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FISH AND WILDLIFE SERVICE • Arnie J. Suomela, *Commissioner*

FECUNDITY OF THE PACIFIC SARDINE
(*Sardinops caerulea*)

By JOHN S. MACGREGOR

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ABSTRACT

Diameter measurements of ovarian ova were made for 587 female Pacific sardines (*Sardinops caerulea*) obtained from the San Pedro commercial fishery samples for the period November 10, 1945 through February 27, 1946. The number of ova present in the most advanced group of developing ova were counted for 116 sardines that contained a distinct group of such ova. The calculated number of ova present in this group increased with age, length, and weight of the fish. The fecundity-length correlation was better than the fecundity-age correlation, and the fecundity-weight correlation was better than either of these. Fecundity-length regression lines based on four different formulas and fecundity-weight regression lines based on two different formulas are compared.

Data on age and length at first maturity based on the criterion of degree of ovarian ovum development are presented.

CONTENTS

FECUNDITY OF THE PACIFIC SARDINE (SARDINOPS CAERULEA)

By John S. MacGregor, *Fishery Research Biologist*

Extensive studies of the biology of the Pacific sardine (*Sardinops caerulea*), designed to lead to an understanding of the causes of fluctuations in the size and distribution of the population, have been carried on since 1949 under the sponsorship of the California Marine Research Committee. These studies, the California Cooperative Oceanic Fisheries Investigations, have been made by the California Academy of Sciences, the California Department of Fish and Game, Hopkins Marine Station of Stanford University, Scripps Institution of Oceanography of the University of California, and the South Pacific Fishery Investigations of the U. S. Fish and Wildlife Service.

One of the requisites of these studies is a measure of the size of the sardine population. The number of individuals in a spawning population of fishes can be estimated if the following are known: (1) the total number of eggs produced per year by all females in the population, (2) the average number of eggs produced per year by each female in the population and (3), the sex ratio in the population. This method has been one of those used for several years by the South Pacific Fisheries Investigations to estimate the size of the Pacific sardine population along the coast of California and Baja California. To determine the average number of eggs produced per year by each female it is necessary to determine the average number of eggs spawned per batch and the number of batches produced. The annual egg production per female used in the population estimates has been based on fecundity data for eight female sardines given by Clark (1934). The purpose of the present paper is to record more extensive data on the fecundity of the Pacific sardine (item number 2 above).

I wish to express my appreciation to my colleagues, E. H. Ahlstrom and T. M. Widrig for helpful suggestions, F. E. Felin for making the age determinations, A. M. Vrooman for assisting in counting and measuring the eggs and preparing the figures, and W. M. Morton for collecting the material, and to members of cooperating agencies for their assistance.

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MATERIAL AND EQUIPMENT

The 13 samples of sardines examined were taken from the commercial fishery at San Pedro, Calif., in November and December, 1945, and January and February, 1946, and included 1,270 individuals. These fish, originally collected for a morphometric study, were fixed and preserved in formalin in gallon jars. Some of them were subsequently transferred to alcohol.

Ovaries and ovary samples for ovum counts and diameter measurements were weighed on a Sartorius Selecta balance. The ovum counts and diameter measurements were made on projected images of the ova using the scale reading device described by Mosher (1950).

The ovary samples were placed on microscope slides for weighing and projection. Slides were prepared by placing two threads parallel to each other and to the long axis of the slide, along one surface of the slide, and securing them at the ends with cellophane tape. The threads were spaced a distance apart somewhat less than the diameter of the microscope field and served as guide lines. The use of threads rather than etched lines kept the ova from falling on the line and controlled the spread of the mounting medium.

METHODS

A pair of ovaries was drained for a few minutes on paper toweling and weighed to the nearest 0.001 gram. A small sample from one ovary was then placed on a microscope slide and weighed to the nearest 0.0001 gram. A drop of glycerin was placed over the sample; the ova were teased out and spread into three strips separated by the two guide-line threads. A second microscope slide was then placed over the first and the two slides were fastened at the ends with cellophane tape. The formalin-hardened ova were not distorted between the slides prepared in this manner so long as the pressure applied to the slides was not excessive. A second mount was prepared in a similar manner, using a sample from the other of the pair of ovaries. The use of two samples for each pair of ovaries

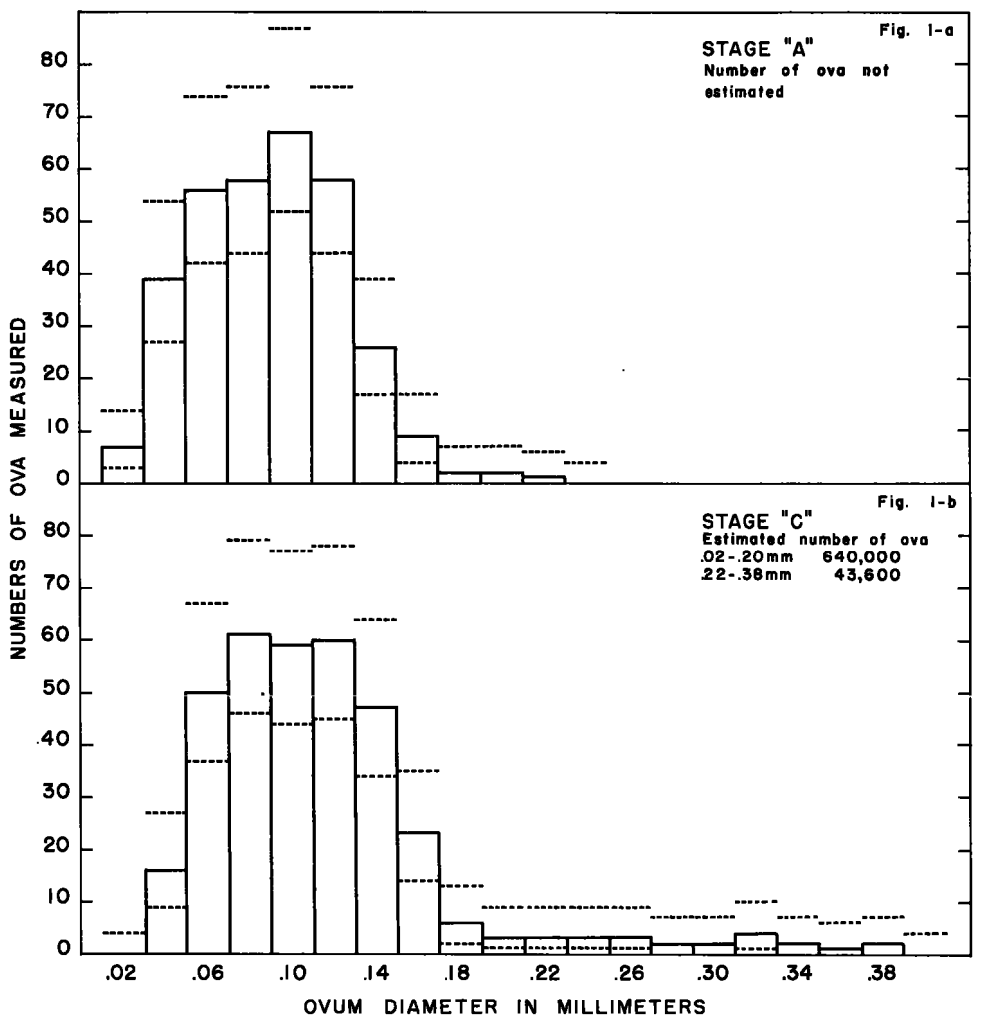

Figure 1-a, b.—Sardine intra-ovarian ovum diameter frequencies.

provided a check on the accuracy of the ovum counts and yielded a larger sample than could have been easily examined on one slide.

Each sample of ova was projected in the scale projector at a magnification of 50X. The projected ovum diameters were measured to the nearest millimeter. When doubled, this measurement gives the actual ovum diameter in hundredths of a millimeter by 0.02 mm. units.

If the sample of ova contained no distinct (by size) group of developing ova, the diameters of the larger ova in the sample were measured. The largest ovum diameter was used as a measure of the ovarian development for these early stages when no modal or other central value could be obtained. Figure 1–a and b and figure 2–a and b show ovum diameter frequencies from ovaries in these stages of development. The dotted lines in figures 1 and 2 represent 95 percent confidence limits of the counts.

If the ovary was advanced enough so that a distinct group of yolked ova had differentiated by size from the smaller yolked ova, enough ova (generally 100 to 200) 0.22 mm. or larger (i. e., containing yolk) were measured to delimit clearly this most advanced group of developing ova. When the size range of this group was determined, all ova in that size range on the slide were counted. Figure 2-c, d, e, f, g, and h shows ovum diameter frequencies from ovaries in these stages of development.[1] The most advanced groups of ova shown in these figures consist of opaque ova except the group shown in figure 2–h which consists of translucent ova. No perivitelline space has formed in

[1] The multimodal distribution of diameters of developing intraovarian ova of the Pacific sardine was first demonstrated and figured by Clark (1934).

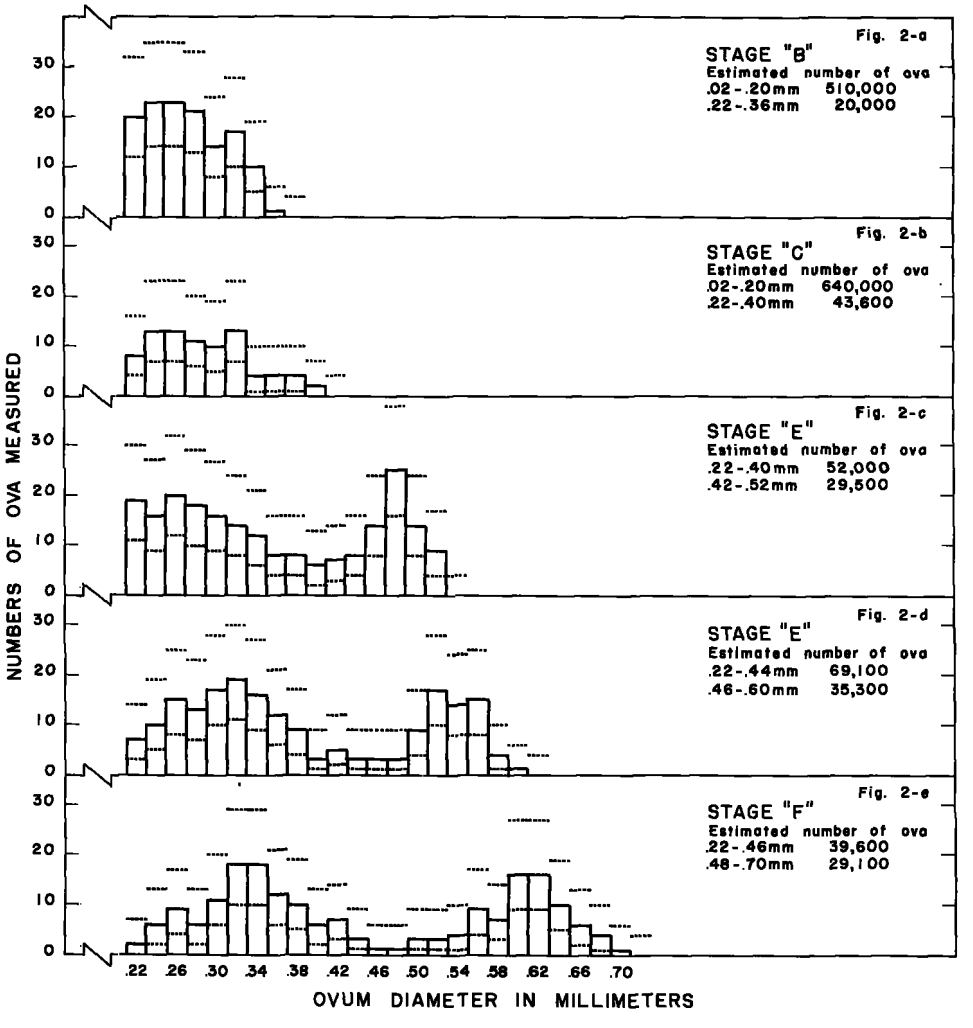

Figure 2–a, b, c, d, e.—Sardine intra-ovarian ovum diameter frequencies (see p. 430).

the intraovarian ova, and hence the ovum diameters are also yolk diameters. In figure 2–i yolk-diameter distributions of 343 planktonic sardine ova in early developmental stages are shown for comparison with figure 2–h.

Figure 2–j shows the ovum diameter distribution of degenerating ova from the ovaries of a sardine taken in May of 1951. None of the San Pedro 1945–46 sardines used in this study were found to be in this condition.

Clark (1934) grouped developing ova in the largest mode into twelve stages of maturity. As I will have occasion to refer to some of these stages in comparing my observations with those of Clark, I am including a description of these stages:

IMMATURE

Stage A: Frequencies with a mode between 0 and 0.2 mm. only.

MATURING (OPAQUE EGGS)

Stage B: Frequencies with the last mode between—0.22 and 0.26 mm.

Stage C: Frequencies with the last mode between—0.26 and 0.34 mm.

Stage D: Frequencies with the last mode between—0.34 and 0.44 mm.

Stage E: Frequencies with the last mode between—0.44 and 0.54 mm.

Stage F: Frequencies with the last mode between—0.54 and 0.64 mm.

Stage G: Frequencies with the last mode between—0.64 and 0.74 mm.

Stage H: Frequencies with the last mode between—0.74 and 0.84 mm.

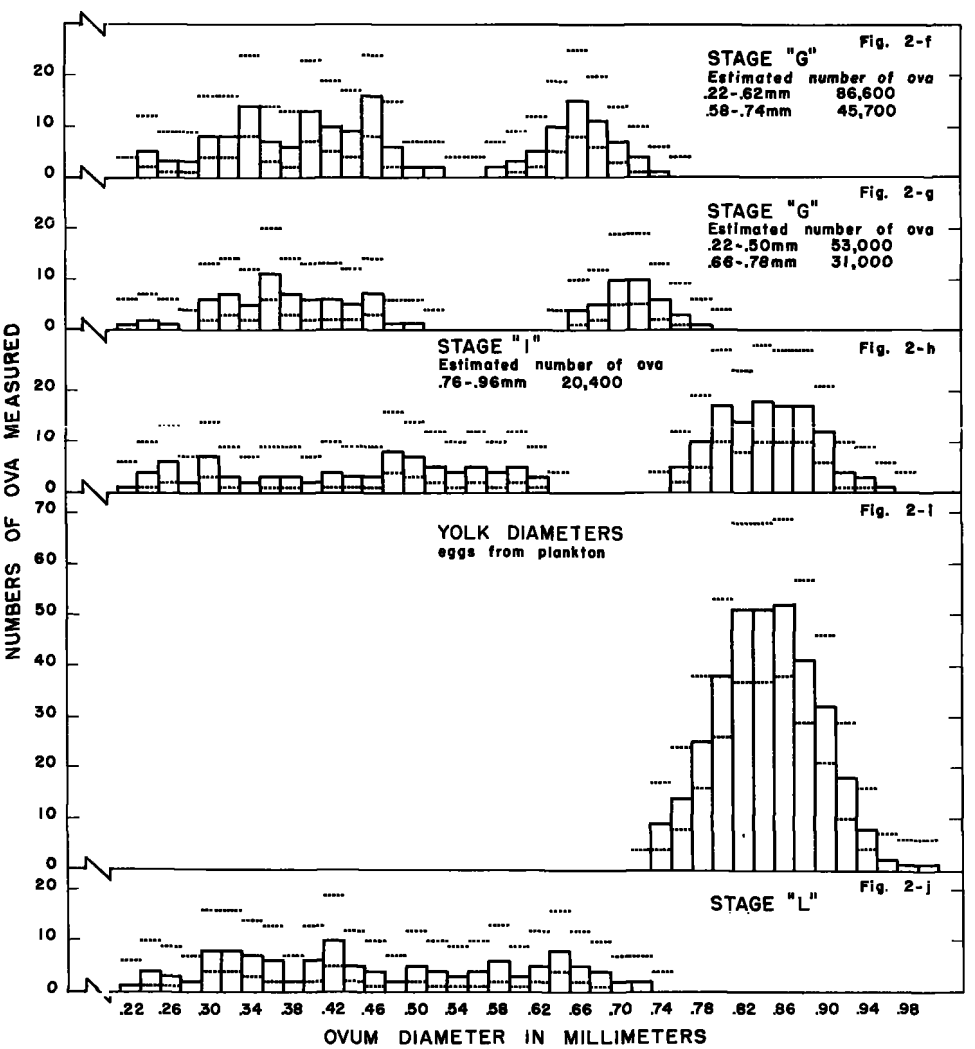

FIGURE 2–f, g, h, i, j.—Sardine ovum diameter frequencies.

MATURING (TRANSPARENT EGGS)

Stage I: Frequencies with the last mode between 0.84 and 0.94 mm.

Stage J: Frequencies with the last mode above 0.94 mm.

MATURE (TRANSPARENT EGGS FREE IN THE OVIDUCT)

Stage K: Frequencies with the last mode above 0.94 mm. and the ripe eggs segregated.

SPENT

Stage L: Frequencies with ova larger than 0.20, but these eggs degenerating.

The number of ova in the most advanced group was calculated by multiplying the weight of the ovaries by the number of these ova in both samples and dividing by the total weight of both samples. It was also determined from each of the two samples separately as a check on the sampling variation.

All (587) of the female sardines in the 13 samples were used for ovum diameter measurements. Ovum counts were made for all fish (116) that contained a distinct group of developing ova. The weight of both samples from a pair of ovaries equalled approximately 2 percent of the weight of that pair of ovaries. The deviations of the 116 pairs of ovum estimates from their respective combined estimates was 1,700 eggs at one standard deviation level. The right and left ovaries of each pair were at the same stage of maturity in every case, and neither ovary gave a consistently higher or lower count than the other. As pointed out by Clark (1934), there are no apparent differences in the relative numbers of ova in each size group in the different parts of the ovary.

RELATION BETWEEN FECUNDITY AND LENGTH

Figure 3 shows 116 fecundity observations obtained from the January and February, 1946, samples plotted against their respective fish lengths. The regression line, fitted by the method of least squares, of the form $Y=a+bX$ (where Y=the number of ova in the most advanced mode in thousands, X=the fish length in millimeters and a and b are constants) is also shown. Clark's (1934) S observations are plotted for comparison. It is apparent from figure 1 that the fecundity of individual fish of the same length can vary considerably. This variation

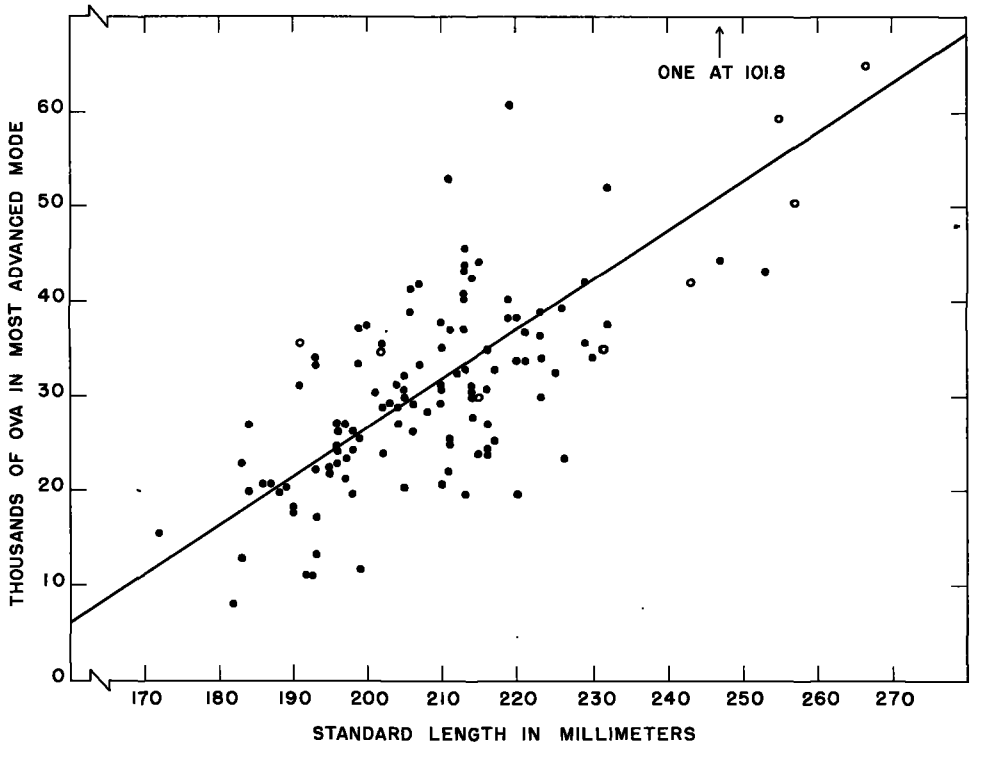

FIGURE 3.—Relation between fecundity and standard length for 116 sardines (San Pedro, Jan.-Feb., 1946). Open circles are Clark's (1934) observations.

(S_y=8.76 thousands of ova) is more than 5 times as large as the variation attributable to sampling and counting techniques.

There has been some differences of opinion among various authors as to whether length, length squared, or length cubed should give the best straight line correlation with fecundity. Lehman (1953) correlated the fecundity of 22 shad (*Alosa sapidissima*) with their lengths. His equation (least squares) for the line of average relationship is $Y=-462.691+40.090X$ in which Y=the number of ova in thousands, and X=the length in inches.

Clark (1934:21), referring to eight fecundity observations on the Pacific sardine, states:

> By the method of least squares from the formula $N=FL^x$, where N indicates the number of eggs; L, the length; F, a constant; and x, the exponent expressing the relationship between the number of eggs and the length of the fish; x was found to have a value of 1.9868. This suggests that the numbers of ova produced by individual sardines increase as the square of the length. But because the calculations were based on very scanty data, these conclusions can be tentative only.

Simpson (1951) expressed fecundity observations for 256 plaice (*Pleuronectes platessa*) by the formula $F=KL^3$, where F=the number of ova; K, a constant; and L^3, the cube of the length of the fish.

The line of best fit (least squares) for the 116 sardine fecundity observations is plotted in figure 4 for each of four different relationships.

Table 1 gives the Y-intercepts (a), slopes (b), standard errors of estimate of Y (S_y) and coefficients of correlation (r) of the four lines for the 116 fish and for each of the five samples which together constitute the 116 fish. The standard errors of estimate of Y for 10-millimeter length intervals are presented in table 2. Table 3 gives the number of ova in the most advanced group calculated by each of the four different formulas at each of 9 different 10-millimeter length intervals. It is apparent from these comparisons that convenience, rather than theoretical considerations should be the deciding factor in selecting one of the regression formulas to describe these data. The same is true for Lehman's (1953) fecundity

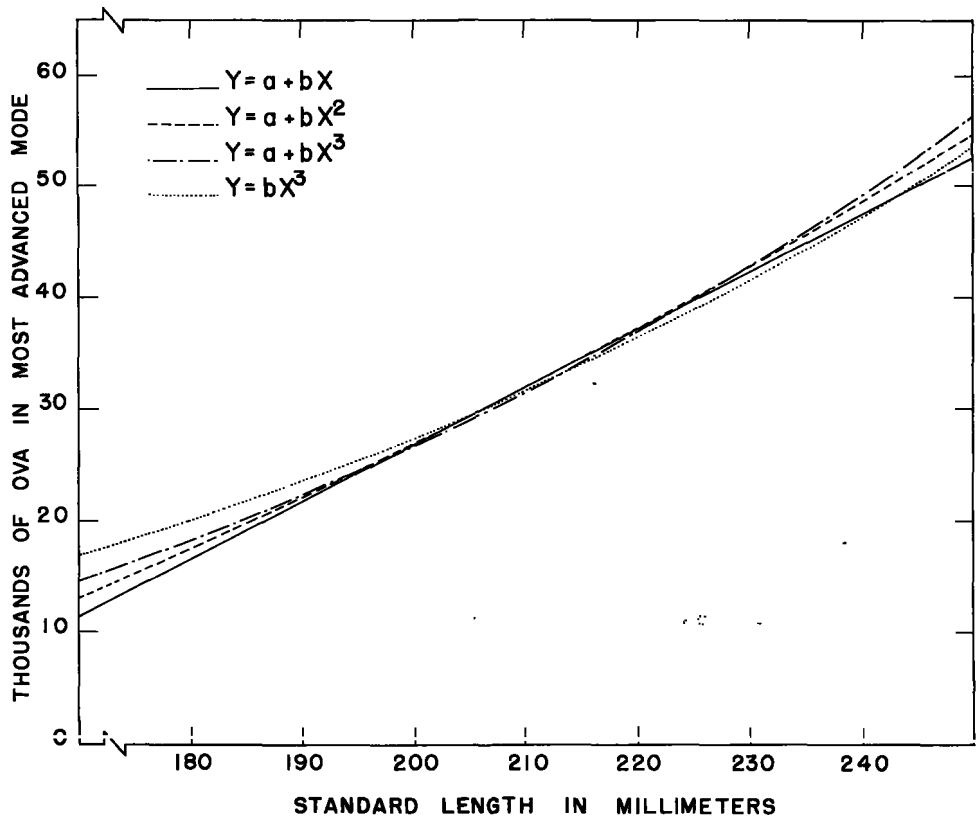

FIGURE 4.—Comparison of fecundity-length regression lines.

data for shad. Using his formula $Y=a+bX$, $S_y=40.2$ and $a=-462.7$. Using $Y=a+bX^3$, $S_y=39.3$ and $a=19.0$. As a approaches zero the formula $Y=bX^3$ would also give an S_y approximating the above two.

Theoretically the number of ova is dependent upon the volume of the ovary, a three-dimensional function, and therefore should better correlate with the cube of the length, length itself being, of course, only linear. In Simpson's (1951) paper on the fecundity of the plaice, the straight line regression of fecundity on length cubed is considerably better than that of fecundity on length squared or length. The significant differences between the regressions in this case are brought out by the greater relative range in sizes of fish used in calculating the regression lines. Measured as a percentage of the length of the shortest fish used, the range of Simpson's plaice is 162 percent, that for Lehman's shad is only 66 percent and for the 116 sardines 48 percent (56 percent including Clark's 8 fish).

TABLE 1.—*Comparison of some possible fecundity-length relationships*

Sample	$Y=a+bX$	$Y=a+bX^2$	$Y=a+bX^3$	$Y=bX^3$
SP-8 (17 fish)				
a (thousands)	−25.4	−1.4	+6.6	0.0
b	.239	.000594	.00000195	.00000267
S_y (thousands)	5.33	5.32	5.30	5.48
r	.547	.549	.553	.510
SP-9 (9 fish)				
a (thousands)	−112.9	−44.9	−22.3	0.0
b	.068	.00164	.00000534	.00000265
S_y (thousands)	5.02	5.02	5.03	5.97
r	.786	.786	.785	.677
SP-11 (41 fish)				
a (thousands)	−43.1	−4.3	+8.6	0.0
b	.358	.000825	.00000253	.00000338
S_y (thousands)	5.49	5.50	5.49	5.60
r	.478	.476	.478	.445
SP-12 (5 fish)				
a (thousands)	−87.8	−27.7	−7.4	.0
b	.574	.00137	.00000430	.00000352
S_y (thousands)	4.09	4.16	4.29	4.44
r	.839	.833	.822	.808
SP-13 (44 fish)				
a (thousands)	−104.3	−32.1	−8.0	0.0
b	.674	.00156	.00000475	.00000386
S_y (thousands)	10.2	10.3	10.4	10.6
r	.730	.725	.719	.703
All samples (116 fish)				
a (thousands)	−76.0	−22.9	−4.3	0.0
b	.514	.00124	.00000386	.00000341
S_y (thousands)	8.76	8.74	8.75	8.79
r	.641	.643	.642	.638

TABLE 2.—*Standard error of estimate of Y for ten millimeter length intervals using formula:* $Y=a+bX$

[Y=No. of ova in thousands; X=length in mm.]

Length (mm.)	Fish (number)	S_y (thousands)
170–179	1	
180–189	10	4.68
190–199	27	6.60
200–209	21	6.80
210–219	36	8.91
220–229	15	7.33
230–239	3	
240–249	2	
250–259	1	
Total	116	8.76

TABLE 3.—*Calculated number of ova in most advanced mode for sardines of different lengths*

Length (mm.)	Number of ova (in thousands)			
	$Y=a+bX$	$Y=a+bX^2$	$Y=a+bX^3$	$Y=bX^3$
170	11.4	12.9	14.7	16.8
180	16.5	17.3	18.2	19.9
190	21.7	21.9	22.2	23.4
200	26.8	26.7	26.6	27.3
210	31.9	31.8	31.4	31.6
220	37.1	37.1	36.8	36.3
230	42.2	42.7	42.7	41.5
240	47.4	48.5	49.1	47.1
250	52.5	54.6	56.0	53.3

Obtaining a sample of Pacific sardines suitable for fecundity determinations with a size-range comparable to that of plaice would be an impossibility. The size range of the sample of spawning sardines might be doubled by including large fish (270 to 290 mm.) from the northern part of the sardine's range and small spawning fish from the southern part of the range. (I have examined some 145–155-mm. sardines taken off the southern tip of Baja, California, that had apparently developing gonads.) This procedure could introduce a considerable error. Simpson found that there were geographical differences in fecundity among stocks of plaice, those from the Baltic containing many more eggs than those of comparable sizes from the North Sea.

In figure 5 the data for each of the 5 samples have been described by regression lines, using the

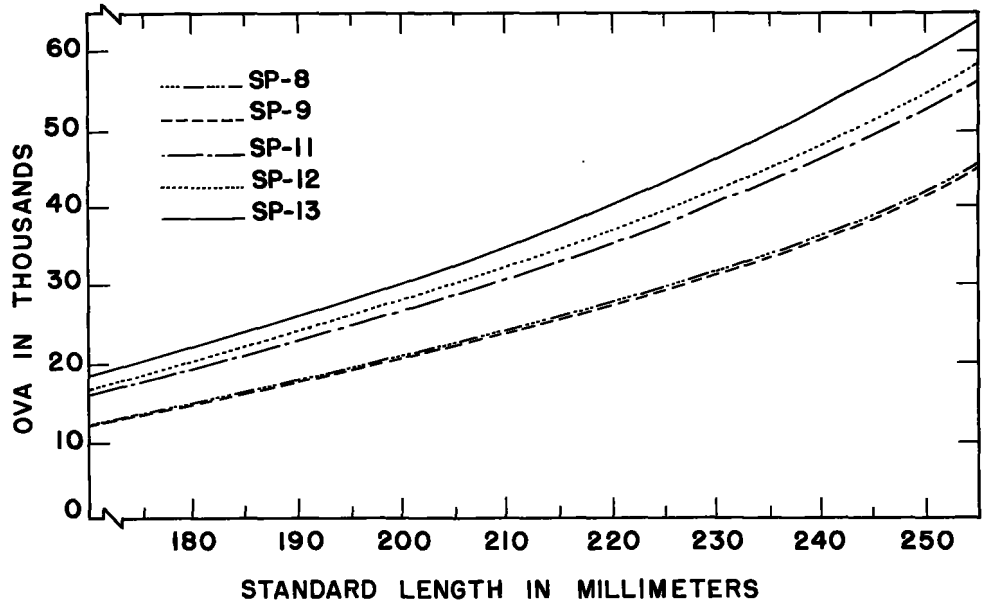

FIGURE 5.—Fecundity-length regression $Y=bX^3$.

formula $Y=bX^3$. The use of this formula makes the curves much easier to compare, since the Y-intercept is taken as zero for all samples and the slopes may be compared directly.

When the curve is fitted by the least squares method to the data, using the formula $Y=a+bX^3$, both the a and b values are determined by the data. The sum of the plus deviations will equal the sum of the minus deviations, while the sums of the squares of the deviations will be at a minimum. When the formula $Y=bX^3$ is used, the Y-intercept is forced to be zero, and both of these conditions cannot be met if the distribution of data is at all skewed. A regression line about which the sum of the plus deviations equals the sum of the minus deviations can be obtained using a value obtained from the formula $b=\frac{\Sigma Y}{\Sigma(X^3)}$. A line about which the sum of the squares of the deviations is at a minimum can be obtained using $b=\frac{\Sigma(X^3Y)}{\Sigma(X^3)^2}$. Although there is little difference between the b values derived by these two methods [2] from the data for the 116 sardines, the latter method has been used because the standard errors of estimate and correlation coefficients based upon it should theoretically be more nearly comparable with those obtained in conjunction with the least squares methods in which the Y-intercept is determined by the data.

Figure 5 shows that samples SP–8 (Jan. 11) and SP–9 (Jan. 24) almost coincide and that samples SP–11 (Feb. 9), SP–12 (Feb. 21), and SP–13 (Feb. 27) show an apparent increase in fecundity as the season progresses. Because of the restricted range of lengths and the great variation in ovum count at any given length, no significance is attached to this apparent temporal fecundity increase. In figure 6 are plotted the regression lines for each of the 5 samples, fitted (least squares) by the formula $Y=a+bX$ (which differs most from the formula $Y=bX^3$). In table 4 each of the 10 possible combinations of pairs of b's is compared by t test for the possibility of significantly different slopes for both formulas. There are no pairs of regression slopes that are significantly different when both formulas are taken into consideration. The apparent significant differences in the slopes of the pairs, SP–8 and SP–9, and SP–8 and SP–13, when the formula $Y=a+bX$ is used are primarily a result of the comparatively great variation in Y values and the restricted range in X values.

[2] Simpson apparently used the formula $b=\Sigma\left(\frac{Y}{X^3}\right)\div N$ which also gives a b value differing very little from the other two for the 116 sardines.

TABLE 4.—*Comparison of regression coefficients*

Sample	n	$Y=a+bX$		$Y=bX^3$	
		t	P	t	P
SP-8	22	1.944	<.05	0.0085	<.9
SP-9					
SP-8	54	0.834	<.4	0.652	<.5
SP-11					
SP-8	18	1.359	<.1	0.433	<.6
SP-12					
SP-8	57	2.411	<.01	0.803	<.4
SP-13					
SP-9	46	1.381	<.1	0.400	<.6
SP-11					
SP-9	10	0.313	<.7	0.321	<.7
SP-12					
SP-9	49	0.016	<.9	0.404	<.6
SP-13					
SP-11	42	0.859	<.3	0.072	<.9
SP-12					
SP-11	81	0.559	<.4	0.363	<.7
SP-13					
SP-12	45	0.235	<.8	0.100	<.9
SP-13					

RELATION BETWEEN FECUNDITY AND WEIGHT

The fish used for this fecundity study had originally been preserved in formalin, but many of them were subsequently transferred to alcohol. The fish in alcohol were noticeably different in appearance from those in formalin. The subcutaneous fat deposits of the formalin preserved fish showed through the skin and scales as a white background wherever pigment did not conceal them. These fat deposits were not apparent in the alcohol preserved fish. The formalin preserved fish also weighed considerably more than alcohol preserved fish of comparable lengths from the same sample.

Only a few fish from sample SP–11 were in a jar containing alcohol, and of these only one was a female for which ovum counts were made. The weights of the other 40 females for which ovum counts were made are plotted in figure 7 as the independent variable, with numbers of ova as the dependent variable. Two different regression lines have been fitted to the data.

As will be shown for this sample, the weight [3] of a sardine is a much better indicator of its fecundity than is its length. It can also be shown that for practical purposes the Y-intercept can be taken as zero in the fecundity-weight regression without any significant loss of accuracy (table 5).

TABLE 5.—*Comparison of two fecundity-weight regressions*

Item	$Y=a+bX$	$Y=bX$
a	+2.94	0.0
b	.2402	.2628
S_y	4.91	4.92
r	.624	.622

The use of the formula $Y=bX$ enables one to determine directly the total weight of spawning

[3] The weight used is round weight. If the ovary weight is subtracted from the round weight, the regression is not changed significantly ($a=+3.3$, $b=0.25$, $S_y=5.1$, $r=0.60$).

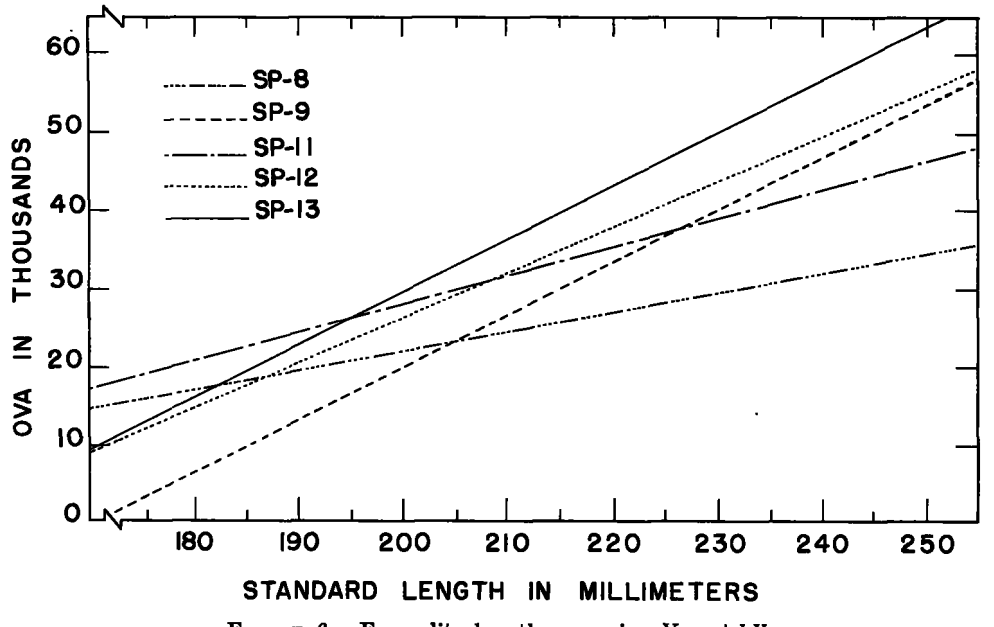

FIGURE 6.—Fecundity-length regression $Y=a+bX$.

female sardines required to produce the estimated number of ova present on the spawning grounds for any one season (assuming that each sardine spawns only the most advanced mode of ovarian ova). If the weight-fecundity relation of sample SP–11 is taken as representative of that of the stock of spawning sardines, the weight of spawning females can be easily estimated on the basis of 262.8 ova per gram or 238.4 million ova per ton of spawning female sardines.

COMPARISON OF FECUNDITY-LENGTH AND FECUNDITY-WEIGHT REGRESSIONS

It has been shown that for the size-range of sardines in these samples, there is very little difference among the regression lines of fecundity on length, on length squared, or on length cubed. For purposes of comparison, the fecundity-length regression line was computed for the same 40 fish used for the fecundity-weight regression line. The partial regression coefficients and the multiple regression of fecundity on length and on weight [4] were also computed (table 6). It would appear from this comparison that the fecundity of these sardines is not only better correlated with their weights, but that the correlation with length is merely a reflection of the very good correlation between length and weight.

This comparison may be tested further by the use of condition factors (Clark 1928). In the present case the condition factor, K,[5] equals the weight of the fish in grams divided by the cube of the length in millimeters and multiplied by 10^7 (to give a three-digit whole number). Condition

[4] Over this length-weight range the cubic relation of length to weight is obscured, and the length-weight regression will approximate a straight line.

[5] The use of condition factors "corrected" by subtracting the ovary weight from the fish weight before computing K gives results that are almost identical to those obtained from K computed from round weight. Theoretically it might also be argued that the fish which contained more ovarian ova or larger ova, or both, had produced them at the expense of other tissues and therefore the inclusion of ovary weight in fish weight should have a corrective value rather than the opposite.

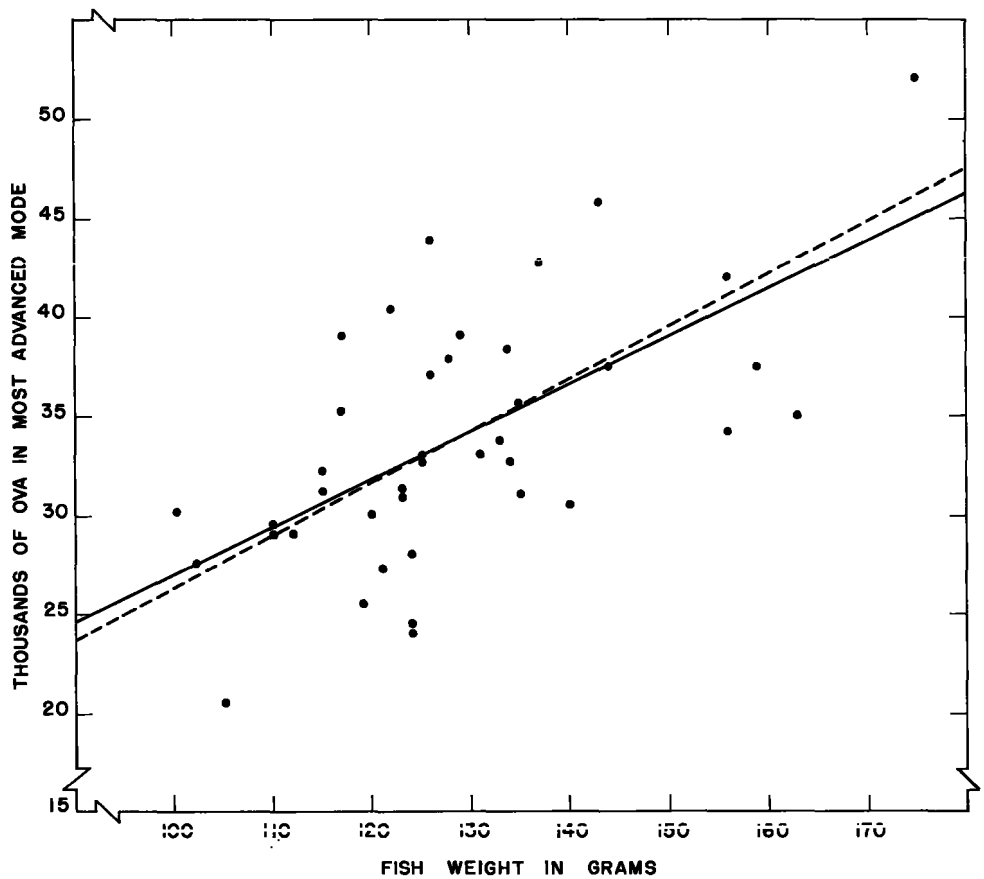

FIGURE 7.—Relation between fecundity and fish weight for 40 sardines (San Pedro, Feb. 9, 1946). (Dashed line, $Y=.2628X$; solid line, $Y=2.94+.2402X$).

factors in theory (assuming isometric growth in all dimensions) should be comparable for all lengths of fish. It appears that condition factors actually are comparable among sexually mature fish but not between adult and juveniles. The latter usually have lower condition factors.

In figure 8 the deviation (observed number of ova minus calculated number of ova) of each of the 40 fecundity-length pairs is plotted against the respective K value for each fish. The regression line is described by $d=.3720K-47.91$ ($S_y=4.81$; $r=.500$). If this equation is added to the fecundity-length regression as a correction for differences in K values among the sardines, the resulting equation is $Y=.3534X+.3720K-90.06$. S_y is decreased from 5.55 (for the fecundity-length equation alone) to 4.81, and r is improved from .469 to .644.

TABLE 6.—*Comparison of fecundity-length and fecundity-weight regressions*

Item	Fecundity-length	Fecundity-weight	Length-weight	Fecundity-length-weight
a	−42.15	+2.94		+41.98
b (length)	+.3534			−.2469
b (weight)		+.2402		+.3494
S_y	5.55	4.91		4.80
r	+.469	+.624	+.875	+.646
r (partial)	−.204	+.500	+.844	

In figure 9 the deviation (observed number of ova minus calculated number of ova) of each of the 40 fecundity-weight pairs is plotted against the K value for that fish. The regression line is described by $d=.2565K-33.03$ ($S_y=4.71$; $r=.282$). When this equation is added to the fecundity-weight regression, S_y is decreased from 4.91 to 4.71 and r is improved from .624 to .663.

The comparatively large improvement resulting from applying this K value correction to the fecundity-length correlation, the magnitude of the correlation coefficient, and the positive slope of the regression of fecundity-length deviation on K value, all demonstrate that when two fish are the same length, the heavier fish contains more ova. The positive slope of the regression of K value and fecundity-weight deviation suggests that when two fish are the same weight, the shorter fish will have a higher fecundity, but the low r value (P between .05 and .1) and the small improvement resulting from applying the correction to the fecundity-weight correlation throw doubt on the significance of this correction. It would probably be safe to say that within reasonable limits the fecundity of the sardine is more closely associated with weight than with length.

When fecundity data obtained in one year are used in estimating sardine populations in other years, either the fecundity-weight or fecundity-length relation, adjusted for K, should give a more nearly accurate estimate of ova spawned per female than the unadjusted fecundity-length rela-

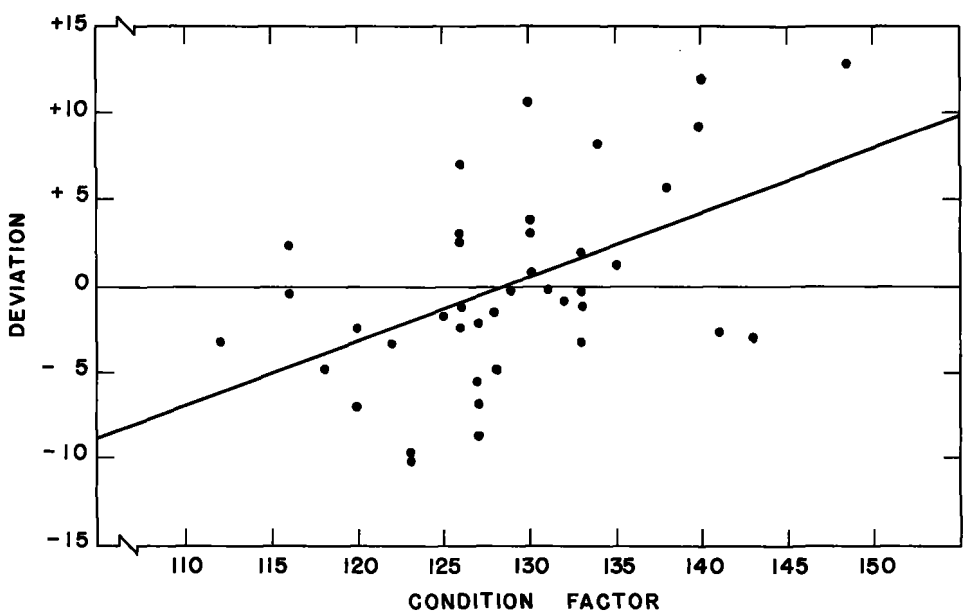

FIGURE 8.—Deviations of fecundity-length regression plotted against condition factor (sample SP–11).

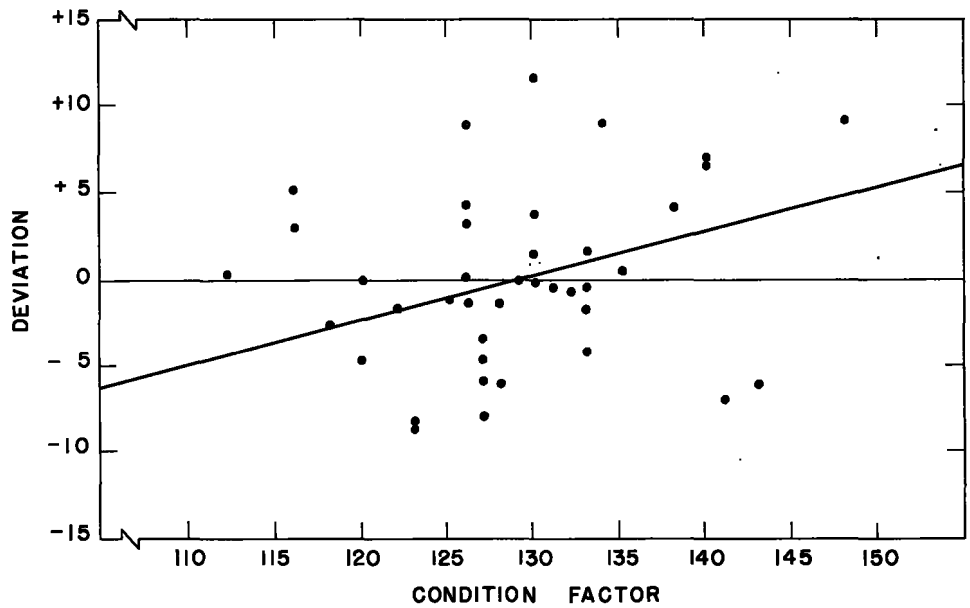

FIGURE 9.—Deviations of fecundity-weight regression plotted against condition factor (Sample SP-11).

tionship. From an examination of weight-length data of commercial fishery sardine samples over a 12-year period, it is evident that the average K value of the sardine population varies greatly not only within a year but also from year to year.

Included in the data recorded in the course of routine sampling of the commercial sardine fishery are the individual lengths of the 50 sardines that make up a sample and their total weight. An approximate K value can be obtained for any sample by dividing the mean-sardine-weight of that sample by the cube of the mean-sardine-length of that sample. An approximate K obtained by this method for the 40 sardines used for the weight-fecundity regression in this paper is 128.87; the mean K value for these same fish is 128.55. Approximate K values obtained from the San Pedro commercial fishery samples for January of various years illustrate how much year to year variation can occur (table 7).

TABLE 7.—*Condition factors of sardines collected in January during 1941–42 to 1953–54*

Season	Month and year	Average length in millimeters of sardines in 50-fish sample—													
		170–179		180–189		190–199		200–209		210–219		220 and above		All sizes	
		No. samples	Av. K	No. samples	Av. K	No. samples	Av. K	No. samples	Av. K	No. samples	Av. K	No. samples	Av. K	No. samples	Av. K
1941–42	Jan. 1942	2	117	12	116	39	117	6	117	1	110			60	117
1942–43	Jan. 1943	1	112	5	118	30	118	17	118	1	120			54	118
1943–44	Jan. 1944			16	121	30	122	12	124	3	124	2	123	63	122
1944–45															
1945–46	Jan. 1946					2	126	9	124	8	127	1	128	20	126
1946–47	Jan. 1947			2	115	1	126	5	129	6	128	2	128	16	127
1947–48	Jan. 1948	1	123	3	131			2	132	4	132			10	131
1948–49	Jan. 1949			1	129	4	128	5	127	1	132			11	128
1949–50	Jan. 1950			2	113	3	121	6	124	4	127			15	123
1950–51	Jan. 1951							1	124	28	127	1	128	30	127
1951–52	Jan. 1952							8	129	2	125	9	130	19	129
1952–53	Jan. 1953											5	137	5	137
1953–54	Jan. 1954											3	134	3	134

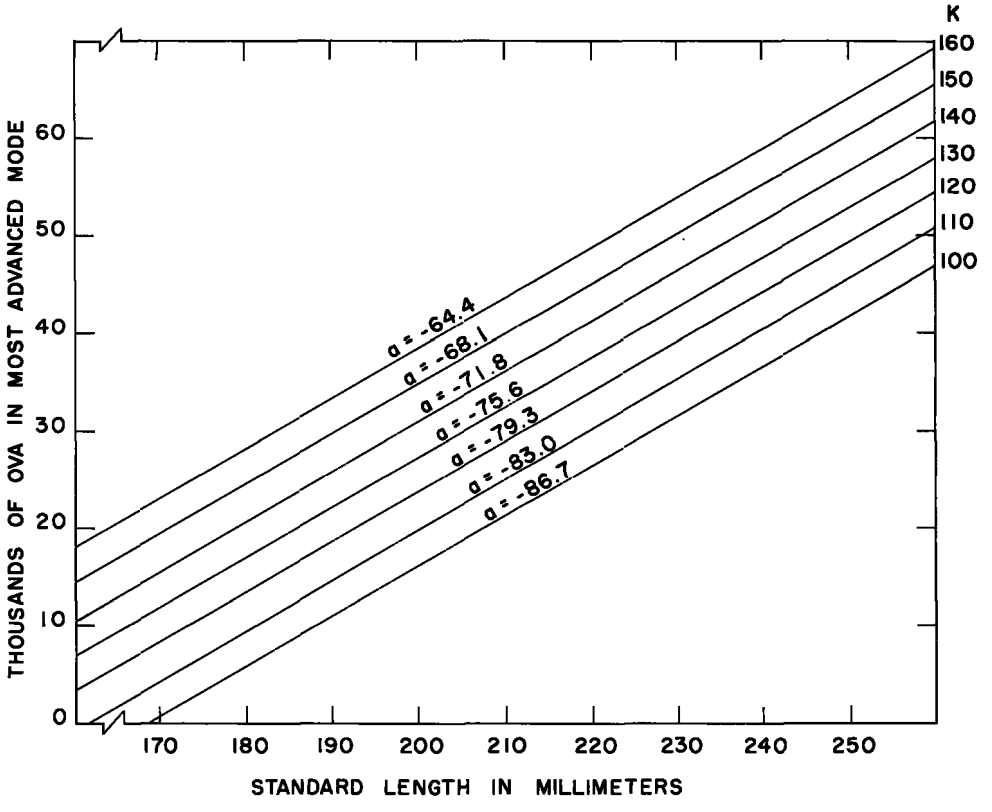

FIGURE 10.—Regression line $Y=0.514X-76.0$ adjusted for various K values by formula deviation $=.372K-47.9$.

In figure 10 are plotted the regression lines of fecundity-length for the 116 sardines adjusted for various K values on the basis of the computed deviation values owing to K (weight correction) found in sample SP–11. On the basis of this figure it can be seen that a 20-unit K value difference between two groups of sardines of similar length distribution would result in a difference of 7.4 thousands of ova in the most advanced group of developing ovarian ova for each fish. The above is, of course, purely theoretical when applied to years other than 1946. Sample SP–11 is probably representative of the population present in the San Pedro area in January and February of 1946 with respect to K. The mean K value of sample SP–11 (taken on Feb. 9, 1946) is 128.6. The approximate mean K value obtained from thirty-four 50-fish samples from the San Pedro commercial fishery in January and February of 1946 is 128.1. What actually happens in years of very high or very low K values of the Pacific sardine may be very different from what can be postulated to happen on the basis of fecundity values extrapolated to these high or low K values. The pre-spawning-season condition of a fish may determine not only how many ova will develop per batch of developing ova, but also how many batches will spawn, or if spawning, will take place at all in that season.

RELATION BETWEEN FECUNDITY AND AGE

The mean lengths of each age group are compared with those obtained by Phillips (1948) for the 1945–46 commercial sardine fishing season at San Pedro in table 8. The sampling method upon which Phillips' data are based was designed to sample the commercial catch representatively throughout the fishing season. Although he used fewer fish, a much larger number of samples are included in his data.

Age-fecundity data are presented in figure 11 and table 9 for the 113 sardines for which both fecundity data and age data were available. These show that the correlation between fecundity and age is not so good as that between fecundity and length or weight for these samples. Simpson (1951) also found a poorer correlation between age and fecundity than between fecundity and length or weight for plaice. On the other hand, Lehman (1953) obtained a better correlation between fecundity and age than between fecundity and length or weight for shad.

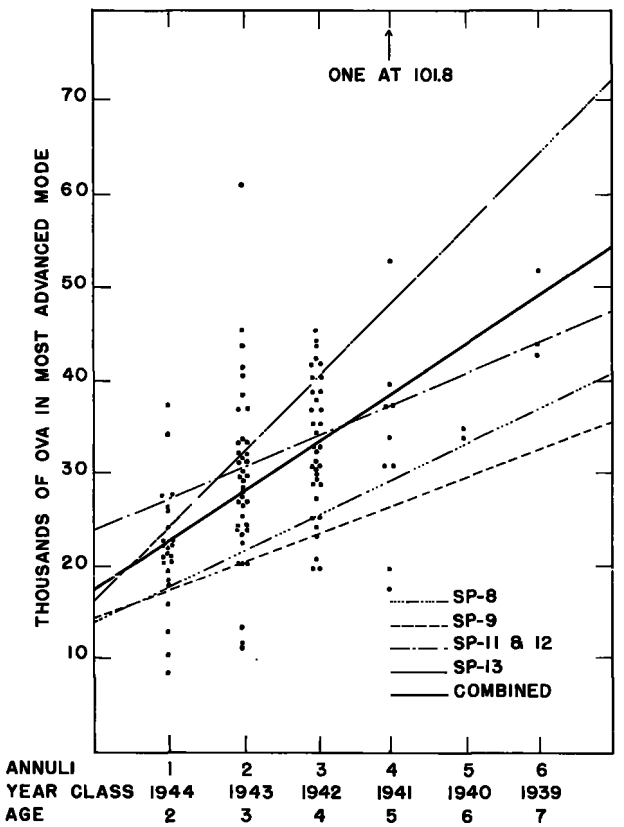

FIGURE 11.—Relation between fecundity and age.

TABLE 8.—*Mean lengths of 9-year classes of sardines taken in the 1945–46 commercial fishery at San Pedro*

	Samples SP-1 through 13			Phillips	
Number of annuli	Year Class	Number of fish [1]	Mean length	Number of fish [1]	Mean length
			Mm.		*Mm.*
0	1945	256	161.1		
1	1944	299	184.0	105	182
2	1943	369	199.4	337	200
3	1942	215	210.7	242	206
4	1941	74	213.4	151	213
5	1940	22	227.1	31	218
6	1939	10	244.0	14	224
7	1938	4	237.5	1	248
8	1937	4	245.5	1	254
		1,259		895	

[1] Males and females.

TABLE 9.—*Age-fecundity regression data using formula* $Y=a+bX$ ($Y=$*No. of ova in most advanced mode:* $X=$ *No. of annuli* [1])

Sample	Number of fish	*a*	*b*	*Sy*	*r*
SP-8	17	14.0	3.83	5.64	0.438
SP-9	9	14.5	2.97	7.52	.377
SP-11	39	24.0	3.36	5.66	.448
SP-12	5	23.8	3.38	5.56	.674
SP-13	43	16.4	8.00	11.28	.665
All	113	17.7	5.28	9.82	.525

[1] Number of annuli+1=age.

NUMBER OF SPAWNINGS PER YEAR

The maturing ovaries of a sardine contain yolked ova of two or more size groups. This point was illustrated in figure 2. Clark (1934) pointed out this fact and used it as a basis for concluding that individual sardines spawn more than once during each spawning season. As the number of batches of ova spawned per season is as critical a point in determinations of fecundity as the number of ova spawned per batch, and much more difficult to assess, I will review evidence for and against multiple spawnings.

The data presented in this paper are based on sardines collected during the period November 1945 through February 1946. It is unlikely that any of the sardines had spawned during this period. These months, with the possible exceptions of January and February (when nominal amounts of spawning have been found), are in advance of the sardine spawning season in the southern California area. As no samples were available after February in 1946, the changes that took place during and after the spawning season could not be studied. However, some of the data obtained from the January and February samples do bear on the problem of multiple spawning, and these will be summarized.

It is assumed by workers on fecundity that only ova in the most advanced mode will be spawned at a given time or batch. Hence, the number of ova in this mode is taken to represent the number of ova spawned per batch. The ratio of number of smaller yolked ova to number of ova in the most advanced mode has been taken as an indication of the number of batches that could potentially be spawned in a season. The number of yolked ova found in a mature ovary just prior to the initial spawning of a season would represent the total number of ova spawned in that season if (1) all the yolked ova were subsequently matured and spawned, and (2) if no ova were subsequently added to the group of yolked ova.

Although the 1946 data are too restricted in time to show any trend in ratios of ova in the largest mode to smaller yolked ova during the spawning season, they are of value in showing the ratios found in maturing ovaries during January and February. The data are summarized by stage of development in table 10.

There are three aspects of this tabulation to which I would like to call attention: (1) There is no change in ratio between stages *E*, *F*, and *G* (as defined by Clark 1934:13). This indicates that no additional ova were being added to the group of smaller yolked ova while the more advanced group was developing from stage *E* to *G*. (2) There is marked variation in the ratio of large ova to small in different fish; this is equally true if the largest mode is in stage *E*, *F*, or *G*. The range in ratios is from 0.3 to 3.2. (3) The ratios are markedly lower than those reported for San Pedro in January–February of 1929 and 1930 by Clark (1934).

The ratios given by Clark for 3 ports and several seasons are summarized in table 11. Clark compared the ratio of ova in stage *G* (the last abundant stage before the ova become translucent and are spawned) to those of all smaller yolked ova. The ratios reported by Clark (table 11) during January and February 1929 and 1930 at San Pedro are about twice as large as those I found for the same months in 1946 (table 10). A discussion of Clark's data is given in the latter part of this section.

TABLE 10.—*Frequencies of ratios of all smaller yolked ova to the number of yolked ova in the most advanced group at San Pedro in January and February 1946*

Ratio	Stage (after Clark 1934) of most advanced group of developing ova				Total
	D	*E*	*F*	*G*	
	Median diameters				
	.34–.43	.44–.53	.54–.63	.64–.73	.34–.73
0.0					
.1					
.2					
.3				1	1
.4		1			1
.5			1		1
.6					
.7		1	2		3
.8		2	1	1	4
.9		1	1	2	4
1.0		1	4	2	7
1.1	1	4	1	2	8
1.2		2	3	3	8
1.3		4	5	2	11
1.4	1	3	5	4	13
1.5		4	5		9
1.6			4	1	5
1.7		2	3	2	7
1.8		4	3	1	8
1.9		3		1	4
2.0		2	2		4
2.1		1		2	3
2.2			3	1	4
2.3					
2.4			1		1
2.5				1	1
2.6			1		1
2.7		1			1
2.8					
2.9		2		1	3
3.0					
3.1					
3.2				1	1
Number	2	38	45	28	113
Mean ratio	1.3	1.5	1.5	1.5	1.5

TABLE 11.—*Ratios of all ova between 0.20 and 0.59 mm. (stages B to F) to all ova larger than 0.59 mm. for all females in stage G (from Clark, 1934, table 1, p. 17) and number and percentage of adult female sardines in stage G (mode .64–.73 mm.) and stages A (resting-mode between 0 and 0.20 mm.) and L (spent) (after Clark, 1934, table 7, San Pedro, p. 27; table 8, Monterey, p. 30; table 9, San Diego, p. 32)*

Date	Monterey					San Pedro					San Diego				
	Ratio stages B–F/G	Stage G		Stages A and L		Ratio stages B–F/G	Stage G		Stages A and L		Ratio stages B–F/G	Stage G		Stages A and L	
		Number	*Percent*	*Number*	*Percent*		*Number*	*Percent*	*Number*	*Percent*		*Number*	*Percent*	*Number*	*Percent*
1929															
I:26–II:23	-------	0	0	2	7	3.36	9	17	0	0	-------	-------	-------	-------	-------
II:24–III:25	5.06	3	10	0	0	3.80	18	33	0	0	-------	-------	-------	-------	-------
III:26–IV:23	-------	1	33	1	33	2.87	10	50	1	5	-------	-------	-------	-------	-------
IV:24–V:23	3.96	2	7	22	76	2.38	5	9	1	2	-------	-------	-------	-------	-------
V:24–VI:21	4.16	2	10	18	90	2.26	6	17	6	17	-------	-------	-------	-------	-------
VI:22–VII:21	2.17	0	0	30	97	2.39	2	25	2	25	-------	-------	-------	-------	-------
VII:22–VIII:20	2.88	0	0	20	95	2.07	5	14	6	17	-------	-------	-------	-------	-------
VIII:21–IX:18	-------	0	0	42	100	2.11	2	4	36	77	-------	-------	-------	-------	-------
IX:19–X:18	-------	0	0	33	100	-------	0	0	40	100	-------	-------	-------	-------	-------
1930															
I:15–II:13	3.88	2	4	8	14	2.95	9	18	0	0	2.34	8	28	0	0
II:14–III:14	3.72	5	14	5	14	3.06	17	33	2	4	2.71	32	65	0	0
III:15–IV:13	2.85	16	47	2	6	2.02	20	37	5	9	3.12	13	62	0	0
IV:14–V:12	2.22	14	44	9	28	2.92	2	9	3	13	-------	-------	-------	-------	-------
V:13–VI:11	2.42	2	7	23	85	2.84	16	48	7	21	-------	-------	-------	-------	-------
1931															
I:5–II:3	-------	0	0	16	37	-------	2	5	4	11	-------	-------	-------	-------	-------
II:4–III:4	-------	2	6	2	6	-------	12	27	0	0	-------	-------	-------	-------	-------
III:5–IV:2	-------	19	60	0	0	-------	15	34	0	0	-------	-------	-------	-------	-------
IV:3–V:2	-------	20	69	1	4	-------	2	6	0	0	-------	-------	-------	-------	-------
V:3–V:31	-------	2	6	27	84	-------	2	6	2	6	-------	-------	-------	-------	-------

I interpret the differences in the ratios between 1929–30 and 1946 as real. I seriously question that they could be due to differences in techniques or interpretation of modes by Clark and myself. There have been three investigators working on the data I have presented in table 10, and the three of us have obtained comparable results. If the ratios are any indication of the average number of batches spawned per female sardine, then the number of batches must vary considerably from year to year. One implication of this is that when basing population estimates on egg surveys and fecundity data, it may be necessary to have current determinations of both egg abundance and average fecundity for that season.

I find that there is no significant difference among ratios of the 113 females considered in table 10 when grouped by size (standard length) rather than stage of maturity (table 12). Clark postulated that larger fish mature earlier than the smaller fish and spawn over a longer time interval. My study does not indicate a higher ratio (of smaller ova to ova in the most advanced mode) in larger female sardines. Hence, if larger fish spawn more batches of eggs in a season than smaller fish, these additional batches are not evident in maturing ovaries. Therefore if larger fish are to spawn more batches of ova than smaller fish, one of the following two conditions must be fulfilled: either additional ova are added to the mass of smaller yoked ova from the reservoir of non-yoked ovocysts, or, if this does not occur, then larger fish must spawn a larger proportion of the smaller yoked ova present in the initial maturation period than do smaller fish. If the first condition obtains, then there would be little significance to ratio changes during the season. If the second condition obtains, then only part of the smaller yoked ova initially present in the developing ovary would eventually mature and be spawned. Hence, smaller fish should have a larger number of batches of degenerating ova at the termination of their spawning than the larger fish. With regard to the 1946 samples, the average ratio of 1.5 to 1 shows that an average of only 2.5 batches could be spawned if all yolked ova were matured and spawned, and no additional yolked ova were added during the spawning season. If a portion of these degenerate, then the average number of batches spawned per female sardine must be between 1 and 2.5 batches.

Andreu (1951) postulated that the peak spawning season of the European sardine, as measured by the occurrence of planktonic eggs (Hickling 1945) off Plymouth, was too restricted in time to allow the sardines to mature and spawn more than one modal group of eggs in a spawning season. This could also be inferred for the Pacific sardine from table 12, and the ovum growth rates postulated by Clark (1934:29): ". . . probably slightly more than two months are necessary for eggs to grow from stage C [last mode between 0.26 and 0.34 mm.] to stage G [last mode between 0.64 and 0.74 mm.]," and ". . . approximately three or four weeks will elapse before females in stage G reach maturity."

Clark's figures show modal egg diameters for groups of translucent ova ranging from 0.80 to over 1.30 mm. According to Ahlstrom (1950:134–135), "Fertilized eggs average about 1.70 mm. in diameter (range 1.35–2.05 mm.)," pre-cleavage eggs "taken during the four hour period before midnight are considerably smaller in diameter than are those with some embryonic development. Since the yolks are of similar size in both groups,

TABLE 12.—*Frequencies of ratios of number of all smaller yolked ova to the number of yolked ova in the most advanced group (taken as unity) grouped by fish size (standard length)*

Ratio	Fish length in millimeters									
	170–179	180–189	190–199	200–209	210–219	220–229	230–239	240–249	250–259	Total
0.0										
0.1										
0.2										
0.3		1								1
0.4					1					1
0.5								1		1
0.6										
0.7			1		2					3
0.8		1	2			1				4
0.9		2	2							4
1.0			2	1	2	2				7
1.1			1	5	1				1	8
1.2		1	1	3	3					8
1.3		1	4	1	2	3				11
1.4	1		3	4	4		1			13
1.5			1		6	2				9
1.6			3	1	1					5
1.7		1	2	1	2			1		7
1.8			1	2	3	2				8
1.9		1	1		2					4
2.0					1	2	1			4
2.1			1	1	1					3
2.2				1	1	2				4
2.3										
2.4					1					1
2.5						1				1
2.6		1								1
2.7					1					1
2.8										
2.9			1		1		1			3
3.0										
3.1										
3.2					1					1
Total	1	9	26	20	36	15	3	2	1	113
Mean ratio	1.4	1.3	1.4	1.4	1.6	1.6	2.1	1.1	1.1	1.5

the difference lies in the width of the perivitelline space, which is nearly wanting in pre-cleavage eggs taken during this period; such eggs averaged only 1.20 mm. in diameter (range 1.02–1.38 mm.)."

Measurements of the yolk diameters of 343 sardine eggs (fig. 2i) from 8 plankton samples taken at various times and localities showed the mean yolk diameter to be .84 mm. (range .74–1.00). The mean egg diameter was 1.66 (range 1.40–1.90), indicating that this group of eggs is comparable with those constituting Ahlstrom's data (mean=1.70 mm.). One sardine of those used for this study contained translucent yolked ovarian ova. The mean of 118 diameter measurements of these ova was .84 mm. (range .76–.96 mm.). As there was no perivitelline space, these measurements are also yolk diameter measurements. Clark's (1934) larger diameter measurements of ovarian ova apparently include a perivitelline space as well as the yolk and therefore are not comparable with the ovarian ova, .20 to .84 mm. (mean diameter), which include yolk diameter only. Referring to sardines containing translucent, yolked ovarian ova, Clark (1934:11) states, "In the 11 years of study only 39 have been found among the thousands of females which have passed under observation." This would indicate that this stage is very transitory.

In table 13 I have summarized data on the length of the spawning season off southern California as determined from sardine egg surveys. Between 70.7 and 97.2 percent of the spawning in this area occurred within a period of two months, and between 88.2 and 99.6 percent occurred within a period of 3 months. The peak month (italicized in table 13) was different in each year, indicating the amount of variation that can occur in the time of spawning.

Clark (1934:19) bases the case for multiple spawning in the sardine on four lines of evidence: "The multiplicity of modes in the ova diameter frequency curves; the high degree of correlation between the growth of these successive groups of eggs; the occasional presence in the ovary of a few ripe unspawned eggs accompanied by a new ripening group; and the decrease, as the breeding season advances, in the numerical ratio between succeeding batches of eggs and the largest size group . . ."

TABLE 13.—*Percent of spawning occurring in each month of 1940 and 1941, 1950, and 1951 spawning seasons off southern California* [1]

Year	Feb.	Mar.	April	May	June	July	Aug.
1940	11.0	29.7	*41.0*	18.3			
1941	17.0	*47.1*	24.1	8.7	3.1		
1950	0.0	0.0	2.4	21.3	*75.9*	0.4	0.0
1951	0.0	1.3	1.3	*69.5*	25.9	2.0	0.0

[1] Based on sardine egg survey data given by Sette and Ahlstrom (1948) and Ahlstrom (1954).

The presence of different size-groups of yolked ova in the developing ovaries of any species of fish has been accepted by various authors as a, if not the criterion of the existence of multiple spawning in that species. However, it is also known that in a number of species of fishes at least some of the yolked ova of intermediate size are not spawned, but instead degenerate and are resorbed. This does not necessarily mean that none of the intermediate-sized ova will be spawned. Clark (1925) concluded that multiple spawning occurred in the grunion (*Leuresthes tenuis*). The ovaries of these fish contained a group of intermediate-sized yolked ova from which a group of ova to be spawned developed and segregated by size at approximately two-week intervals. At the end of the spawning season Clark (1925:22) found that, "In all cases, eggs in the intermediate group were undergoing a process of degeneration and resorption."

Hart and McHugh (1944) figure the distribution of ovum diameters for three species of Osmeridae found along the Pacific Coast of British Columbia. As these three species participate in inshore runs their spawning activities are much better known than those of species that spawn offshore.

One of these species, the eulachon (*Thaleichthys pacificus*), migrates into rivers to spawn. The spawning migration lasts from mid-March to mid-May. Each female apparently spawns only one batch of ova; the ovaries of a ripe female contain only the group of matured ova to be spawned and very small ova that contain no yolk.

A similar condition is found in the Pacific herring (*Clupea pallasi*). I had the opportunity to examine five ripe females of this species. I found only one mode of yolked ova, all larger than 1.00 mm. in diameter and the residual non-yolked ova, all smaller than 0.20 mm. This species is a demersal spawner, the eggs being deposited on eel grass and seaweed. The spawning of the one group of matured ova may take

place over a period of several days (Fraser 1922).

Another Osmerid studied by Hart and McHugh (1944) is the silver smelt (*Hypomesus pretiosus*). These fish spawn on beaches during high tides and in most months of the year. The ovaries contain yolked ova of intermediate sizes. Schaefer (1936) has also figured the ovarian ova diameter distributions of this species. The above three authors concluded that this species spawns several batches per season.

The third Osmerid for which ovarian ova diameters are figured by Hart and McHugh (1944) is the capelin (*Mallotus catervarius*). Of this species the authors say, "Spawning takes place in various localities in the strait of Georgia during late September or the month of October . . . Spawning takes place in the evening at high tide right at the water's edge . . . The size frequencies of the eggs [fig. 10] suggest that the mature capelin spawns more than one batch of eggs as there appears to be one group of small eggs becoming differentiated from the general mass which comprise the residual ovarian tissue after the ripe eggs are spawned out. It is not known at the present time whether any such second spawning occurs. It is possible that more or less nomad schools of capelin move around the southern part of the strait of Georgia spawning on suitable beaches as the eggs ripen. There is no racial evidence against such a belief but the only evidence in favor of such a supposition is the observations on the ovaries taken in conjunction with the lack of second spawnings occurring on the same beaches."

Thus we find three possible types of spawning occurring among these shore spawning species: (1) only one group of yolked ovarian ova with only one known spawning (eulachon, herring); (2) more than one group of yolked ovarian ova with multiple spawning (grunion, silver smelt); (3) more than one group of yolked ovarian ova with only one known spawning (capelin).

The degree of correlation between the modal value of the most advanced group of developing ova and the modal value of the secondary group of developing ova was used by Clark (1934) as an indication of multiple spawning in the Pacific sardine. June (1953) also used this method for the yellowfin tuna (*Neothunnus macropterus*). By this method of correlating modal values, Clark (1934) obtained a coefficient of correlation of 0.70 for modal diameters below 0.80 mm. and 0.72 for modal diameters above 0.80 mm.; June (1953) obtained a coefficient of correlation of 0.855 for his tuna data.

There may be some doubt concerning the interpretation of these correlations because of the mathematical restrictions imposed upon the plotting of the data. Although there are biological limits to the plotting of any biological data there should be no mathematical limitations; that is, it should not be mathematically impossible to plot any point. In the present case the convention of always plotting the larger diameter on one axis and the smaller on the other limits the plots to a triangular area rather than a rectangular area. It can be demonstrated that while a regression line based on a random plotting of points (positive numbers) in a rectangular area will have a Y-intercept (a) equal to the mean of Y, a slope (b) of zero and a coefficient of correlation (r) of zero, a regression line based on a random plotting of points in a traingular area with a hypotenuse of slope 1.00 passing through zero (i. e., coincidence of the two modes in the present case) will have a Y-intercept of zero, a slope of .500 and a coefficient of correlation of .500.

Regarding the "decrease, as the breeding season advances in the numerical ratio between succeeding batches of eggs and the largest size group," Clark (1934:19) states: "The change in the ratio from approximately 4–1 to 2–1 suggests that each fish may mature an average of three batches of eggs, although this number may be higher, for this study furnishes no data to determine whether growth from the immature to the maturing class accompanies growth within the maturing sizes."

Her ratio data are given in table 11 along with data on the numbers and percentages of fish in stage G (the last abundant stage before the eggs become translucent and are spawned) and in stages A (resting) and L (spent). The data for numbers and percentages are based on sardines larger than 199 mm. in length; the ratios apparently include a few smaller sardines in some months.

High percentages of stage G fish were shown for Monterey between March 15 and May 13 in 1930 and between March 5 and May 2 in 1931 (the 1929 Monterey data are not used as they are based on only 8 stage G fish for the season), followed in each case by high percentages of stages A

(resting) and *L* (spent) fish in the next lunar period. This would indicate a short peak spawning period in the Monterey region during these two years. Clark shows a decrease in ratios in 1930 at Monterey from 3.88 in the January–February lunar period (I:15–II:13) to 2.22 in the April–May lunar period (IV:14–V:12). Assuming that the values adequately represent the ratios during the two periods (the higher is based on 2 specimens), the decrease in ratios amounts to 1.66, hence the average number of batches spawned per female could approximate 2.66 batches.

The situation at San Pedro is more difficult to interpret. In 1929 Clark shows a high ratio of 3.80 (based on 18 *G* stage fish sampled between II:24–III:25), a low of 2.07 (based on 5 stage *G* fish sampled between VII:22–VIII:20) for a total decrease in ratios of 1.73; this approximates the decrease given above for Monterey in 1930. It should be noted that most of the decrease in ratios in 1929 at San Pedro also occurred during a two-month period. The ratio of 3.80 had decreased to 2.38 by lunar period IV:24–V:23 for a drop in ratios of 1.4. During the four succeeding lunar months the further drop in ratios amounted to only 0.3. The 1930 data show no real change in ratios during the season. A drop in ratios from 3.06 to 2.02 occurred between two lunar periods (between II:14–III:14 and III:15–IV:13), but the ratios again jumped to 2.92 and 2.84 in the two following lunar periods.

At the end of the spawning period at both ports spawning females still contained several modes that had not been spawned. These yolked ova must have degenerated and been resorbed. In fact, it may be characteristic of fish which mature several modes of ova, that one or more of the modes will be resorbed eventually rather than spawned.

LENGTH AT FIRST MATURITY

To facilitate handling of the data, the samples have been grouped by lunar periods [6] in table 14.

Clark (1934) considered as maturing all those fish having a group of ovarian eggs with a modal diameter of .22 mm. or larger (i. e., yolked ova). Using this criterion, the 250 fish taken in lunar periods 325 and 326 are compared in table 15 with Clark's data for the months of February, March, April, and May of the years 1929, 1930, and 1931.

[6] The Pacific sardine fishery in California is carried on at night, when the fish schools can be located by luminescence. There is generally no fishing during the full-moon period. Lunar periods are assigned numbers in connection with the sampling program of the California Cooperative Oceanic Fisheries Investigations.

TABLE 14.—*Samples grouped by lunar periods*

Lunar period	Sample	Date	Number of females
322	SP-1	Nov. 10, 1945	96
	SP-2	Nov. 13, 1945	
323	SP-3	Nov. 26, 1945	119
	SP-4	Dec. 5, 1945	
	SP-5	Dec. 10, 1945	
324	SP-6	Dec. 28, 1945	123
	SP-7	Jan. 5, 1946	
	SP-8	Jan. 11, 1946	
325	SP-9	Jan. 24, 1946	146
	SP-10	Feb. 1, 1946	
	SP-11	Feb. 9, 1946	
326	SP-12	Feb. 21, 1946	104
	SP-13	Feb. 27, 1946	

Maximum ovum diameter, the measurement used to describe the stage of maturity for the 1946 material, is the diameter of the largest ovarian ovum present in a sample of the ovary. An average value (mode, mean, or median) of the group of developing ova cannot be determined accurately for early developmental stages when the developing ova are not completely differentiated from the mass of immature, non-yolked ova that are always present in the ovary. For developing groups of ova that have differentiated enough from these immature ova to form a distinct size group, the maximum ovum diameter is about .07 mm. greater than the median ovum diameter of that size group. This difference is probably less for developing groups of smaller ova than for groups of larger ova.

TABLE 15.—*Numbers of sardines and percentages containing developing ova*

[San Pedro, Calif.]

Standard length (in millimeters)	Lunar period 325 (Jan. 24, Feb. 1 and 11)		(1946) Lunar period 326 (Feb. 21 and 27)		Lunar periods 325 and 326		1929–1930–1931 Clark (1934) (Feb. through May)	
	Total number	Percent maturing	Total number	Percent maturing	Total number	Percent maturing	Total number	Percent maturing
120–129	0		0		0		1	0
130–139	0		0		0		0	
140–149	0		1	0	1	0	4	0
150–159	11	9	24	17	35	14	4	0
160–169	34	29	23	43	57	35	21	24
170–179	8	63	2	100	10	50	21	38
180–189	6	100	10	100	16	100	36	58
190–199	13	92	20	100	33	97	62	89
200–209	25	96	9	100	34	97	83	94
210–219	31	97	9	100	40	98	94	99
220–229	13	100	3	100	16	100	85	100
230–239	4	100	0		4	100	79	99
240–249	1	100	2	100	3	100	75	97
250–259	0		1	100	1	100	67	100
260–269	0		0		0		54	98
270–279	0		0		0		36	100
280–289	0		0		0		10	100
290–299	0		0		0		2	100

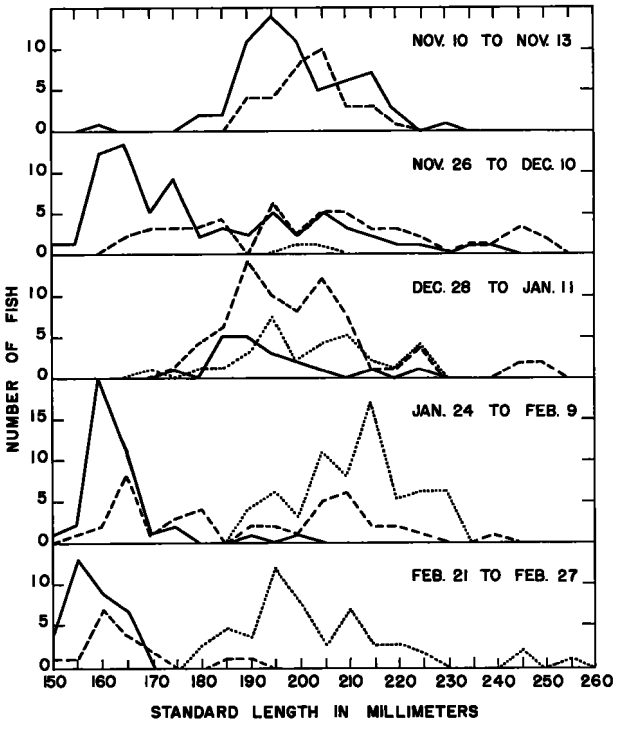

FIGURE 12.—Sardine length frequency distribution for each of three maximum ova diameter ranges (ova to 0.20 mm. solid lines, 0.22 to 0.40 mm. dashed lines, 0.42 mm. and larger dotted lines).

Figure 12 shows fish length-frequency distributions for each of three maximum ovum size ranges and for each of the five lunar periods. The first category of ovum diameters, to 0.20 mm., covers the range of non-yolked ova. The maximum ovum diameter observed for any fish during lunar period 322, when the ovaries were in a "resting" stage, was 0.40 mm.; this size was used as a break between the two categories of yolked ova. This is also the maximum ovum diameter attained by any fish less than 175 mm. in length during lunar period 326, when all but two of the larger fish contained ova that exceeded this value. Table 16 compares maximum ovum diameters of fish more than 175 mm. in length from the November 10 and 13 samples with those under 175-mm. and those over 175 mm., taken in the February 21 and 27 samples.

TABLE 16.—*Comparison of maximum ovum diameters*

Range of ovum maximum diameters	Lunar period 322 Nov. 10 and 13		Lunar period 326, Feb. 21 and 27			
	Fish more than 175 mm. long		Fish less than 175 mm.		Fish more than 175 mm.	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
to 0.20 mm.	62	65	33	69	0	0
0.22 to 0.40 mm.	33	35	15	31	2	4
0.42 and above	0	0	0	0	51	96
Total	95	100	48	100	53	100

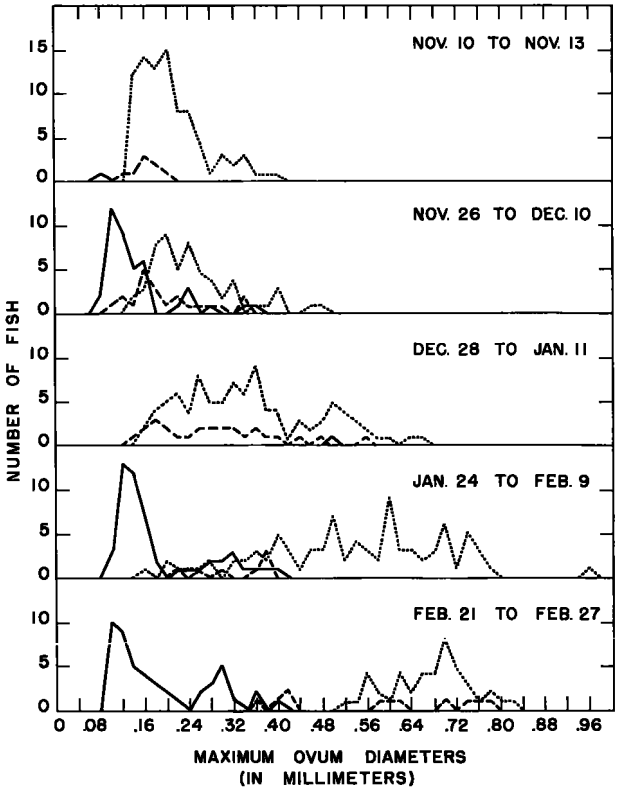

FIGURE 13.—Maximum ovum diameter frequency distribution for each of three sardine length ranges (148–174 mm. solid line, 175–189 mm. dashed line, 190–253 mm. dotted line).

Figure 13 shows the maximum ovum diameter frequency distribution for each of three fish size ranges. The above data show a very definite growth of the ova in fish more than 175 mm. in length and negligible growth of the ova in fish less than 175 mm. The state of development of the ovaries of the fish less than 175 mm. long in lunar period 326 (late February) is very similar to the

state of development of the ovaries of the fish above 175 mm. in length in lunar period 322 (mid-November). Clark (1934:22) states that, " * * * adolescent fish may start to mature eggs but these eggs may fail to reach a ripe state and eventually degenerate. Such a condition has been claimed for the hake by Hickling (1930), but we have not been able either to prove or disprove the possibility for the sardine." As no samples are available for the 1946 spawning season after February 27, the ultimate fate of the ovarian ova of these smaller sardines cannot be determined. If the presence of yolked ova in the ovary is the criterion of maturity, all fish more than 175 mm. in length and 31 percent of the fish under 175 mm. in length from the samples of February 21 and 27 had attained maturity. If a maximum ovum diameter exceeding 0.40 millimeters (i. e., the maximum ovum diameter attained by any fish in the samples of November 10 and 13, when the ovaries are "resting") is the criterion of maturity, all fish 190 mm. or more in length, 82 percent of the fish 175 to 189 mm. in length and none of the fish 174 mm. or less in length from the samples of February 21 and 27 had attained maturity.

AGE AT FIRST MATURITY

Numbers and percentages of sardines at each of three maturity stages for each age group and each lunar period are presented in table 17. If the presence of yolked ova in the ovary is the criterion of maturity, 28 percent of the one-year-old fish and 100 percent of the two-year-old and older fish were maturing in lunar period 326 (samples of February 21 and 27). But the presence of yolked ova in the ovaries may not necessarily mean that a fish will develop and eventually spawn those ova. Actually the one-year-old fish were less advanced in respect to ovarian development in lunar period 326 (samples of February 21 and 27) than the two-year-old and older fish were in lunar period 322 (samples of November 10 and 13).

In any case the one-year-old fish taken by the commercial fishery cannot be considered representative of the one-year-old fish in the population at large. One-year-old sardines are not often taken by the commercial fishery, and those that are taken are undoubtedly the larger specimens of that age group.

TABLE 17.—*Age at first maturity*

Age and year class	Maximum ovum diameter (in millimeters)	Lunar period 322		Lunar period 323		Lunar period 324		Lunar period 325		Lunar period 326	
		Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1-year-old (1945)	0 to .20			25	100			37	82	31	72
	.22 to .40			0	0			8	18	12	28
	.42 and over			0	0			0	0	0	0
Total				25	100			45	100	43	100
2-years-old (1944)	0 to .20	17	71	23	61	4	19	0	0	0	0
	.22 to .40	7	29	15	39	14	67	7	70	5	17
	.42 and over	0	0	0	0	3	14	3	30	24	83
Total		24	100	38	100	21	100	10	100	29	100
3-years-old (1943)	0 to .20	22	59	12	46	13	21	1	3	0	0
	.22 to .40	15	41	13	50	35	56	12	33	0	0
	.42 and over	0	0	1	4	14	23	23	64	17	100
Total		37	100	26	100	62	100	36	100	17	100
4-years-old (1942)	0 to .20	9	47	3	21	3	9	1	3	0	0
	.22 to .40	10	53	10	71	15	43	5	16	0	0
	.42 and over	0	0	1	7	17	49	26	81	6	100
Total		19	100	14	99	35	101	32	100	6	100
5 to 9 years old (1934–41)	0 to .20	9	69	5	31	0	0	0	0	0	0
	.22 to .40	4	31	11	69	8	80	2	15	0	0
	.42 and over	0	0	0	0	2	20	11	85	5	100
Total		13	100	16	100	10	100	13	100	5	100

SUMMARY

1. Ovarian ovum counts and diameter measurements are presented for 13 samples of sardines containing 587 females taken by the San Pedro commercial fishery during the period November 10, 1945 to February 27, 1946.

2. Throughout the size range of fish studied there are no significant differences among the regression lines of fecundity expressed as the number of ova in the most advanced group of yolked ova on length, on length squared, or on length cubed.

3. The estimated number of ovarian ova present in the most advanced group of yolked ova in a sardine 200 millimeters in length is 26.8 thousands (using the formula $Y=a+bX$). The rate of increase or decrease in estimated numbers of ova is 5.14 thousands per increase or decrease of 10 millimeters of length. There is considerable variation in the number of ova produced by individual fish at any given length. The standard error of estimate of y is 8.76 thousands of ova for the above formula.

4. The correlation between fecundity and fish weight is better than that between fecundity and fish length. The number of ova present in the most advanced group of yolked ovarian ova equals 263 ova per gram weight of sardine.

5. Both the fecundity-length and fecundity-weight correlations are better than the fecundity-age correlation.

6. No conclusions can be drawn from the material used in this study regarding the number of groups of ova that a sardine will spawn in one spawning season. The evidence presented in the literature by various authors is inconclusive and their conclusions are contradictory.

7. All fish two or more years old and all fish more than 175 mm. in length from the February 21 and 27 samples contained yolked ovarian ova (0.22 mm. or larger in diameter); 28 percent of the one-year-old fish and 31 percent of those less than 175 mm. in length also contained yolked ovarian ova. None of the fish in these latter groups contained ova greater than 0.40 mm. in diameter, while 91 percent of the two-year-old and older fish and 96 percent of the fish greater than 175 mm. in length contained ova greater than 0.40 mm. in diameter. The stage of ovarian development of the one-year-old sardines less than 175 mm. in length on February 21 and 27 was much like that found in the older and larger fish taken about 3 months earlier (on November 10 and 13, 1945).

LITERATURE CITED

AHLSTROM, ELBERT H.
1950. Influence of temperature on the rate of development of pilchard eggs in nature. U. S. Dept. Interior, Fish and Wildlife Service, Spec. Sci. Rept.: Fisheries No. 15, pp. 132–167.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. U. S. Dept. Interior, Fish and Wildlife Service, Fishery Bull. 93, vol. 56, pp. 83–140.

ANDREU, BUENAVENTURA.
1951. Consideraciones sobre el comportamiento del Ovario de sardina (*Sardina pilchardus* Walb.) en relacion con el proceso de meduracion y de freza. Boletin del Instituto Espanol de Oceanografia, No. 41, 16 pp.

CLARK, FRANCES N.
1925. The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. California Division of Fish and Game, Fish Bulletin No. 10, 51 pp.
1928. The weight-length relationship of the California sardine (*Sardina caerulea*) at San Pedro. California Division of Fish and Game, Fish Bulletin No. 12, 58 pp.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. California Division of Fish and Game, Fish Bull. No. 42, 49 pp.

FRASER, C. MCLEAN.
1922. The Pacific herring. Contributions to Canadian Biology, No. VI, pp. 103–111.

HART, J. L., and J. L. MCHUGH.
1944. The smelts (Osmeridae) of British Columbia. Fisheries Research Board of Canada, Bull. 64, 27 pp.

HICKLING, C. F.
1930. The natural history of the hake. Part III: Seasonal changes in the condition of the hake. England. Min. Agri. Fish., Fish Invest., Ser. 2, vol. 12, No. 1, 78 pp. Ref. from Clark (1934).
1945. The seasonal cycle in the Cornish pilchard, *Sardinia pilchardus* Walb. Journal Mar. Biol. Assn., vol. XXVI, No. 2, pp. 115–138.

JUNE, FRED C.
1953. Spawning of yellowfin tuna in Hawaiian waters. U. S. Dept. Interior, Fish and Wildlife Service, Fishery Bull. 77, vol. 54, pp. 47–64.

LEHMAN, BURTON A.
1953. Fecundity of Hudson River shad. U. S. Dept. Interior, Fish and Wildlife Service, Res. Rept. No. 33, 8 pp.

MOSHER, KENNETH H.
1950. Description of a projection device for use in age determination from fish scales. U. S. Dept. Interior, Fish and Wildlife Service, Fish. Bull. 54, vol. 51, pp. 405–407.

PHILLIPS, JULIUS B.
1948. Growth of the sardine (*Sardinops caerulea*), 1941–1942 through 1946–1947. California Fish and Game, Fish Bull. No. 71, 32 pp.

SETTE, OSCAR E., and ELBERT H. AHLSTROM.
1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. Sears Foundation: Journal of Marine Research, vol. VII, No. 3, pp. 511–542.

SIMPSON, A. C.
1951. The fecundity of the plaice. Ministry of Agriculture and Fisheries, Fishery Invest. No. 5, vol. 17, Series II, 27 pp.

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