can clearly be variable and will be influenced by many factors, so that it is difficult to generalize about them. Two features are of interest, however. One of these concerns the fact that when fishing mortality is imposed on a population, natural mortality is to some extent replaced by fishing mortality. That is, some of the fish which would have died naturally during a given time interval are caught instead. The other feature, and by far the most important one, is that as far as we can judge from all the observations that have been made, fishing and natural mortality exert their greatest influence on the size of the population existing at the time they occur. Opinions differ about their effect on the size of future additions to the population, i.e., year-class which will be produced subsequent to the time the mortalities occur.

There must, of course, be some "critical," minimum spawning stock size below which year-class size is a function of stock size, as we have already stated. This critical stock size has not yet been measured for any marine fishes. Above this minimum stock size all present evidence indicates that the magnitude of additions to the population (the size of individual year-classes) is not determined by the number of eggs spawned, but rather by variations in survival rate between the time the eggs are spawned and the time the resulting fish have grown large enough to enter the population. This means that the size of any particular year-class is determined, not by the number of adult fish

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(above minimum) which produce it, but rather by variations in the environment which affect survival rate after the eggs are spawned.

Clark and Marr were unable to agree on whether the size of the spawning stock determined the size of the year class. Their disagreement centered on whether or not large spawning stocks produced large year classes and small spawning stocks produced small year classes. The present paper extends their data from 19 to 26 years and re-examines the problem from a different point of view.

SOURCES OF DATA

The index of spawning population size and the index of year-class size used in this paper are essentially those used by Clark and Marr (1955), which they call "accumulated age estimates." The spawning-stock size in any given season is considered to consist of all fish having scales with three or more annuli taken in the following fall-winter fishery and all fish of these year classes taken in subsequent years plus one-half of the fish having two annuli taken in the following fall-winter fishery and one-half of the fish of this year class taken in subsequent years.

The northern fishery of the earlier years was actually a summer-fall fishery, and the expanded Mexican fishery of more recent years is pursued throughout the year although the heaviest landings generally coincide with the southern California fall fishery.

Estimates of a year class are derived by summing all fish of that year class caught during its life span with the following exceptions: only one-half of the fish with one annulus and one-fourth of the fish with no annuli are included. Fish in their first year were seldom taken by the commercial fishery, and fish with only one annulus were taken in appreciable quantities in only a few years. Most of the commercial sardine catch is made up of 2- and 3-annulus fish.

The above measure of spawning-stock size is used because it is the same as that used by Clark and Marr (1955). Actually age at first spawning varies over the geographic range of the sardine, apparently occurring earlier in the south and later in the north; it also varies from year to year. Also if the spawning-stock size is considered to be either all fish 2 years old or older or all fish 3 years old or older, and if the year class either includes or excludes fish taken at less than 2 years of age, the correlations obtained between year-class size and spawning-stock size are as good as those obtained from the measurements used in this paper.

The age composition of the commercial sardine catch was obtained from the following sources:

Year:	*Author*
1932 through 1937–38	Eckles (1954).
1938–39 through 1940–41	Wolf (1961).
1941–42 through 1946–47	Felin and Phillips (1948).
1947–48	Mosher et al. (1949).
1948–49 through 1955–56	Felin et al. (1949, 1950, 1951, 1952, 1953, 1954, 1955, 1958).
1956–57	Wolf et al. (1958).
1957–58	Daugherty and Wolf (1960).
1958–59	Wolf and Daugherty (1961).

Data for the 1959–60 and 1960–61 seasons were made available by Robert Wolf of the Bureau of Commercial Fisheries, and data for the Mexican fishery not already in the above reports by Makoto Kimura also of the Bureau of Commercial Fisheries. The only data available for some ports in a few of the earlier years are tons landed. These have been converted to age and numbers of fish on the basis of known age compositions of landings at the nearest ports having similar age composition landings in other years.

ANALYSIS OF DATA

The magnitude of the commercial catch depends upon 1) sardine population size, 2) fishing effort, and 3) availability of sardines to the fishing fleet. Over the 26-year period covered by this paper, the population size is the primary factor determining catch. Effort and availability may be considered as sampling errors whose effect is not great enough to negate the use of an index of population size based on catch. During the early years covered by the data, effort was increasing. This would cause earlier estimates of population size and year-class size to be lower with the latter less underestimated because of the 2-year lag. During the late 1940's to the present there have been first considerable fluctuation in fishing effort and finally a decrease in effort, both of which appear to be primarily responses to population size (as measured by catch) in the immediately preceding fishing seasons.

Although the range of the sardine has contracted considerably, and these fish are no longer available in commercial quantities in the northern portions of their former range, the sardine population still shifts northward in the summer and southward in the winter.

The population as a whole has shown fluctuations in availability as evidenced by changes in total mortality rates from year to year. In some years all year classes in the catch show a negative total mortality which cannot be accounted for by increased effort. This must result from increased availability. The seasonal shifts in sardine population do not seem to be constant from year to year, and consequently availability has its greatest effect in the most northern portion of the range.

The method of accumulating ages tends to offset the errors of changing effort and availability but not as much as it would in a longer lived species of fish. Changes in both availability and effort undoubtedly account for some of the variation in the correlations between spawning-stock size and year-class size.

Direct correlation methods are usually applied to frequency series rather than time series unless, in the latter case, neither of the time series is marked by a definite secular trend. The direct correlation of time series data can easily give a fortuitously high correlation. One method of circumventing this difficulty is to determine trends for the data and correlate the deviations from the trends. This method applies only when the parameters involved react to one another relative to their trends, rather than absolutely without regard to trends.

A third degree parabolic trend line, $Y_c=5.079+0.5475X-0.06670X^2+0.001497X^3$, in which Y_c =calculated spawning-stock size index in billions of fish and X=trend year, was fitted to the spawning-stock size indices (fig. 1). Similarly a third degree parabolic trend line, $Y_c=2.463+0.6050X-0.06754X^2+0.001614X^3$, in which Y_c=calculated year class size index in billions of fish and X=trend year was fitted to the year-class size indices (fig. 2).

The deviations of the observed values from calculated values were obtained. These data are presented in table 1. In figure 3 the two sets of deviations are plotted as anomalies from their trends. Year-class size deviations are plotted against spawning-stock size deviations in figure 4. The least squares regression line $Y_c=0.000136-0.6774X$ is also plotted. The correlation coefficient, r, equals -0.699, with a probability that such a correlation could be obtained by chance alone of less than one in a thousand.

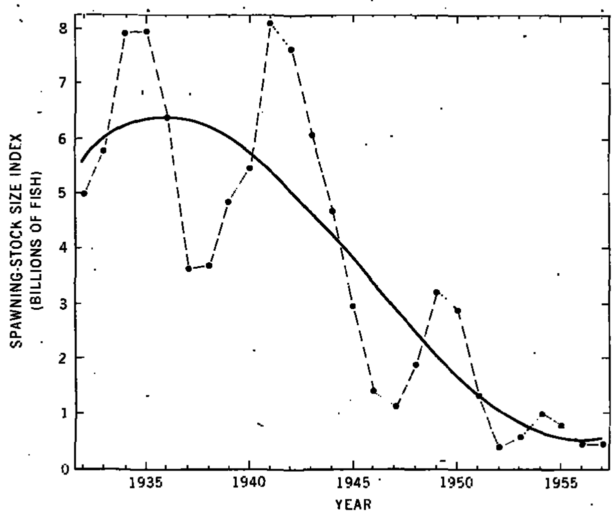

FIGURE 1.—Apparent trend of sardine spawning-stock size index, 1932–57.

As stated above the method of correlating deviations from trend guards against spuriously high correlations that may be obtained if trend data are directly correlated. In the present case the fact that two sets of parameters having such closely coincident trends do not have a high direct positive correlation is in itself significant. As we have seen this is caused by the fact that the parameters are inversely related with respect to trend.

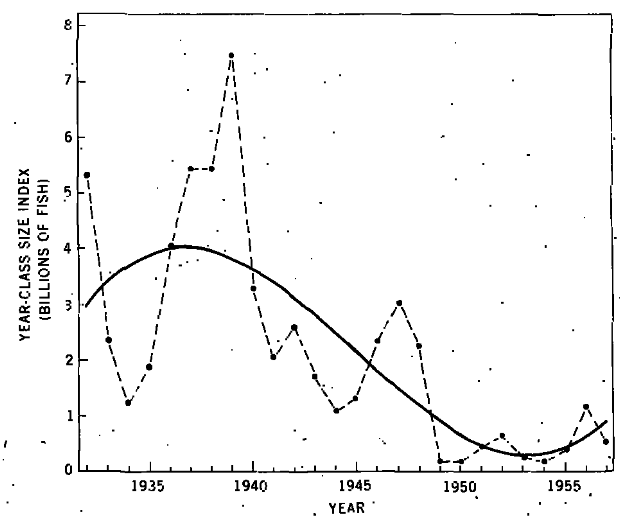

FIGURE 2.—Apparent trend of sardine year-class size index, 1932–57.

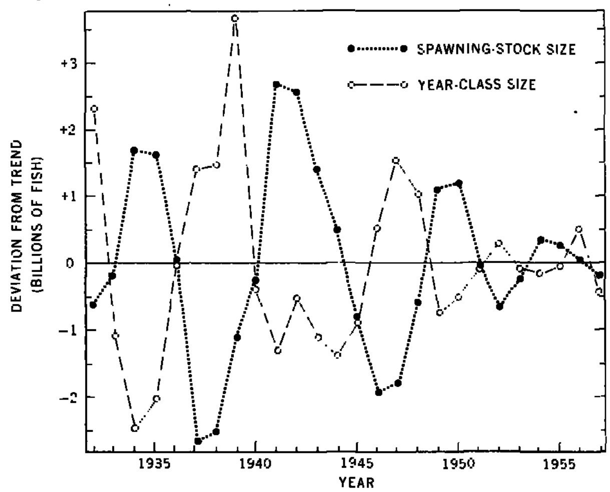

FIGURE 3.—Deviations from trends of sardine spawning-stock size index and year-class size index, 1932–57.

TABLE 1.—*Indices of spawning-stock size and year-class size of the Pacific sardine. Observed and computed values and deviations*

[Billions of fish]

Year	Trend year	Spawning-stock size			Year-class size		
		Observed	Calculated	Deviation	Observed	Calculated	Deviation
1932	1	4.96	5.56	−0.60	5.33	3.00	2.33
1933	2	5.76	5.92	−.16	2.37	3.42	−1.05
1934	3	7.87	6.16	1.71	1.26	3.71	−2.45
1935	4	7.94	6.31	1.63	1.89	3.91	−2.02
1936	5	6.34	6.34	.00	4.03	4.00	.03
1937	6	3.64	6.29	−2.65	5.44	4.01	1.43
1938	7	3.67	6.16	−2.49	5.42	3.94	1.48
1939	8	4.83	5.96	−1.13	7.47	3.81	3.66
1940	9	5.44	5.70	−.26	3.27	3.61	−.34
1941	10	8.09	5.38	2.71	2.07	3.37	−1.30
1942	11	7.61	5.02	2.59	2.59	3.10	−.51
1943	12	6.04	4.63	1.41	1.69	2.79	−1.10
1944	13	4.69	4.22	.47	1.07	2.46	−1.39
1945	14	2.95	3.78	−.83	1.27	2.13	−.86
1946	15	1.39	3.34	−1.95	2.32	1.79	.53
1947	16	1.11	2.90	−1.79	3.03	1.47	1.56
1948	17	1.88	2.47	−.59	2.22	1.16	1.06
1949	18	3.18	2.06	1.12	.14	.89	−.75
1950	19	2.89	1.68	1.21	.15	.65	−.50
1951	20	1.31	1.33	−.02	.41	.46	−.05
1952	21	.39	1.03	−.64	.63	.33	.30
1953	22	.58	.79	−.21	.22	.27	−.05
1954	23	.97	.61	.36	.16	.29	−.13
1955	24	.78	.50	.28	.36	.40	−.04
1956	25	.43	.48	.05	1.16	.60	.56
1957	26	.41	.55	−.14	.52	.91	−.39

As also stated above, the trend method cannot be applied to parameters that react to one another absolutely, which is generally the case when biological parameters are involved. In fact, one would expect this to be the case in the present instance. As will be shown later, the period of years involved may be divided into three more or less distinct phases of population contraction. The same phenomena of population dynamics seem to be functioning within successively smaller population ranges. This permits the population data to be treated as a trend that allows the data for all years to be included in a single correlation.

By using the trend method, the total fish caught spawning-stock size index may be compared to a second, more frequently used population size index, catch per unit of effort. Such data are available for 23 seasons for the California fishery from 1932–33 through 1954–55 (Marr, 1960).

Catch per unit of effort data (tons of sardines landed per boat-month) are presented in table 2. A third degree parabolic trend line ($Y_c=693.76-28.854X-0.034874X^2-0.0047127X^3$ in which $Y_c=$ computed catch per unit of effort and $X=$trend year) was fitted to these data (fig. 5). When the deviations from trend of spawning-stock size index are correlated with the deviations from trend of catch per unit of effort for the 23 seasons, a positive correlation coefficient of 0.822 is obtained. The data were fitted to the least squares regression line, $Y_c=-0.0057656+0.011304X$, in which $Y_c=$computed spawning stock size deviation and $X=$catch per unit of effort deviation (fig. 6).

There is no reason to believe that catch per unit of effort is necessarily a better measure of

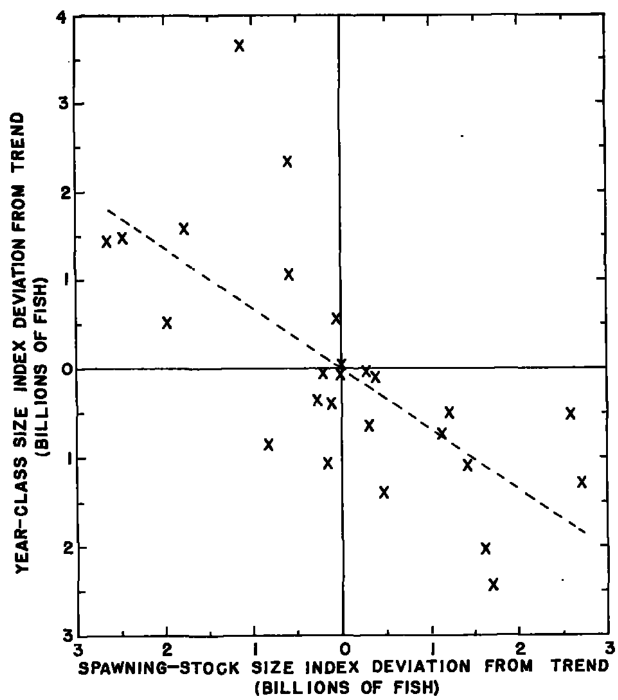

FIGURE 4.—Deviation from trend of year-class size plotted against deviation from trend of spawning-stock size for 26 years (1932–57).

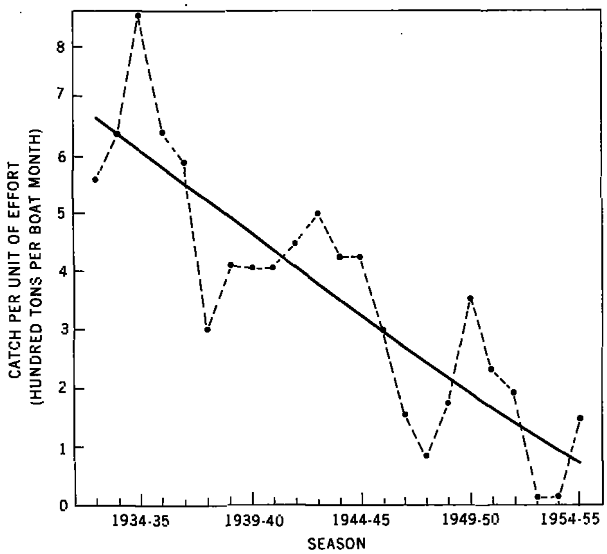

FIGURE 5.—Apparent trend of sardine catch per unit of effort, 1932–33 through 1954–55 seasons.

population size than the total fish caught index. The former accounts for changing effort but measures only the population available to the fishery in that year. The latter tends to average the effects of both effort and availability over several years. At relatively low levels of fishing effort directed against a stable fish population one might reasonably expect that changes in effort would result in directly proportional changes in catch. However, at relatively high levels of fishing effort a "saturation point" is reached above which relatively large changes in effort result in relatively small changes in catch. This effort saturation point seems to have been exceeded throughout most of the period covered in this paper as later data will indicate. The above conditions will tend to impair the accuracy of the catch per unit of effort index to a greater extent than the total fish caught index. The excellent correlation between the two indices, however, is evidence of their validity as measures of population size.

TABLE 2.—*Observed and calculated California catch per unit of effort data (tons per boat-month) and deviations compared with spawning-stock size index deviations*

Year	Trend year	Observed catch per unit of effort	Computed catch per unit of effort	Deviation	Spawning-stock size index deviation
1932–33	1	557	665	−108	−0.60
1933–34	2	636	636	0	−.16
1934–35	3	835	607	228	1.71
1935–36	4	638	578	60	1.63
1936–37	5	586	549	37	.00
1937–38	6	302	520	−218	−2.65
1938–39	7	409	492	−83	−2.49
1939–40	8	405	463	−58	−1.13
1940–41	9	404	435	−31	−.26
1941–42	10	447	406	41	2.71
1942–43	11	497	378	119	2.59
1943–44	12	422	351	71	1.41
1944–45	13	420	323	97	.47
1945–46	14	302	296	6	.83
1946–47	15	153	269	−116	−1.95
1947–48	16	81	242	−161	−1.79
1948–49	17	173	216	−43	−.59
1949–50	18	352	191	161	1.12
1950–51	19	229	165	64	1.21
1951–52	20	187	140	47	−.02
1952–53	21	10	116	−106	−.64
1953–54	22	11	92	−81	−.21
1954–55	23	145	69	76	.36

Another method of demonstrating the relation between year-class size and spawning-stock size (fig. 7) involves fitting a parabola directly to the data. Ricker (1954) gives a number of examples of reproduction curves of somewhat similar nature. The curve I have fitted in figure 7 is a transformation of the straight line fitted to recruits per spawner plotted against spawning-stock size. That is, if Y equals year-class size and X equals spawning-stock size, a straight line may be fitted to $\frac{Y}{X}=1.28867-0.12658X$. Multiplying through by X gives a second degree parabola: $Y=1.28867X$

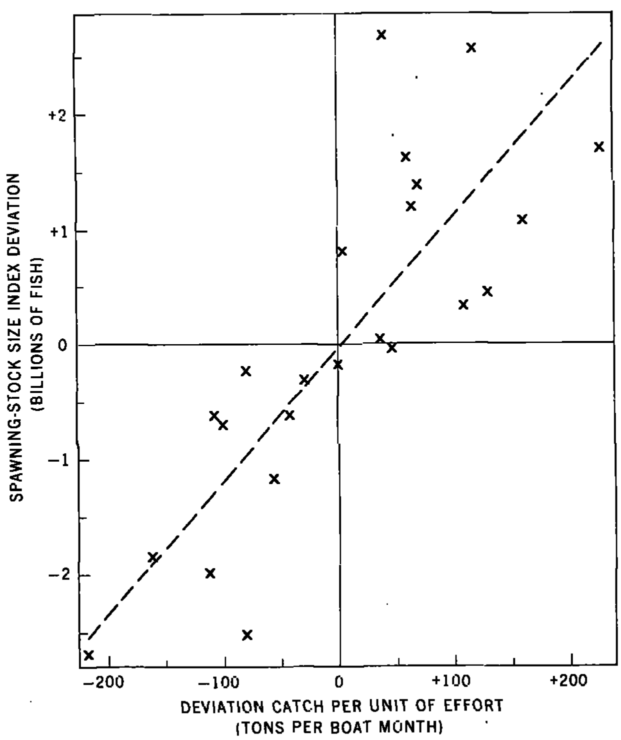

FIGURE 6.—Deviation from trend of spawning-stock size plotted against deviation from trend of catch per unit of effort for 23 seasons (1932–33 through 1954–55).

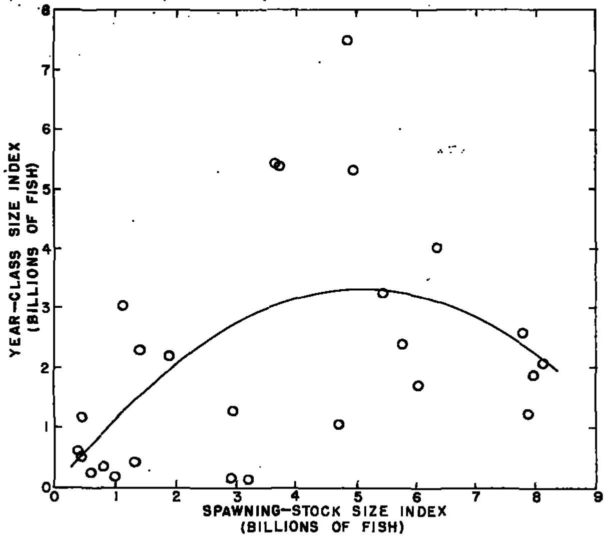

FIGURE 7.—Sardine year-class size plotted against spawning-stock size with fitted second degree parabola, $Y=1.28867X-0.12658X^2$, $r=0.539$, $p<.01$.

$-0.12658X^2$. A straight line may be fitted to random numbers as above and will yield a significant correlation if enough pairs of random numbers are used, but the transformation of such a line will, of course, no longer show a significant correlation.

In figure 8 spawning-stock size and year-class size indices are plotted against time for the sardine data. In figure 9 the observed spawning-stock size index and the computed values for year-class size obtained from the curve in figure 7 are plotted against time. A comparison of these two figures indicates that the curve is not an adequate description of the data. It is difficult to see how this curve would describe such a relationship when the fish species is fairly short-lived, year-class size is measured after the fish enters the fishery, and the data follow a somewhat cyclical pattern. In order for the population to pass over from the right limb of the curve to the left limb, it would have to move through a period of large year-class production which would throw it back to the right limb again.

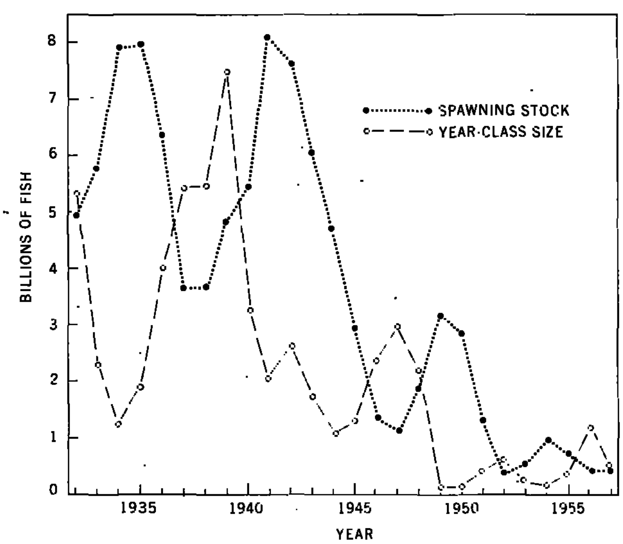

FIGURE 8.—Sardine year-class size and spawning-stock size plotted against time, 1932–57.

Although the method of analyzing the data by trend deviation is satisfactory for the entire period covered, a more illuminating analysis may be obtained by breaking the data down into three periods of no trend which may be treated separately. The data are presented in this manner in figure 10. The straight line on the right is fitted to the data for the 11 years 1932–42; the line in the middle is fitted to the 6 years 1945–50; and the line on the left is fitted to the 6 years 1952–57. The years 1943 and 1944 marked the beginning of the first collapse of the fishery. Both of these collapses were associated with reductions in the range of the sardine. In the mid-1940's the sardine disappeared in commercial quantities from British Columbia to Central California and the Central California fishery became sporadic. The

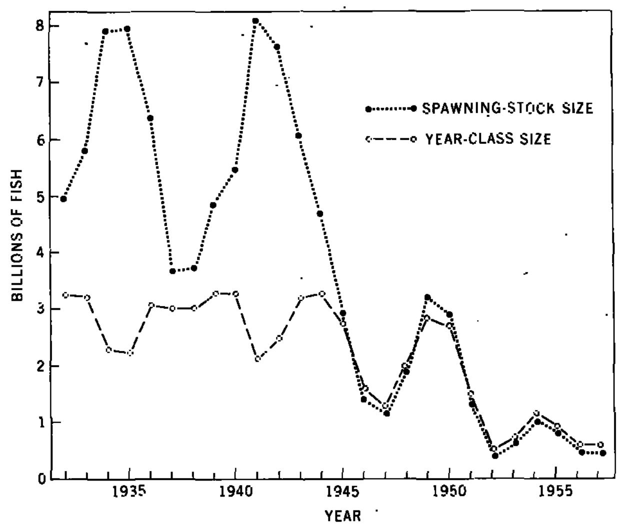

FIGURE 9.—Sardine year-class size index computed from curve (fig. 7) and observed spawning-stock size index plotted against time (1932–57).

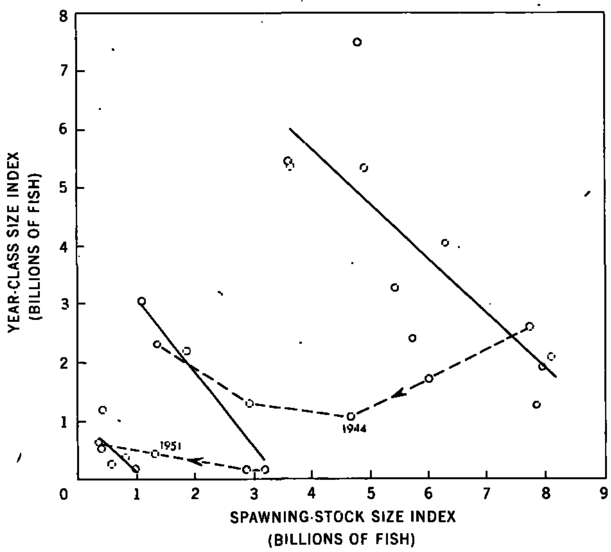

FIGURE 10.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of the three periods 1932–43, 1945–50 and 1952–57.

San Pedro fishery remained relatively unaffected. In the early 1950's the Central California landings became negligible or absent and the San Pedro fishery became sporadic. It appears, however, that the same inverse relationship between spawning-stock size and year-class size persisted but within reduced ranges.

In figure 11 spawning-stock size and year-class size indices based on San Pedro landings only are plotted against time. Two fishery periods and one collapse are evident here. In figure 12 a

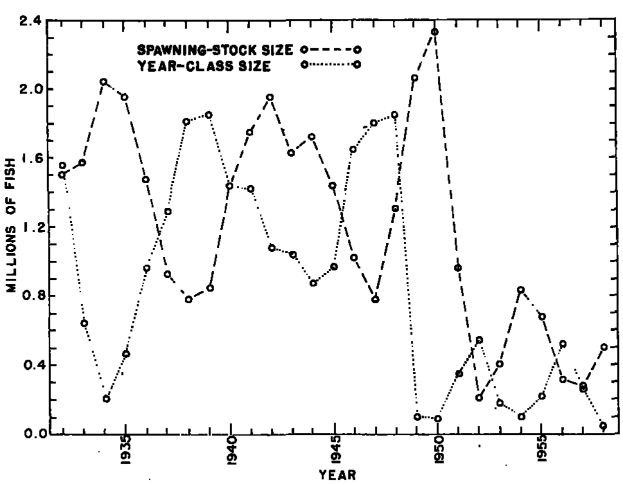

FIGURE 11.—Sardine year-class size index and spawning-stock size index plotted against time (1932–57) San Pedro, California, only.

straight line has been fitted to the 19-year period 1932–50 on the right, and a second straight line to the 7-year period 1952–58 on the left.

The three fitted lines ($Y=a+bX$) for all ports and the two for San Pedro are presented in figure 13. Correlation data for these lines are presented in table 3. It is noteworthy that the regression lines all have about the same slope and that the periods of fishery collapse originate and cross over from the lower right-hand area of the regression lines rather than going "over a curve."

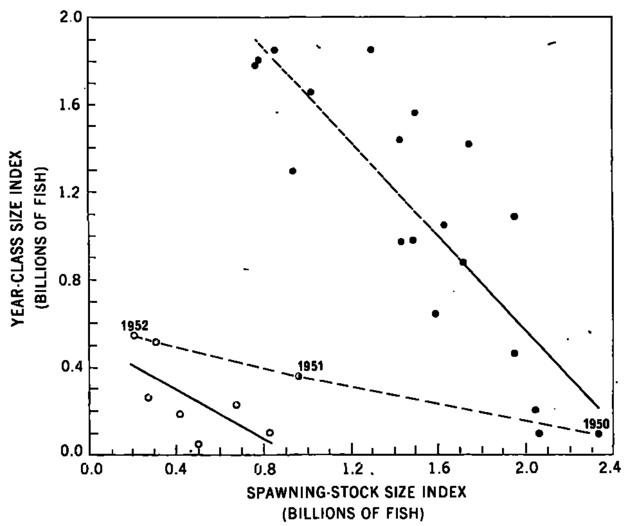

FIGURE 12.—Sardine year-class size index plotted against spawning-stock size index and lines fitted to each of two periods, 1932–50 and 1952–58, San Pedro only.

TABLE 3.—*Correlation between spawning-stock size and year-class size*

	N	r	P
Index based on—			
All ports:			
1932–42	11	−0.820	0.001
1945–50	6	−.936	.01
1952–57	6	−.669	.1
San Pedro:			
1932–50	19	−.845	.001
1952–58	7	−.691	.1

The existence of good correlations between spawning-stock size and year-class size does not in itself mean that spawning-stock size necessarily affects year-class size. On the other hand it is axiomatic that year-class size (as measured after the fish have entered the fishery or spawning stock) affects spawning-stock size a few years later. By using the method of correlating deviations from trend, an excellent negative correlation

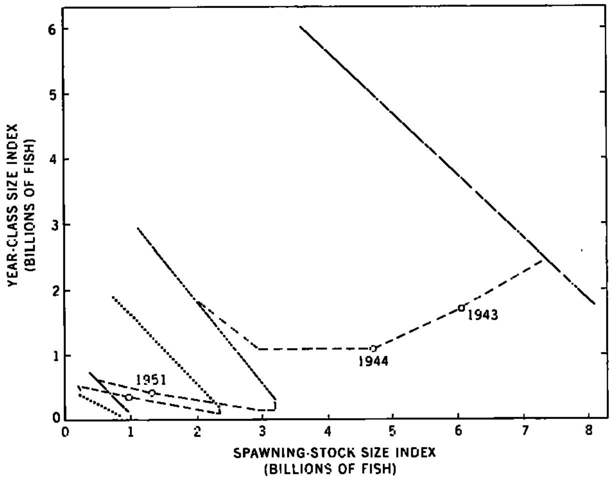

FIGURE 13.—Comparison of computed lines for three periods shown in figure 10 (all ports) and two periods shown in figure 12 (San Pedro) with transitional years plotted.

was found between spawning-stock size and year-class size. A slightly better positive correlation, however, may be found between year-class size and spawning-stock size 3 years later. Correlation coefficients of year-class size on spawning-stock size for a series of lagged and advanced years are presented in figure 14.

From the above we may hypothesize either 1) that the apparent cause and effect relationship between spawning-stock size and year-class size is merely a byproduct of the known effect of year-class size on subsequent spawning-stock or 2) that spawning-stock size actually determines year-class size. If the former is true, year-class size could either fluctuate or follow cycles. If the latter is true, year-class size would follow a cycle. Examination of the data reveals that they do appear to follow a cyclical pattern, and, in fact, if they did not, the excellent negative correlation between spawning-stock size and year-class size could not be found. Also this correlation would not result unless the length of the cycle was approximately twice the mean age of the spawning stock.

Therefore, although the effect of year-class size on subsequent spawning-stock size could cause the apparent relationship between spawning-stock size and year-class size, the circumstances under which this could occur are limited. If this hypothesis were true the factors determining year-class size would have to occur in cycles approximately equal to twice the mean age of the spawning stock. At present, the only known factor that follows this pattern is spawning-stock size.

Figure 15 presents eight population models based on the sardine data. These models illustrate what correlations would exist between spawning-stock size and year-class size if there were no cause and effect relationship between these two parameters and if the correlation resulted from the cause and effect relationship between year-class size and subsequent spawning-stock size alone. Figure 15 shows that the length of cycle determines whether or not the cycles are in or out of phase and consequently the degree and direction of the correlation. These data are presented in somewhat different form in figure 16 to which the plot of the observed correlation coefficient has been added. The factors controlling the cyclical pattern of year-class size would have to vary in approximately an 8- to 10-year cycle in order for the high observed correlation coefficient to obtain. No environmental factor varying in such a manner has yet been found.

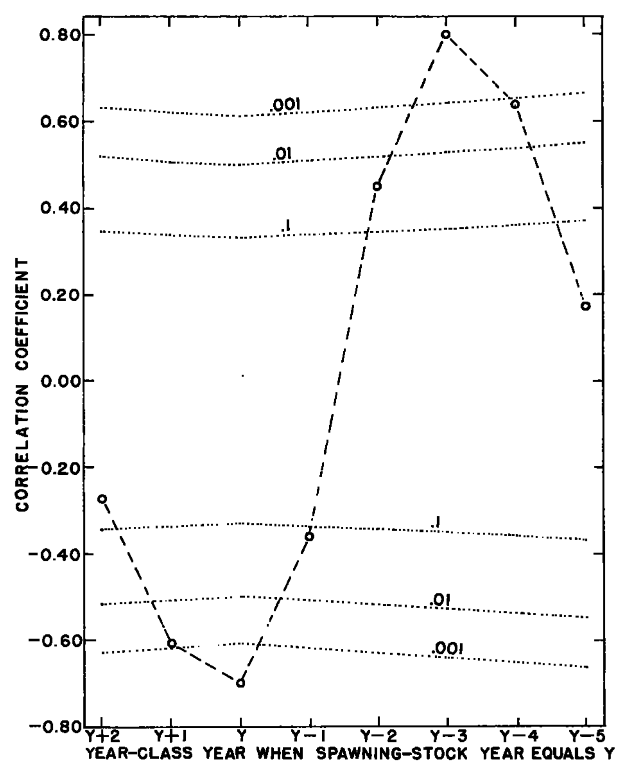

FIGURE 14.—Correlations between year–class size index deviations from trend in year, y, each of the 2 succeeding years and each of the 5 preceding years and spawning-stock size index deviations from trend in year, y.

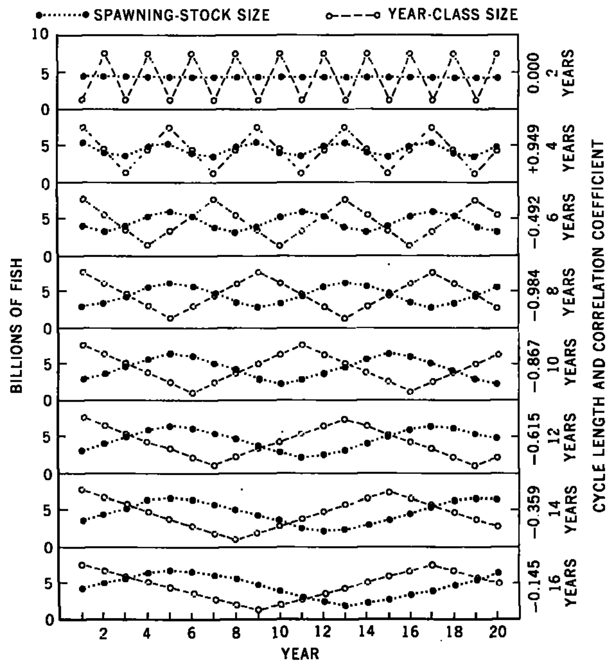

FIGURE 15.—Population models (based on sardine data) illustrating the effect (for eight cycles of different lengths) of year class strength on subsequent spawning stock size when spawning stock size exercises no influence on year-class size.

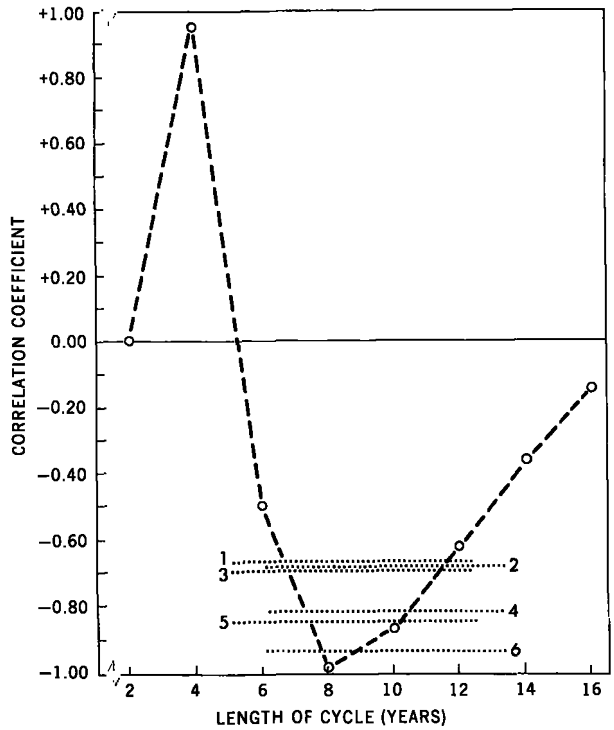

FIGURE 16.—Correlation coefficients plotted against length of cycle for data in figure 15. Observed correlation coefficients for spawning stock size index and year class size index indicated by dotted lines: No. 1 all ports 1952–57, No. 2 San Pedro 1952–58, No. 3 all ports 1932–57 (deviations from trend), No. 4 all ports 1933–42, No. 5 San Pedro 1932–50, No. 6 all ports 1945–50.

On the other hand, if spawning-stock size causes year-class size, Ricker (1954) has pointed out that the length of the cycle should be twice the mean length of a generation (interval from egg to egg). This appears to be applicable to the present data. In fact there is a shortening of the cycle length over the period covered coincident with a decrease in the mean age of spawning stocks resulting from the disappearance of the longer lived later maturing northern fish.

If it is assumed that spawning-stock size alone causes year-class size the population model, based on the sardine data, shown in figure 17 would prevail. Starting with the largest observed spawning-stock size index spawning-stock size and year-class size would fluctuate inversely in cycles of constant length but decreasing amplitude until, after many years, an equilibrium population was attained. Any environmental factors that affected the spawning-stock composition would, of course, once again initiate the fluctuating cycles.

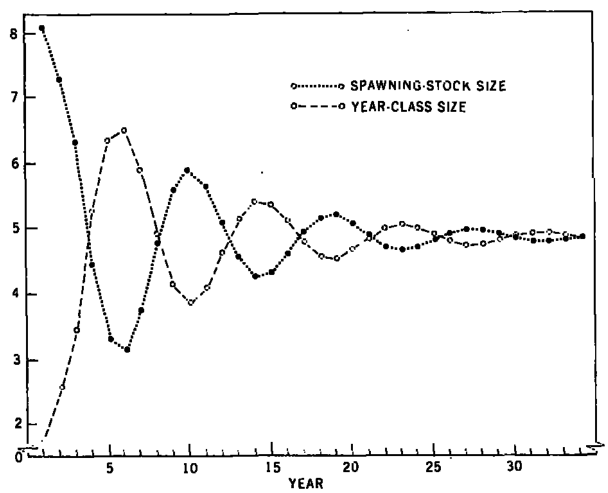

FIGURE 17.—Population models (based on sardine data) illustrating the effect of spawning-stock size on year-class size when spawning stock size determines year class size according to the straight line formula determined for sardines for all ports, 1932–43.

Data comparable to those presented for the sardine may be found for the haddock (Herrington, 1948). Catch per unit of effort indices for haddock

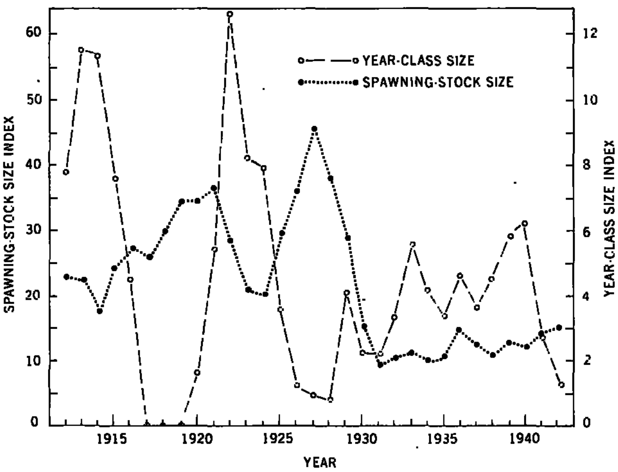

FIGURE 18.—Haddock spawning stock size index and year class size index plotted against time.

spawning-stock size and year-class size plotted against time are shown in figure 18. According to Ricker (1954) there was a radical change in fishing methods about 1930. The good inverse correlation between spawning-stock size and year-class size that prevailed until 1929 is no longer apparent after that date (figs. 18 and 19). The haddock has not undergone any great reduction of range comparable to that exhibited by the sardine.

The use of spawning-stock size and year-class size indices assumes that total sardines caught

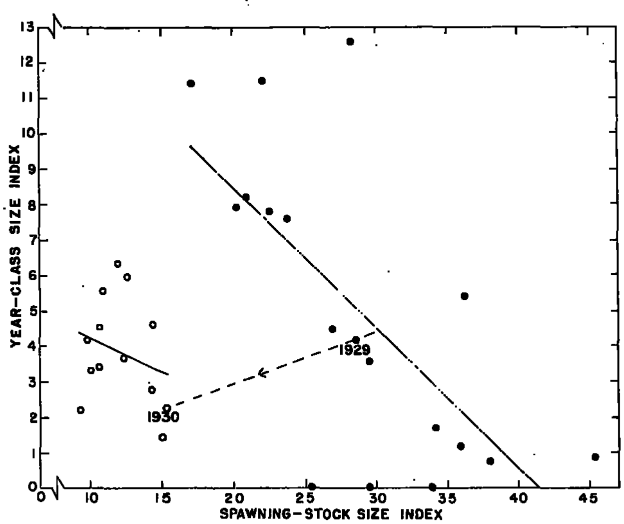

FIGURE 19.—Haddock year-class size index plotted against spawning-stock size index and computed regression lines for two periods (1912–29 and 1930–42).

adequately reflects the actual population size and year-class size present in the ocean. Although this certainly appears to be true in the case of the sardine, there are several other factors that may cause some error in the estimates. One of these is effort.

California catch (thousands of tons) and effort (boat months) (Marr, 1960) are plotted in figure 20 and also presented in table 4.

When these values are directly correlated a correlation coefficient of 0.533 ($P.=0.01$) is obtained. However, if catch is correlated with effort 1, 2, or 3 years later, even higher correlations are obtained as follows:

Catch year	*Effort year*	*Years*	*r*
y	$y-1$	22	0.172
y	y	23	.533
y	$y+1$	22	.631
y	$y+2$	21	.636
y	$y+3$	20	.538
y	$y+4$	19	.419

These data are plotted with levels of probability in figure 21.

The above correlations appear to be caused at least in part by trend. Third degree parabolas were fitted to catch and effort data, and deviations obtained. These deviations are plotted for the 23 years in figure 22. The coefficient of correlation and the rank coefficient of correlation for various lagged and advanced series of years are as follows:

Catch year	*Effort year*	*Years*	*r*	*Pr*
y	$y-2$	21	-------	−0.472
y	$y-1$	22	−0.366	−.570
y	y	23	.208	.081
y	$y+1$	22	.197	.206
y	$y+2$	21	.106	.221
y	$y+3$	20	-------	.178

These data are plotted with levels of probability in figure 23. The great deviation in effort in the 1950–51 season tends to depress the correlation coefficients especially those of effort years $y+1$ and $y+2$ of trend deviations. The effort peaks also seem to follow the catch peaks in the earlier years and more nearly coincide with them in latter years. If the deviations from trend are correlated directly for the 1932–33 through 1948–

TABLE 4.—*California sardine catch and effort 1932–33 through 1954–55*

Season	Catch	Effort
	Thousands of tons	*Boat months*
1932–33	248	447
1933–34	382	600
1934–35	597	715
1935–36	557	874
1936–37	724	1,236
1937–38	413	1,368
1938–39	572	1,401
1939–40	531	1,312
1940–41	455	1,125
1941–42	584	1,306
1942–43	505	1,008
1943–44	479	1,123
1944–45	555	1,304
1945–46	404	1,313
1946–47	234	1,487
1947–48	121	1,356
1948–49	184	918
1949–50	334	948
1950–51	351	1,531
1951–52	127	594
1952–53	4	466
1953–54	3	296
1954–55	66	458

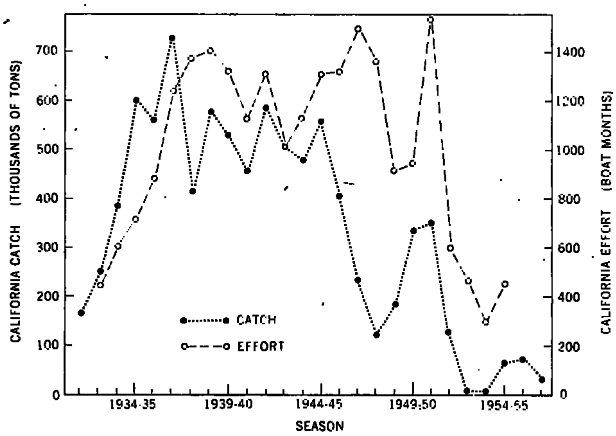

FIGURE 20.—California catch and effort plotted against time for 23 seasons.

49 period only, the following correlation coefficients are obtained:

Catch year	*Effort year*	*Years*	*r*
y	*y*−3	14	−0.062
y	*y*−2	15	−.434
y	*y*−1	16	−.618
y	*y*	17	−.171
y	*y*+1	16	.117
y	*y*+2	15	.618
y	*y*+3	14	.569

These data are plotted with levels of probability in figure 24.

The above analysis of catch and effort data indicates that catch causes effort rather than vice versa. The lag in effort appears to be more nearly 3 years at the beginning of the period and closer to 1 year at the end of the period. It is especially

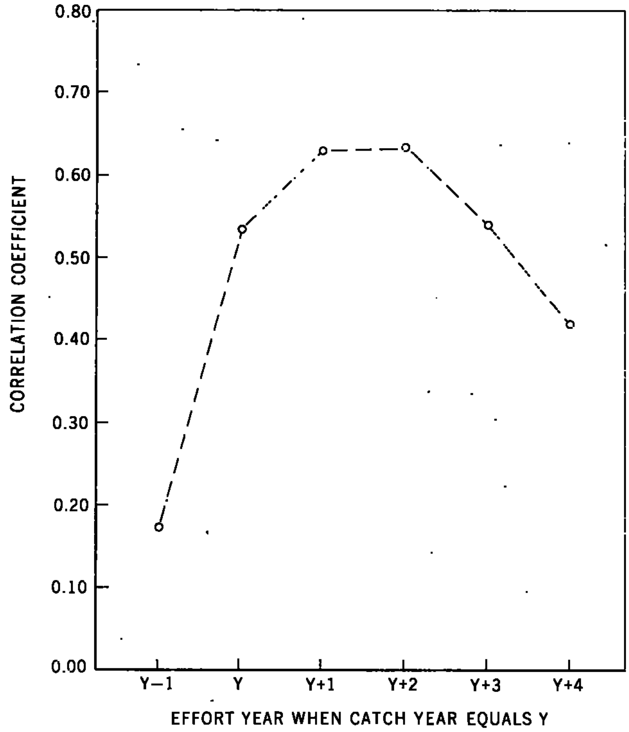

FIGURE 21.—Correlations between California catch in year, *y*, and effort in year, *y*, the preceding year, and the 4 subsequent years.

noticeable also that toward the end of the period effort is low in some years because of the scarcity of fish in those same years. When preseason evidence indicates a scarcity of fish, many boats will not begin to fish and others will stop fishing within the first month or two of the season; and conversely, when fish are abundant, effort will remain high throughout the season.

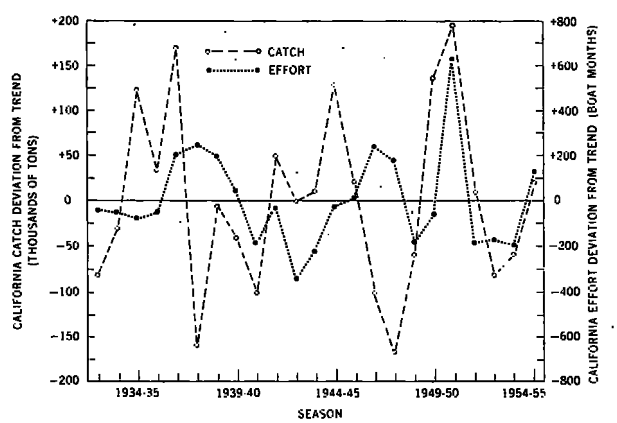

FIGURE 22.—Deviations from trend of California catch and effort, 1932–33 through 1954–55 seasons.

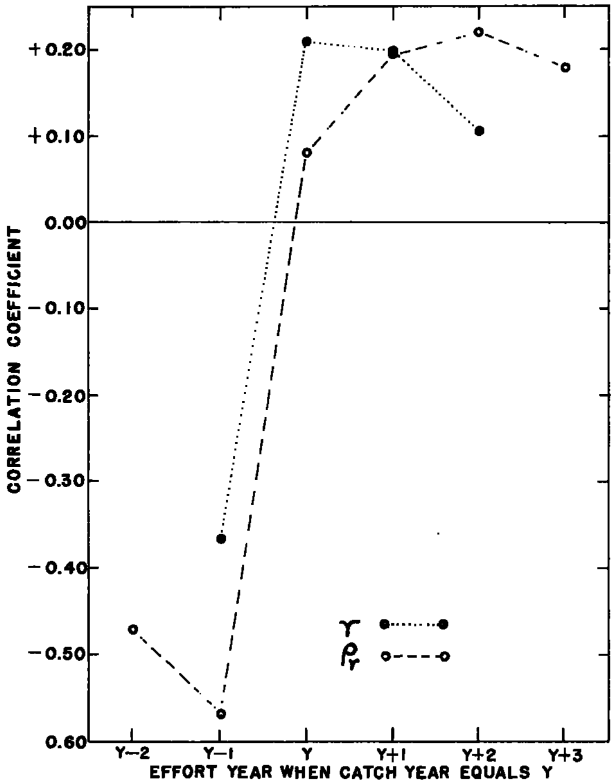

FIGURE 23.—Correlation and rank correlation between deviations from trend of California catch and effort 1932–33 through 1954–55 seasons.

It is also noteworthy that the 1934–35 effort of 715 boat-months yielded the second highest catch of the 23-year period despite the fact that effort did not drop below the 1934–35 figure until 1951–52 and averaged 54 percent higher during these 16 years. The high negative correlations between effort in one year and catch the following year may mean that high effort in one year will reduce the catch in the following year or it may only be a manifestation of the cyclical nature of the data.

Two-annulus sardines are not fully available to the fishery. This may be seen from the following 28-year average (geometric mean) survival rates for sardines based on all ports:

Percent	*From annuli—*	*to annuli—*
109	2	3
46	3	4
37	4	5
30	5	6
22	6	7
10	7	8

A survival rate of 109 percent would be impossible if the fishery sampled the 2-annulus fish equally as well as the older fish. There may also be some selectivity of larger fish by fishermen.

Table 5 presents correlation coefficients obtained from direct correlations of various pairs of parameters based on the San Pedro sardine fishery for the 14-year period 1937–38 and 1950–51. These parameters exhibit negligible trend over this period.

TABLE 5.—Correlation coefficients [1] for various pairs of parameters, San Pedro sardines 1937–38 through 1950–51 seasons

	Spawning-stock size index	Effort	Catch
Percent of year class taken as 2-annulus fish	−0.773	−0.007	+0.137
Effort	−.342		+.309
Spawning-stock size index		−.342	−.031

[1] Probability levels: N=14 n=12 P=0.1 0.01 0.001
r=0.458 .661 .780

There is an excellent negative correlation between spawning stock size index and the percent of a year class taken as 2-annulus fish. None of the other pairs of parameters involved yields a significant correlation for this period of years.

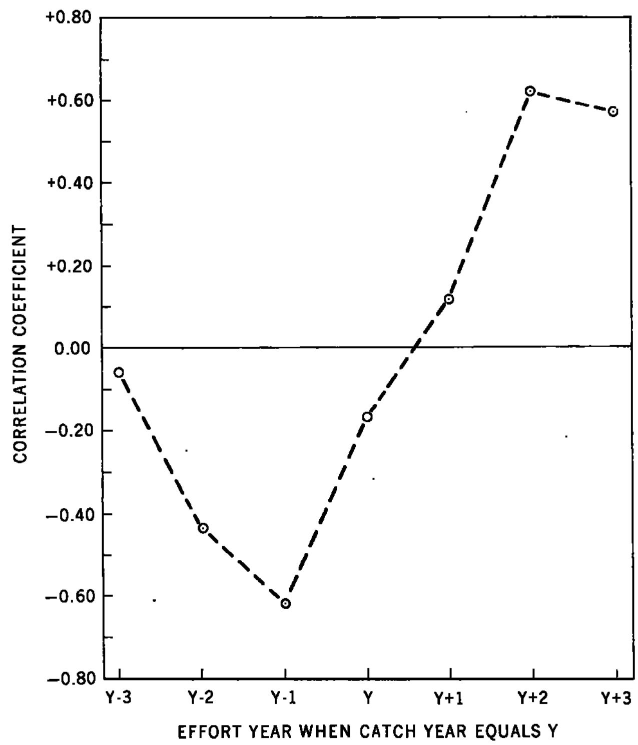

FIGURE 24.—Correlations between deviations from trend of California catch in year, y, and effort deviations from trend in year, y, the preceding 3 years and the succeeding 3 years.

These data indicate that catch was maintained relatively high during periods of low spawning-stock size by directing more fishing effort against the 2-annulus fish which were entering the fishery at that time.

A measure of survival or mortality may be obtained by comparing the number of sardines having three or more annuli caught in one season with the number of sardines having four or more annuli caught in the following season. This measure includes the effect of changing effort and availability. This is shown by the fact that in some years survivals in excess of 100 percent (or negative mortalities) may be obtained.

Survival data, computed as above, are presented in table 6 and figure 25 for all ports and for San Pedro only. Logarithmic second degree parabolic trend line values fitted to these data are also plotted. The apparent high survival values during 3 of the first 4 years are probably caused by increasing effort as the fishery was developing. Following that period, effort appears to be saturated with respect to population size and its effects become secondary. In theory effort should affect survival rates both absolutely and relatively. A high effort should increase total mortality thus decreasing survival, and a low effort should con-

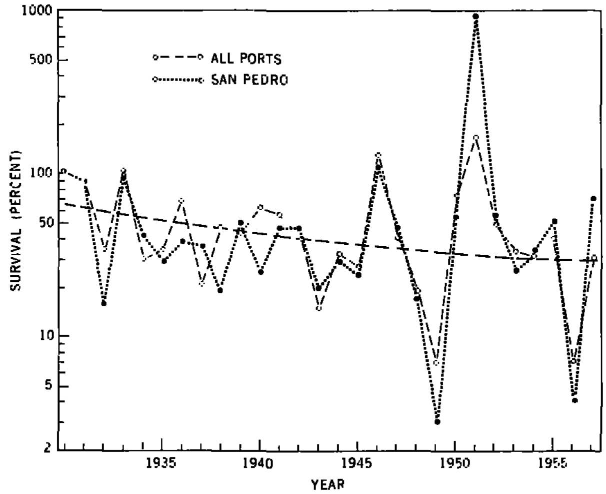

FIGURE 25.—Apparent survival trends for all ports and San Pedro only, 1933 through 1960.

versely increase survival. Also a change from a lower effort to a higher effort should cause apparent survival to increase. These relationships are not apparent in the survival data.

In addition to being affected by the increasing effort during the early years, the trend lines are also influenced by the changing age composition of the population. In the earlier years a greater proportion of the population was made up of the

TABLE 6.—*Sardine survival as measured by 4-annulus and older fish caught in one year expressed as a percent of 3-annulus and older fish caught the preceding year*

Season		All ports				San Pedro			
		Population size (millions of fish)		Survival (percent)		Population size (millions of fish)		Survival (percent)	
3-annulus and older	4-annulus and older	3-annulus and older	4-annulus and older	Observed	Computed	3-annulus and older	4-annulus and older	Observed	Computed
1932–33	1933–34	1,401	1,459	104	65.1	473	489	103	56.1
1933–34	1934–35	1,769	1,532	87	62.1	578	509	88	52.9
1934–35	1935–36	2,807	981	35	59.3	877	142	16	50.0
1935–36	1936–37	2,829	2,918	103	56.7	719	678	94	47.4
1936–37	1937–38	3,861	1,151	30	54.3	861	369	43	45.1
1937–38	1938–39	1,672	645	39	52,0	510	149	29	43.1
1938–39	1939–40	890	604	68	50.0	206	78	38	41.3
1939–40	1940–41	1,875	399	21	48.0	244	88	36	39.7
1940–41	1941–42	1,544	799	47	46.2	409	78	19	38.4
1941–42	1942–43	2,378	1,075	45	44.6	543	269	50	37.2
1942–43	1943–44	2,981	1,862	62	43.1	941	237	25	36.1
1943–44	1944–45	2,893	1,627	56	41.6	587	276	47	35.2
1944–45	1945–46	2,384	948	40	40.3	797	370	46	34.5
1945–46	1946–47	1,819	270	15	39.1	740	151	20	33.9
1946–47	1947–48	654	210	32	37.9	471	137	29	33.4
1947–48	1948–49	404	109	27	36.9	291	69	24	33.1
1948–49	1949–50	297	380	128	35.9	215	233	108	32.8
1949–50	1950–51	1,210	496	41	35.0	771	364	47	32.7
1950–51	1951–52	1,526	285	19	34.2	1,229	204	17	32.7
1951–52	1952–53	1,017	67	7	33.4	797	20	3	32.8
1952–53	1953–54	89	66	74	32.7	23	12	52	33.0
1953–54	1954–55	108	184	170	32.0	16	148	925	33.4
1954–55	1955–56	409	199	49	31.5	339	185	55	33.9
1955–56	1956–57	467	157	34	30,9	437	110	25	34.5
1956–57	1957–58	247	78	32	30.4	175	60	34	35.2
1957–58	1958–59	162	67	41	30.0	109	56	51	36.1
1958–59	1959–60	338	22	7	29.6	233	9	4	37.1
1959–60	1960–61	181	56	31	92.3	56	40	71	38.3

longer lived northern fish. As an example, the geometric mean of survival for the 7 years 1942–48 was 54 percent in the Pacific Northwest and 32 percent in San Pedro. Aside from the effects of changing population composition, effort, and availability, survival probably remained relatively unchanged over the 28-year period.

Although not measurable, the effects of availability may be seen in the increasingly large fluctuations in survival toward the end of the 28-year period in figure 25. It appears that availability has had its greatest effect on the northern periphery of the sardine range, and considerably influenced the catch in British Columbia and the Pacific Northwest throughout the existence of the fisheries in these areas. Population size, however, also exerted great influence and was undoubtedly related to availability in this area. Certainly population size was the primary factor influencing the fisheries when all ports are considered. In more recent years the reduction of the range of the sardine has caused the effects of availability to be felt much farther to the south, and the relatively larger proportion of the population affected has caused the greater fluctuation in apparent survival. In at least a few of these later years availability has probably been the dominant factor affecting the fishery, although population size and availability are probably to a certain extent themselves related. Nevertheless, over the period of years treated in this paper, population size has been, without any doubt, the primary and dominating factor influencing the success of the fishery.

SUMMARY

1. For the 26-year period (1932–1957) an excellent negative correlation exists between anomalies of spawning-stock size and year-class size for the Pacific sardine.

2. This correlation may be demonstrated by correlating deviations from trends of the two parameters or by directly correlating the parameters for three (all ports) or two (San Pedro only) periods of no no trend separated by fishery failures and a reduction in sardine range.

3. The data indicate that the good negative correlation existing between spawning-stock size and year-class size is not a secondary result of year classes occurring in cycles which generate cycles of population size several years later.

4. The indices of year-class size and spawning-stock size are based on catch, which is determined primarily by actual population size. Catch may also be influenced by fishing effort and availability. During the period of study effort seems to have been near saturation, and changes in effort had little effect on catch. On the other hand, catch appeared to have considerable effect on the amount of effort expended, especially in the two immediately following seasons, with large catches causing increased effort and small catches causing decreased effort. Availability seems to have been secondary to population size in determining catch, although the effects of availability as evidenced by apparent total mortality rates appeared to increase during the latter half of the 26-year period.

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