DIVISION OF FISH AND GAME OF CALIFORNIA
BUREAU OF COMMERCIAL FISHERIES
FISH BULLETIN No. 42

Maturity of the California Sardine (Sardina caerulea),Determined by Ova Diameter Measurements

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CONTENTS

INTRODUCTION

Because the California sardine is seldom taken in a ripe condition, a study of the maturity of this fish has proved a very complicated problem. Since 1919 the California State Fisheries Laboratory has conducted an intensive investigation of the sardine but in the 12 seasons covered by the study only 39 ripe or nearly ripe females have been observed. As the gross observations of the state of maturity of the gonads of the sardine have not proved satisfactory, this detailed study of the diameters of the eggs in the ovaries was made.

The study has established the dates of the spawning season, the size at first maturity, and the amount of spawning in each locality. Also, the maturity studies have thrown further light on the movements of sardines. The concentration of spawning in the south and a difference between the north and the south in the rate of development of the eggs, indicate that during the winter months sardines are moving southward along the California coast.

Although all the egg measurements were made by the writer, various members of the Laboratory staff aided in collecting the material, and their assistance is gratefully acknowledged. The writer has also benefited from the advice and criticism of staff members and received many valued suggestions from Mr. W. L. Scofield, supervisor of the Laboratory, and from Dr. W. F. Thompson, director of investigations, International Fisheries Commission (United States and Canada), who introduced the use of egg diameter measurements in his study of the Pacific halibut. (Thompson, 1915.)

July, 1931.

1. METHCDS

1.1. Collection of Material

This study is based on measurements of the diameters of the ova from the gonads of female sardines. The material was obtained from two sources—sardines caught for canning purposes and sardines caught for the fresh fish markets. During the fall and winter, collections were made from the cannery catch, but because sardines are not taken during the summer months in sufficient quantities to keep the canneries operating, material was obtained from the fresh fish markets when cannery fish were not available.

The method of collecting the egg samples had to be such that no selection involving maturity occurred, and such that samples were taken from as complete a size range as could be secured on any sampling day. Since 1919, the Laboratory has collected samples from the cannery catch of sardines. These samples, five of which are taken each half week, consist of 50 fish from a fishing boat. From the cannery catch, the ova samples were selected from these regular fish samples. The size range of sardines in each sample was divided into centimeter groups and an ova sample taken from the first female measured in each centimeter category. This gave ova samples collected at random as regards the state of maturity, but which represented all the centimeter size groups found among the 250 fish measured on a sampling day.

As no regular system of sampling is carried on for sardines delivered to the fresh fish markets, a different means was devised to secure egg samples from this class of fish. Ova samples were taken once a week from 10 females. The fish were sorted in the markets, to secure a fairly complete size range, and egg samples taken from 10 females selected for size but not for condition of maturity.

For each ova sample, the date and locality of capture, source of material, length of fish, weight of fish, and state of maturity as determined by a gross examination of the gonad, were recorded. The material was preserved in 10 per cent formalin and allowed to harden several days before the eggs were measured.

1.2. Measurement of the Ova

When the ova sample had hardened in formalin for at least four or five days, a fraction of the ovary was teased out on a slide and the diameters of the eggs measured by means of a micrometer eyepiece in a compound microscope at a magnification which gave a value of 0.02 mm. to each micrometer unit. Due to the effects of preservation, the eggs when measured were not always perfectly symmetrical, and to obviate any selection of the longest or shortest diameter, the micrometer was placed in a horizontal position in the eyepiece and the diameter parallel to the graduations on the micrometer measured. This gave measurements of the longest diameters of some eggs, the shortest of others or measurements intermediate between these two. The writer in a previous study (Clark, 1925), after a careful trial, found this to be a reliable procedure and the most satisfactory for constant use.

Tests were made to determine the effect of the preservative on the diameters of the eggs. No consistent evidence of either shrinkage or swelling was apparent, but to make absolutely certain that all measurements were directly comparable all the material was preserved in 10 per cent formalin.

Test measurements were made of eggs from the anterior, central and posterior portion of an ovary. No differences in the relative numbers of eggs in each size group were found in any of these regions. Consequently the eggs were measured from the central portion of each ovary.

In the ovaries of maturing fish several size groups of eggs larger that the immature ova were present in the ovary at one time. To assure the representation of each of these groups in their true ratios, 200 eggs larger than the immature group were measured from each sample. Fewer than 200 measurements were not adequate to assure the proper representation of these groups. In immature fish only one size group of eggs was present in the ovary and since this group was adequately represented by less data, only 100 eggs were measured from each immature ovary. For immature fish a portion of an ovary was teased out on a slide and 100 eggs measured at random. For maturing fish a portion of an ovary was teased out and all eggs larger than 0.2 mm. measured. Smaller ova were not measured in the latter case.

1.3. Definition of Terms

In any discussion of maturity, confusion arises over the meaning of the words immature and mature. Immature may refer to young fish which have never spawned or it may designate older fish which have spawned previously and as yet show no indication of the onset of maturity for the following spawning season. Similarly, maturity has a double meaning.

In this study, fish which have never spawned are designated as "young" and individuals which have spawned previously or are approaching their first spawning season as "adult" or "adolescent." Eggs which show no growth toward maturity, *i.e.*, smaller than 0.22 mm., and females containing this group of eggs only are termed "immature." "Maturing" refers to eggs larger than 0.20 mm. and to females with eggs of these sizes. "Mature" means completely ripe eggs which have burst from their follicles and lie in the lumen of the oviduct. "Spent" fish are females with eggs larger than 0.20 mm. that are degenerating and being resorbed.

2. LIMITATIONS OF THE STUDY

The time required to measure 200 eggs from each fish placed a limit on the number of individuals which could be used in this study. Although egg measurements were made from 3000 females, these comprised data taken over a period of five years and from four localities. Greater numbers of samples would have made the results more convincing, however, the measurements made constituted the maximum that could be handled by one worker. In spite of the limitation in numbers the repetition of the same maturity conditions in successive seasons justifies the general conclusions here drawn.

Since the methods used in this study could not be applied to the males, conclusions must be based on data for the females only and the work is limited thereby. Gross observations of maturity were made by each investigator sampling sardines, but the problem is so difficult that these results were too inconsistent to be usable even for the females. In only one or two cases did a worker continue his observations on the males throughout a season. Each individual became so dissatisfied with his attempts that he discontinued the work as worse than useless.

This lack of data for the males was most keenly felt in determining the size at first maturity or adulthood. In many species males mature at a smaller size than females, but whether this is true for the sardine we do not know. The scanty observations made indicated a larger size for the males but due to the inaccuracies of the observations no credence can be placed in these results. What sexual differences exist in the size of sardines at adulthood we can not state.

The dates of the spawning season and the percentage of fish spawning in each locality are presumably sufficiently indicated by a study of the female fish only.

3. HISTORY OF THE RIPENING OVA

3.1. Description of a Mature Ovary

Only four mature female sardines have been observed during the 11-year period of the sardine investigation. These fish were sufficient, however, to make clear the appearance of a mature ovary and of the ripe eggs contained therein. Figure 1 is a diagrammatic sketch of a mature ovary found in the San Pedro fresh fish markets on July 13, 1928. Because the mature eggs ran freely when the body of the fish was pressed, presumably most of the ripe eggs had been extruded before the fish was examined. When the fish was opened no ripe eggs were visible on the ventral side of the ovary except in the oviduct near the vent. After the gonad had been removed from the fish, the mature eggs were plainly evident lying in the lumen of the oviduct along the dorsal side of the ovary. If all the mature eggs had still been present in the ovary, probably the oviduct would have been much distended and the ripe eggs would have been apparent on the ventral as well as on the dorsal side of the gonad. The ovary of a second mature female taken May 23, 1929, appeared much as the above.

The ripe eggs were practically transparent, very delicate and easily broken. Each egg contained a single oil droplet, salmon-pink in color, and 0.16 mm. in diameter. The average diameter of the mature ova was 1.24 mm., the range from 0.96 to 1.36. No perivitelline space was evident in the eggs fresh from the ovary, but after they had been placed in sea water this space developed and varied in width from 0 to 0.16 mm. In many eggs the yolk became excentric but this was not true of all. Attempts made to fertilize these ripe eggs met with no success.

This appearance of the ripe sardine egg corresponded in most respects with the description of fertilized sardine eggs found in plankton hauls by Scofield and Lindner (1930). While the latter averaged larger, 1.89 mm. in diameter, and had a larger perivitelline space, this increase in size undoubtedly resulted from an absorption of water by the fertilized

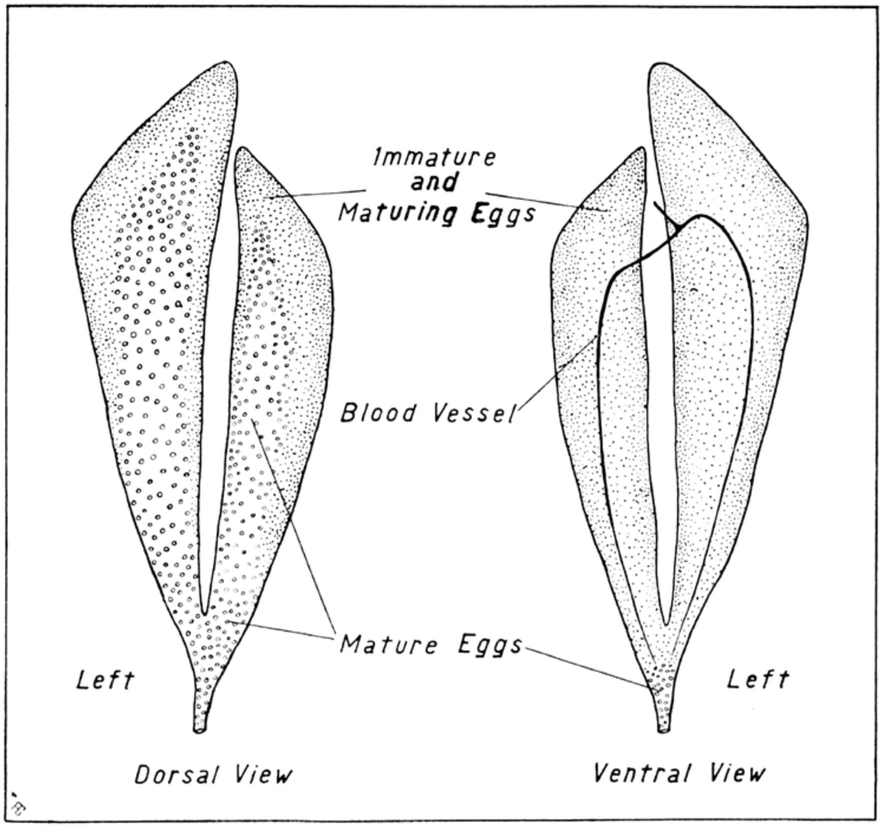

FIG. 1. Diagrammatic drawing of a mature sardine ovary showing the location of different groups of eggs.

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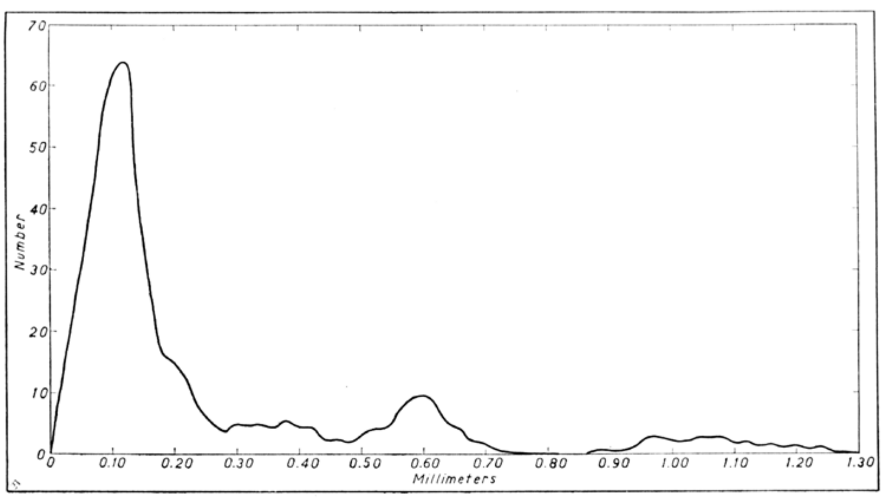

FIG. 2. Frequency polygon of the diameters of 516 ova measured from a maturing sardine, 233 mm. in body length, taken on the west side of San Clemente Island, March 22, 1928.

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egg. In the planktonic eggs the yolk was excentric and the single oil droplet 0.15 mm. in diameter. Similarly the ovarian eggs had a single oil droplet 0.16 mm. in diameter and excentric yolk when placed in sea water. Both types of eggs were transparent. Further measurements made by Scofield, E. C. (1934), on planktonic eggs give an average ova diameter of 1.60 mm. and the diameter of the oil droplet as 0.16 mm.

Since this study is based on egg measurements, the few mature or nearly mature sardines found aided materially in interpreting the state of maturity of eggs from other females. Figure 2 is a frequency polygon of the diameters of 516 ova measured at random from a nearly mature ovary. Four distinct groups are apparent in this frequency. The first, between 0 and 0.2 mm., represents immature eggs, invisible to the naked eye, and present in the ovary throughout the entire year. The next group, between approximately 0.3 and 0.5 mm., comprises opaque, creamy-white eggs, visible without the aid of a microscope. Eggs of this group are found in most adult females from late December to the following July or August. The third group, between approximately 0.5 and 0.7 mm., also opaque and creamy-white in color, consists of egg sizes found in many adult females from late January to July or August. The fourth group, between 0.9 and 1.23 mm., includes eggs almost ready for spawning. These eggs are practically transparent and resemble the mature eggs described in the preceding paragraph. Fish containing this group of eggs are rarely taken in the commercial catch of California sardines. In the 11 years of study only 39 have been found among the thousands of females which have passed under observation.

The measurements for this diameter frequency were made without any size selection and represent with fair accuracy the numerical ratio of eggs in each group. The eggs in the three larger groups were of approximately equal numbers, but the eggs of the first or immature group far exceeded the numbers in all the other groups. This was true in spite of the fact that these very small eggs were easily overlooked and were undoubtedly discriminated against when the measurements were made. This equality in numbers of the various maturing groups occurred with great consistency in the ova diameter frequencies for the many individuals studied.

3.2. Growth from the Immature Stage to Maturity

If all sardines matured at the same time the growth of the ova to maturity could be readily traced, but the state of maturity varied greatly among individuals and on many sampling days fish in all stages of maturity were found. Because of this diversity among individuals in the time of maturity no chronological arrangement of the data could be made to show the various stages through which the eggs pass before spawning. To demonstrate the history of the maturing eggs, the data were grouped according to the location of the largest mode in the diameter frequency of the eggs from each fish. This resulted in the following twelve classes:

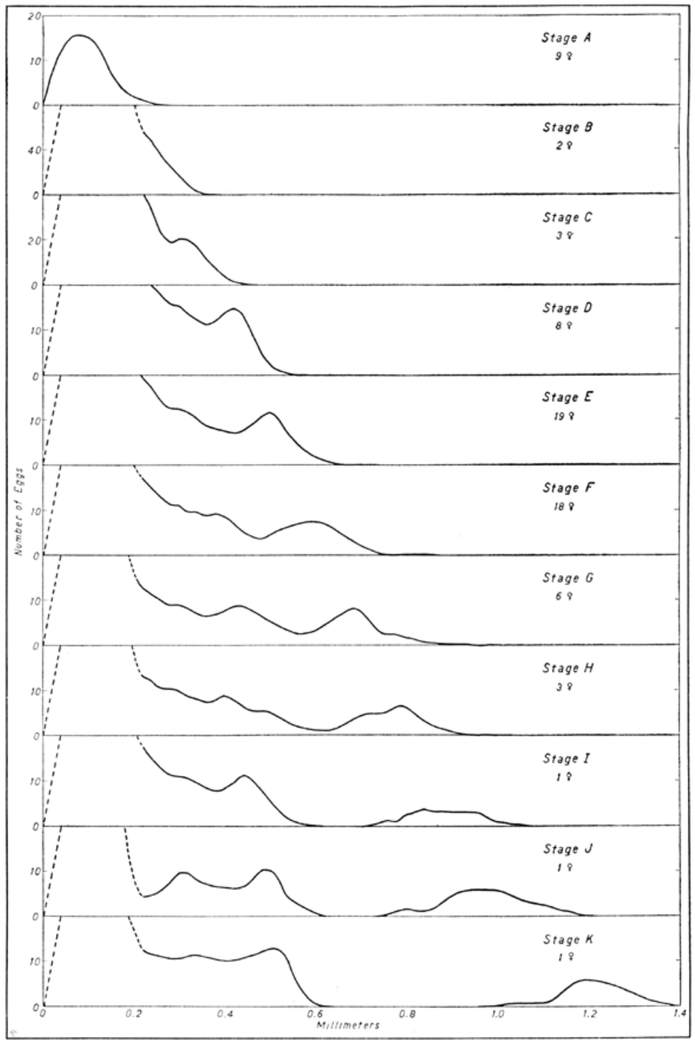

FIG. 3. Ova diameter frequency polygons showing the growth of the eggs to maturity. Each frequency represents measurements of ova from one or more females. Material taken at San Pedro between April 24 and May 23, 1929.

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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.

Maturing (transparent eggs)

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

Stags 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 mm. but these eggs degenerating.

These classifications correspond to the maturity scale adopted by the International Council for the Exploration of the Sea (Wood, 1930) and to the classification adopted by Andrews (MS.), roughly as follows:

International	*Andrews'*	*California*
Council	*Classification*	*Sardine*
Stage I	Class 1	Stage A
II	2	B and C
III	2	D, E and F
IV	3	G and H
V	4	I and J
VI	4	K
VII	5	L

The data for each sampling day were grouped according to the above classification and these groupings further combined by lunar months. In the sardine investigation lunar months are used in preference to calendar months because fishing is suspended for a period of four or five days at the time of each full moon. This natural division of the data into specific time intervals has been found advantageous in many phases of the sardine investigation. (Scofield, W. L., 1926, p. 201.) During one lunar month, April 24–May 23, 1929, fish representing all the maturity groups except L were taken at San Pedro. The ova diameter frequencies for these fish are shown in figure 3. These curves with the exception of the three lower graphs represent the averages of the frequencies for more than one fish. The number of fish included in each curve is indicated on the figure. No actual measurements of ova smaller than 0.22 mm. were made for any except immature fish. These eggs were omitted because they so far outnumbered the maturing eggs that to measure them in their true ratios would have increased the work manyfold. Since immature eggs, smaller than 0.22 mm., are found in the ovary at all times in the year, these eggs are of only minor interest in a study of the growth of the ova to maturity and nothing was lost by not including them in the measurements. Stage

A of figure 3 is based on actual measurements and in the following curves the immature group is suggested by the broken lines. The frequencies are smoothed by a moving average of three.

Figure 3 may be considered a composite picture illustrative of the growth of the ova to maturity for individual sardines. The time required for a group of eggs to develop from stage A to stage K is discussed in the section "Time of the Spawning Season." Figure 3 must not be construed as representing any fixed time but as merely showing the changes taking place in a maturing ovary. At the onset of maturity certain ova in the immature group start growth. These gradually increase in diameter and continue to grow as a unified group until they are mature as in K. The apparent rapid growth from J to K results from the fact that stage J comprises twice as great a size interval as do the other stages. No data illustrating the second half of stage J were available for this lunar month.

Little visible change in the eggs of the maturing group was evident before stage H. Between stages H and I the ova lost their opaqueness and became practically transparent. Stage H represents the point at which sardines disappear from the commercial catch, few fish of this stage were taken in the regular samples, and the following three stages were represented by only 39 fish in all the data observed. The cytological changes which occur within the ova during growth to maturity are described by Andrews (MS.)

By the time the first batch of eggs had increased in size sufficiently to develop a definite mode, stage D, a second class was suggested by the flatness of the curve between 0.2 and 0.3 mm. When the first group had reached stage G, the second group was definitely apparent with a mode at 0.44 mm. The growth rate of the first maturing group was but little faster than that of the second until stage G was reached. From that point onward the first group grew much more rapidly than the second. At stage I when the first lot of eggs had become entirely separated from the second, a third group was again suggested in the flatness of the curve between 0.2 and 0.3 mm. In stages J and K the mode of this third group was clearly evident. The diameter frequency curve of figure 2 suggests the origin of a fourth group at 0.2 mm. This multiplicity of modes appeared in practically all the diameter frequency curves of maturing ova from individual fish and its validity is clearly evident.

4. FREQUENCY OF SPAWNING WITHIN A SEASON

4.1. Multiplicity of Modes

The multiplicity of modes in the frequency curves of ova diameters from maturing females strongly suggests that individual sardines spawn more than once in each spawning season. But this can not be accepted as a fact until it has been shown that these secondary modes do not represent eggs which will be spawned in succeeding seasons, or that they do not comprise eggs which will never ripen but will degenerate and be resorbed at the close of the breeding season. This latter theory of degeneration and resorption is favored by Andrews (MS.).

That the secondary modes are not spawned in later years is very clear. From August, 1928, to June, 1930, egg samples were collected continuously at Monterey and San Pedro. In both localities during the fall months, September and October, no sardines were taken with any eggs larger than the immature group, represented by stage A, figure 3. This was true of all females, both young and adult. Since maturing eggs were present in the ovaries at certain seasons of the year only, the secondary groups of maturing eggs evident during the spawning season can not constitute ova which will mature in succeeding years.

4.2. Growth of Distinct Egg Groups

To establish whether these secondary groups of eggs will be spawned or whether they will degenerate is much more difficult. The fact, as indicated in figure 3, that the groups of smaller eggs increase in size as the batch of largest eggs grows to maturity intimates that these succeeding groups will also mature in their turn. To show this correlation between the progression of the modes of the various groups of maturing ova figure 4 is given.

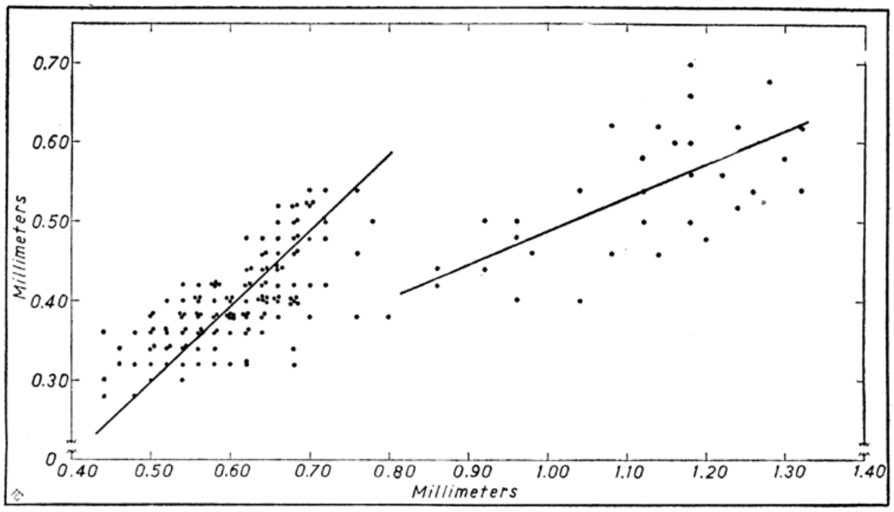

FIG. 4. Scatter diagram showing the correlation between succeeding modes in ova diameter frequency curves for 140 sardines taken at San Pedro. The last mode of each curve is plotted on the abscissa against the immediately preceding mode on the ordinate.

FIG. 4. Scatter diagram showing the correlation between succeeding modes in ova diameter frequency curves for 140 sardines taken at San Pedro. The last mode of each curve is plotted on the abscissa against the immediately preceding mode on the ordinate

The data for this figure were derived from the ova diameter frequency curves of 140 sardines. The curves were smoothed once by a moving average of five to determine the location of the mode of each group of eggs. The mode of the largest group was then plotted on the abscissa against the mode of the next smaller group on the ordinate. For example, since in stage G, figure 3, the mode of the last group of eggs falls at 0.68 mm. and of the next group at 0.44 mm., a dot would be placed at the point where the abscissa 0.68 intersects the ordinate 0.44.

The points to the right of the 0.80 axis represent fish with transparent eggs in stages I to K. The points to the left of 0.80 indicate fish in stages D to H. It is evident that the relationship between the modes before the largest eggs attain a mode at 0.80 differs from the relationship after the mode of this group passes this point. Up to this stage the immediately following group increases in size almost as rapidly as does the largest group of eggs. When the mode of the largest group grows beyond 0.80, the size at which the eggs become transparent, this batch of eggs increases in size more rapidly and for an interval of time the next succeeding group apparently shows little growth. But the data for fish with transparent eggs are unfortunately scanty and it is impossible to determine whether the apparent temporary cessation of growth of the second batch of eggs is valid or whether the appearance results from too few data.

Since the division line at 0.80 marks a visible biological change in the ova, the data were thus divided into two groups and correlation coefficients were calculated for each group. The Pearsonian coefficient for the modes below 0.80 was 0.70±0.03 and for the modes above, 0.72±0.05. These high coefficients, far exceeding their standard errors, demonstrate a close relationship between the progression of succeeding modes in the ova diameter frequency curves. As one group of eggs increases in size other groups grow also, although not necessarily at the same rate.

To obtain some measure of the relative rate of growth between each succeeding batch of eggs, a straight line was fitted to all data below 0.80 and a second line to the data above this point. The units describing the slope of these lines were 0.88 for the first group of data and 0.42 for the second. This indicates that until the largest group of eggs reaches stage H, the next batch increases in size almost, although not quite, as rapidly as the first. If the unit expressing the slope of the line had been 1.00 the progression of the two modes would have been indicated as equal. After the first batch of eggs passes stage H, their growth is apparently slightly more than twice as fast as that of the immediately following group. A value of 0.5 would have indicated twice as rapid a rate of increase for the maturing group. This comparison of growth rate up to stage H with the growth rate from H to maturity, assumes an uninterrupted growth from stages B to H. Probably this growth is modified by complex biological phenomena which this study can not measure.

This evidence, which demonstrates that distinct batches of eggs are successively growing toward maturity in the ovaries of individual sardines, does not prove, however, that more than one batch of eggs is actually spawned each season. Succeeding batches may never grow beyond stage G or H and degenerate at these stages. Degenerating eggs in all stages from B to H were found at the close of the breeding season, but stages B and C were more numerously represented. That the majority of eggs in stages B to H do not degenerate but are spawned out is shown in the following paragraphs.

4.3. Remnants of Ripe Ova from Previous Spawnings

For the grunion and the jack smelt multiplicity of spawning has been demonstrated (Clark, 1925, 1929) by the fact that a second lot of eggs was ripening while there still remained in the oviduct a few ripe ova which had not been extruded at the previous spawning. For the sardine the detection of a remnant of ripe eggs in the oviduct was very difficult. The ripe sardine eggs are so nearly transparent and so delicate that unless they are present in considerable numbers they are easily overlooked. In a few instances, however, scattered, degenerating mature eggs were observed at the same time that a second batch of eggs was developing toward maturity.

4.4. Relative Numbers of Eggs in Each Group

If several groups of maturing eggs are present in an ovary but only one batch of eggs is spawned by each female, the numbers of eggs in the maturing groups should maintain a constant ratio to the numbers of eggs in the mature group throughout the entire breeding season. If, on the other hand, more than one batch of eggs is spawned each season, as the season advances succeeding batches of eggs will progress from the maturing to the mature group and the numbers of eggs in the maturing group should decrease in proportion to the numbers of eggs in the mature group.

TABLE 1

Ratio of All Eggs between 0.20 and 0.59 mm. to All Eggs Larger Than 0.59 mm. for All Females in Stage G. Data Combined by Lunar Months

Lunar month	Ratio			
	San Francisco	Monterey	San Pedro	San Diego
I:26– II:23:'29			3.36 to 1	
II:24– III:25		5.06 to 1	3.80 to 1	
III:26– IV:23			2.87 to 1	
IV:24– V:23		3.96 to 1	2.38 to 1	
V:24– VI:21		4.16 to 1	2.26 to 1	
VI:22– VII:21		2.17 to 1	2.39 to 1	
VII:22–VIII:20		2.88 to 1	2.07 to 1	
VIII:21– IX:18			2.11 to 1	
I:15– II:13:'30		3.88 to 1	2.95 to 1	2.34 to 1
II:14– III:14		3.72 to 1	3.06 to 1	2.71 to 1
III:15– IV:13		2.85 to 1	2.02 to 1	3.12 to 1
IV:14– V:12	2.75 to 1	2.22 to 1	2.92 to 1	
V:13– VI:11		2.42 to 1	2.84 to 1	

TABLE 1

Ratio of All Eggs between 0.20 and 0.59 mm. to All Eggs Larger Than 0.59 mm. for All Females in Stage G. Data Combined by Lunar Months

To determine this point for the sardine, comparisons were made for fish in stage G, the only stage comprising sufficient data to make such a comparison possible. The diameter frequencies for this stage were summed for each lunar month of the spawning season and the numbers of all eggs larger than 0.59 mm. were compared with all eggs between 0.20 and 0.59 mm. The resulting ratios are presented in table 1. At both Monterey and San Pedro the number of eggs in the smaller size groups decreased in proportion to the number in the largest size group as the spawning season advanced. For the Monterey data, at the beginning of the 1929 season and again in 1930, the ratio was practically 4 to 1. This changed to less than 3 to 1 at the close of each season. In the San Pedro region the first ratios were slightly more than 3 to 1 but did not equal 4 to 1. During 1929 the ratios gradually changed to practically 2 to 1 at the close of the season. In 1930 the study was not continued to the close of spawning but as in 1929 with the advance of the season a proportionate decrease in the numbers of the eggs smaller than the largest group was indicated. Only three lunar months are represented in the San Diego data, but these suggest an increase rather than a decrease in the relative numbers of smaller eggs, however, the data are too scanty to justify definite conclusions.

Although table 1 seems to indicate quite definitely that the numbers of smaller eggs decreased with the season in proportion to the numbers of largest eggs, the possibility remains that in the latter part of a spawning season only smaller fish were comprised in the data and that these contain a relatively smaller number of eggs between 0.20 and 0.59 mm. than do the larger fish. That this was not true is shown by table 2. The

TABLE 2

Average Length by Lunar Months of All Females in Stage G

Lunar month	Average length in millimeters		
	Monterey	San Pedro	San Diego
I:26– II:23:'29	----------	225	----------
II:24– III:25	252	255	----------
III:26– IV:23	----------	250	----------
IV:24– V:23	255	222	----------
V:24– VI:21	232	215	----------
VI:22–VII:21	251	238	----------
VII:22–VIII:20	254	234	----------
VIII:21– IX:18	----------	237	----------
I:15– II:13:'30	246	242	244
II:14– III:14	246	237	243
III:15– IV:13	239	253	233
IV:14– V:12	242	244	----------
V:13– VI:11	255	245	----------

TABLE 2

Average Length by Lunar Months of All Females in Stage G

average length of the fish in stage G for each lunar month did not decrease in any consistent manner at either Monterey or San Pedro, and at the close of the season the averages were as great as at the begining. Further, for the San Pedro data for the first two lunar months of the spawning seasons of 1929, 1930 and 1931, the ratios for the two classes of eggs were calculated for fish in each centimeter length range. These calculations, presented in table 3, do not indicate any consistent change in ratios at different length units. Fish smaller than 200 mm. appear to have lower ratios than do larger fish, but these ratios are based on only four fish and many females at larger sizes had as low individual ratios as did these small fish. High ratios are indicated in the 20, 24 and 26 cm. ranges, but these do not signify a consistent increase or decrease in ratios with length changes. The maximum ratio in the 28 cm. class, based on only one individual, did not exceed

TABLE 3

Ratio of All Eggs between 0.20 and 0.59 mm. to All Eggs Larger Than 0.59 mm. for Females in Stage G, Grouped by Centimeters of Length. Data for San Pedro, January 26-March 25, 1929, January 15-March 14, 1930, and February 4-April 2, 1931

Body length, mm.	Ratio	Number of individuals
180–9	2.28 to 1	2
190–9	2.36 to 1	2
200–9	3.61 to 1	5
210–9	2.97 to 1	11
220–9	2.61 to 1	6
230–9	2.96 to 1	9
240–9	3.57 to 1	12
250–9	3.37 to 1	11
260–9	3.65 to 1	11
270–9	2.72 to 1	10
280–9	5.25 to 1	1

TABLE 3

Ratio of All Eggs between 0.20 and 0.59 mm. to All Eggs Larger Than 0.59 mm. for Females in Stage G, Grouped by Centimeters of Length. Data for San Pedro, January 26–March 25, 1929, January 15–March 14, 1930, and February 4–April 2, 1931

individual ratios in other size groups. The gradual decline in ratios from 20 to 22 cm. followed by an upward trend to 24 cm. may have been caused by significant ratio differences at these sizes. But a careful analysis of the ratio data for individual fish suggests that this is merely a chance variation and the possibility that the ratios of different egg groups change with the size of the fish seems remote. A similar comparison of ratios at each centimeter of length for the two succeeding lunar periods of each spawning season showed a decrease in the ratios at all length units, thus indicating that as the spawning season advanced the relative numbers of eggs smaller than 0.59 mm. decreased for sardines at all lengths. We are justified in assuming therefore that the decrease throughout the season in the ratios of the different groups of eggs did not result from changes in the sizes of fish making up the catch but was brought about by the spawning out of successive batches of eggs.

To illustrate the effect on the diameter frequency curves of this change in ratios, figure 5 is shown. These curves give the average frequencies of all females in stage G for the eight lunar months of the 1929 spawning season at San Pedro. The numbers of fish represented by each curve are indicated on the figure. The frequencies were smoothed once by a moving average of three. During the first two lunar months, January 26 to March 25, the largest maturing group was immediately followed by a second group of eggs ranging in size from 0.36 to 0.56 mm. In the next two lunar months, March 26 to May 23, the relative numbers of eggs in this group had decreased and at the close of the season, this group was represented only by eggs between 0.36 and 0.46 mm. The numbers of eggs between 0.20 and 0.36 mm. had also decreased. Presumably as the spawning season advanced, succeeding groups of eggs failed to undergo a corresponding growth and spawning finally ceased after the largest group of eggs had been spawned out.

4.5. Number of Spawnings

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; all furnish sufficient evidence to justify the conclusion that individual sardines spawn more than once in a breeding season. 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. The mode at 0.20 mm. in figure 2 suggests such a growth, as do the successively appearing modes in the curves in figure 3.

5. NUMBER OF EGGS SPAWNED

Because so few sardines are taken in a mature condition and because individual fish spawn more than once in a season, determination of the number of eggs spawned by each fish was difficult. Estimations were attempted, however, for eight females of varying lengths. The procedure was as follows: Both ovaries were carefully removed from

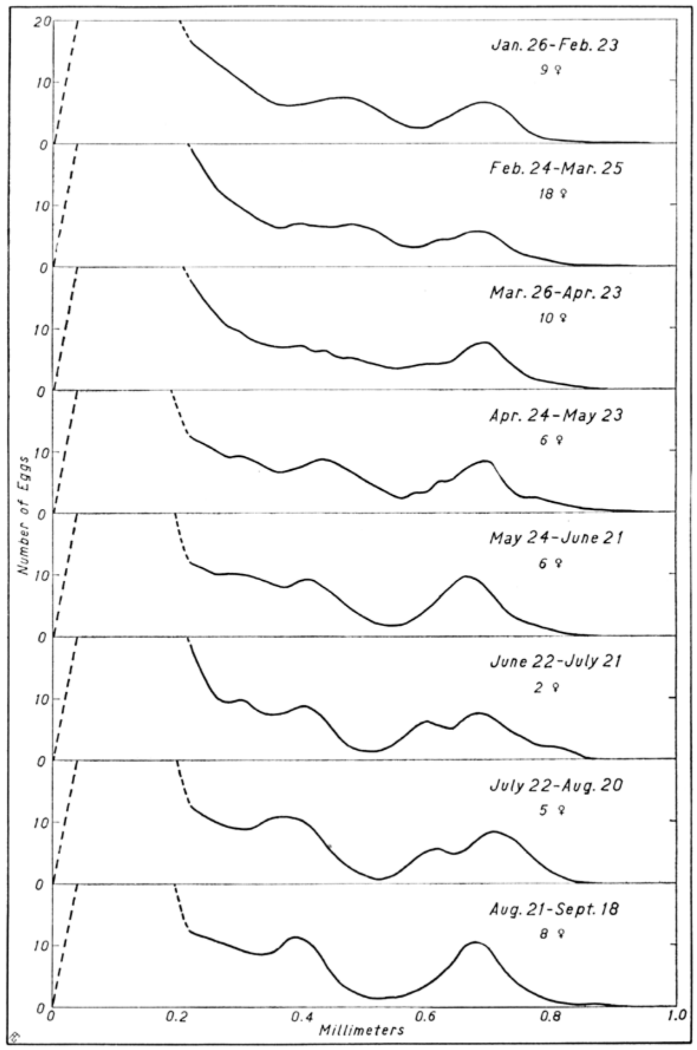

FIG. 5. Ova diameter frequency polygons, combined by lunar months, for all females in stage G taken at San Pedro during the 1929 spawning season.

FIG. 5. Ova diameter frequency polygons, combined by lunar months, for all females in stage G taken at San Pedro during the 1929 spawning season

the fish and preserved in 10 per cent formalin. When sufficiently hardened the excess moisture was drained away and the gonads weighed to the nearest milligram. A small sample of the gonad was then weighed and measurements made of all eggs larger than 0.2 mm. in this sample. The number of eggs in the largest group was then ascertained and multiplied by the factor which expressed the ratio between the weight of the sample and the entire weight of the gonads. This gave the total number of eggs in the largest maturing group. The results are presented in table 4.

TABLE 4

Number of Eggs Matured at Each Spawning and Estimated Number Produced in a Season

Body length, mm.	Number of eggs in one spawning	Number of eggs in three spawnings
191	35,520	106,560
202	34,880	104,640
215	30,000	90,000
231	34,780	104,340
243	42,190	126,570
255	59,540	178,620
257	50,540	151,620
267	65,330	195,990

TABLE 4

Number of Eggs Matured at Each Spawning and Estimated Number Produced in a Season

As is true of many fishes, the number of eggs increased with the size of the sardine. The four smallest females, however, were maturing approximately the same number of eggs. Possibly sardines from 19 to 23 cm. produce an equal number of eggs, but more probably additional data would indicate a differentiation in numbers for fish of this size range.

Other workers, notably Kisselevitch (1923) for the Caspian herring, found that the number of eggs increased as the square of the length. Although the data for the California sardine were very inadequate they were used to estimate roughly this relationship between numbers of eggs and length of the fish. 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 are based on very scanty data, these conclusions can be tentative only.

Inasmuch as each sardine spawns more than once in a season, the number of eggs in one spawning does not represent the total egg production for a breeding year. On a basis of three spawnings for each fish, the total number of eggs matured in a year are presented in the third column of table 4. These totals vary from a minimum of 90,000 to a possible maximum of 200,000.

6. SIZE AT FIRST MATURITY

The size of sardines at first maturity was determined from data collected at Monterey and San Pedro during the 1928–1929, 1929–1930 and 1930–1931 seasons. All females with eggs larger than stage A were considered maturing and classed among fish that would spawn in the season of collection. It is possible that this method introduces some error for 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. Fish with eggs in stage G have been found for all lengths greater than 160 mm., body length, but our percentages of maturing fish may be somewhat in error due to the inclusion of adolescent fish.

TABLE 5

Number and Percentage of Sardines Maturing in Each Ten Millimeters of Length. Data Taken in 1929, 1930 and 1931

Body length, mm.	Monterey			San Pedro		
	Total number	Number maturing	Per cent maturing	Total number	Number maturing	Per cent maturing
120–9	----------	----------	----------	1	0	0
130–9	----------	----------	----------	----------	----------	----------
140–9	----------	----------	----------	4	0	0
150–9	3	0	0	4	0	0
160–9	5	0	0	21	5	23.8
170–9	8	1	12.5	21	8	38.1
180–9	14	9	64.3	36	21	58.4
190–9	23	18	78.2	62	55	88.7
200–9	29	28	96.6	83	78	94.0
210–9	35	34	97.1	94	93	98.9
220–9	36	34	94.4	85	85	100.0
230–9	33	33	100.0	79	78	98.8
240–9	35	35	100.0	75	73	97.3
250–9	35	34	97.1	67	67	100.0
260–9	29	28	96.6	54	53	98.2
270–9	24	24	100.0	36	36	100.0
280–9	4	4	100.0	10	10	100.0
290–9	----------	----------	----------	2	2	100.0
Totals	313	282	----------	734	664	----------

TABLE 5

Number and Percentage of Sardines Maturing in Each Ten Millimeters of Length. Data Taken in 1929, 1930 and 1931

Furthermore, conclusions drawn from the data must be interpreted as applying to the commercial fishery only and not to the population in the ocean. It is possible that the majority of sardines do not appear in the area covered by fishing operations until they are adolescent or adult. Our percentages of fish maturing at each length unit may be higher, therefore, than they would be if we could obtain an unselected sample from the whole oceanic population. Since the latter is not obtainable, our data will measure the size at first maturity of sardines from the commercial catch only.

These percentages of females maturing at each length unit are presented in figure 6. For these calculations, data at the onset and close of the spawning season have been omitted. This omission was necessary because all fish do not start to mature nor cease spawning at the same time. By including only the middle portion of each spawning season the maximum spawning condition was measured. The Monterey percentages include the lunar months corresponding roughly to February, March and April, and the San Pedro data include February, March, April and May. Because of the longer spawning season, one more lunar month could be included in the San Pedro calculations. The data for three seasons are combined to form the percentage curves of figure 6.

These curves indicate that the size of sardines at first maturity is very similar at Monterey and San Pedro. No fish smaller than 160 mm., body length, were found maturing, about 50 per cent of the females were maturing at 180 to 190 mm., 90 per cent at 200 mm., and practically all fish were mature at 210 to 220 mm. The Monterey curve is slightly steeper than the San Pedro curve, and this may indicate

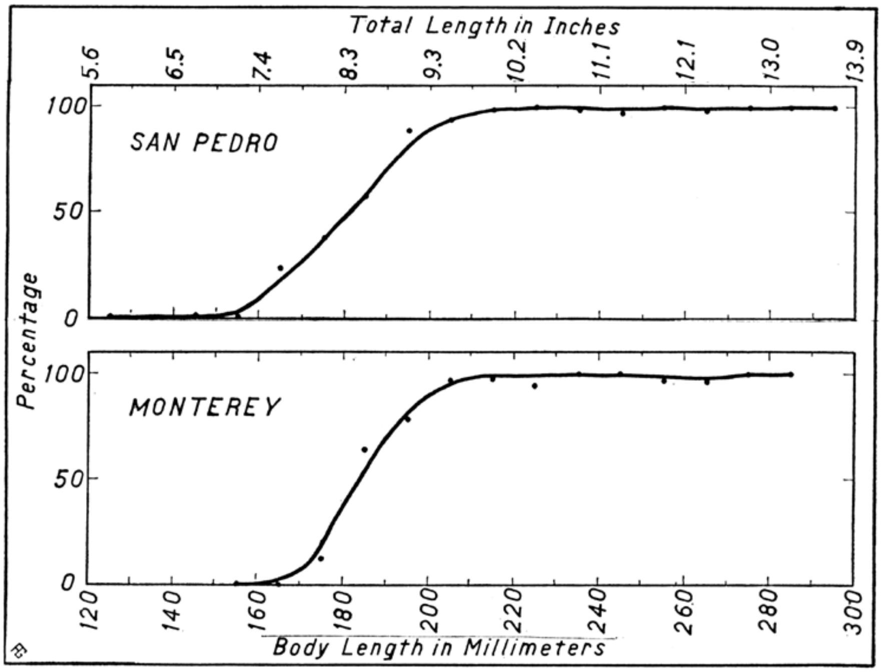

FIG. 6. Size at first maturity of the California sardine, as indicated by the percentage of females maturing in each ten millimeters of length.

FIG. 6. Size at first maturity of the California sardine, as indicated by the percentage of females maturing in each ten millimeters of length

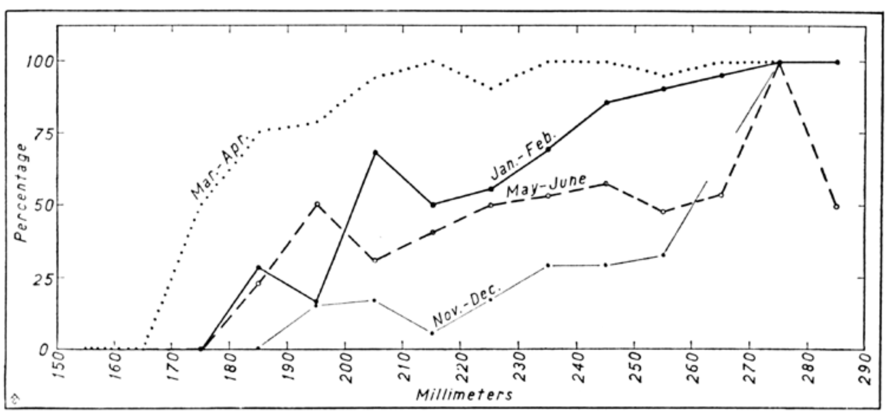

FIG. 7. Percentages of sardines maturing in each ten millimeters of length during each two-month interval. Based on Monterey data for 1928–1929, 1929–1930, 1930–1931.

FIG. 7. Percentages of sardines maturing in each ten millimeters of length during each two-month interval. Based on Monterey data for 1928–1929, 1929–1930, 1930–1931

that more fish between 160 and 180 mm. are maturing at San Pedro than at Monterey. Fish of this size, however, occur only in small numbers in the Monterey catch and the apparent lack of maturing fish at these smaller lengths may merely result from inadequate data.

TABLE 6

Number and Percentage of Monterey Sardines Maturing in Each Ten Millimeters of Length. Data for 1928-1929, 1929-1930 and 1930-1931 Combined in Two-month Intervals

Body length, mm.	November-December			January-February			March-April			May-June		
	Total number	Number maturing	Per cent maturing	Total number	Number maturing	Per cent maturing	Total number	Number maturing	Per cent maturing	Total number	Number maturing	Per cent maturing
150-9							1	0	0	2	0	0
160-9							2	0	0	4	0	0
170-9				3	0	0	2	1	50.0	8	0	0
180-9	1	0	0	14	4	28.6	8	6	75.0	13	3	23.1
190-9	13	2	15.4	18	3	16.7	14	11	78.6	12	6	50.0
200-9	17	3	17.6	25	17	68.0	18	17	94.4	22	7	31.8
210-9	18	1	5.6	32	16	50.0	26	26	100.0	17	7	41.2
220-9	17	3	17.6	32	18	56.3	22	20	90.9	24	12	50.0
230-9	17	5	29.4	33	23	69.7	21	21	100.0	15	8	53.3
240-9	17	5	29.4	35	30	85.7	21	21	100.0	26	15	57.7
250-9	9	3	33.3	32	29	90.6	20	19	95.0	21	10	47.6
260-9				22	21	95.5	16	16	100.0	13	7	53.8
270-9	1	1	100.0	11	11	100.0	16	16	100.0	8	8	100.0
280-9				2	2	100.0	2	2	100.0	2	1	50.0
Totals	110	23		259	174		189	176		187	84	

TABLE 6

Number and Percentage of Monterey Sardines Maturing in Each Ten Millimeters of Length. Data for 1928–1929, 1929–1930 and 1930–1931 Combined in Two-month Intervals

This study of maturity for the California sardine has indicated also that the larger fish mature earlier than the smaller fish and spawn over a longer time interval. The longer spawning season for the larger fish undoubtedly results from the multiplicity of spawnings for individuals. Larger females are able to ripen more batches of eggs than smaller females.

To illustrate this longer spawning season for large fish, only the Monterey data were utilized. Since at the onset of maturity, in the early winter months, few large fish are taken in the San Pedro catch, material from this locality did not demonstrate this point clearly. Figure 7 gives in two-month intervals the percentage of females maturing in each ten millimeters of length. Fish with eggs larger than stage A were classed as maturing. The curves are based on data taken in 1928–1929, 1929–1930 and 1930–1931. In November and December less than 50 per cent of the population were maturing but more large than small fish contained maturing eggs. In January and February a much greater number contained ripening eggs but the higher percentages were among the larger fish. In March and April the maximum state of maturity was reached for Monterey fish. In May and June spent fish, stage L, appeared in the samples and the percentage of maturing fish decreased. But again the higher percentages of maturing fish were among the larger sizes, and it is evident that the first spent fish to appear are among the smaller individuals. At San Pedro also in the latter half of the spawning season, a higher percentage of small fish were spent and more large fish were still spawning.

7. TIME OF THE SPAWNING SEASON

7.1. San Pedro

If mature sardines were taken in the California fishery in appreciable numbers, to determine the time of the spawning season would be relatively simple. But since so few entirely ripe fish have been found we can define the spawning dates only approximately and these approximations must be based on rather complicated calculations. The developing ova have been traced through stage G and the time required for eggs to grow to this stage estimated. By comparing this growth rate with the calculated rate of growth from G to maturity, the dates of the spawning season have been defined for each locality.

The data for the San Pedro region are presented in figure 8. This figure shows by lunar months the percentage of adult females (fish larger than 199 mm.) in each stage of maturity. In the 1928–1929 season fish in stage G were first taken in late January and females in this condition of maturity occurred in the catch until late August. In 1929–1930 the first stage G fish were again taken in late January and these females dominated the catch when collections were discontinued in June. The first spent fish appeared in the latter part of April, 1929, and in early March, 1930. Spent fish did not dominate the catch until August. Spawning must occur therefore sometime between February and August, but estimates of the growth rate of the eggs have determined the dates more accurately.

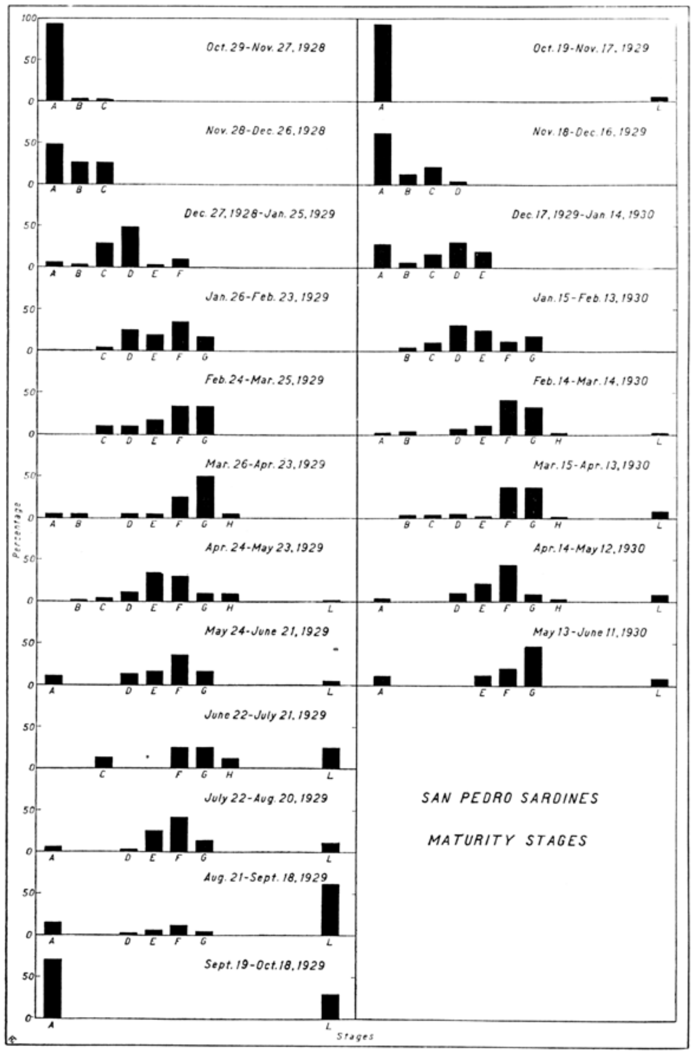

FIG. 8. Percentages of adult San Pedro sardines in each stage of maturity. Data grouped by lunar months.

FIG. 8. Percentages of adult San Pedro sardines in each stage of maturity. Data grouped by lunar months

TABLE 7

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Pedro in 1928, 1929, 1930, and 1931, Grouped by Lunar Months

Date	A		B		C		D		E		F		G		H		L		Total	
	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
1928—																				
X:29– XI:27	31	94	1	3	1	3													33	100
XI:28– XII:26	15	48	8	26	8	26													31	100
XII:27– I:25	2	7	1	3	9	29	15	48	1	3	3	10							31	100
1929—																				
I:26– II:23					2	4	13	25	10	19	18	35	9	17					52	100
II:24– III:25					5	9	5	9	9	16	18	33	18	33					55	100
III:26– IV:23	1	5	1	5			1	5	1	5	5	25	10	50	1	5			20	100
IV:24– V:23			1	2	2	4	6	11	18	34	16	30	5	9	4	8	1	2	53	100
V:24– VI:21	4	11					5	14	6	17	13	36	6	17			2	5	36	100
VI:22– VII:21					1	13					2	25	2	25	1	12	2	25	8	100
VII:22–VIII:20	2	6					1	3	9	25	15	41	5	14			4	11	36	100
VIII:21– IX:18	7	15					1	2	3	6	5	11	2	4			29	62	47	100
IX:19– X:18	28	70															12	30	40	100
X:19– XI:17	32	94															2	6	34	100
XI:18– XII:16	15	62	3	13	5	21	1	4											24	100
1930—																				
XII:17– I:14	9	28	2	6	5	16	10	31	6	19									32	100
I:15– II:13			2	4	5	10	16	31	13	25	6	12	9	18					51	100
II:14– III:14	1	2	2	4			3	6	5	10	21	41	17	33	1	2	1	2	51	100
III:15– IV:13			2	4	2	4	3	5	1	2	20	37	20	37	1	2	5	9	54	100
IV:14– V:12	1	4					2	9	5	21	10	44	2	9	1	4	2	9	23	100
V:13– VI:11	4	12							4	12	7	20	16	47			3	9	34	100
XII:6– I:4	4	19	6	29	7	33	2	9	1	5	1	5							21	100
1931—																				
I:5– II:3	4	11	1	3	6	16	7	19	9	24	8	22	2	5					37	100
II:4– III:4							1	2	7	16	25	55	12	27					45	100
III:5– IV:2									8	18	20	46	15	34	1	2			44	100
IV:3– V:2					1	3	5	14	12	34	15	43	2	6					35	100
V:3– V:31	1	3					9	26	8	24	12	35	2	6	1	3	1	3	34	100

TABLE 7

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Pedro in 1928, 1929, 1930, and 1931, Grouped by Lunar Months

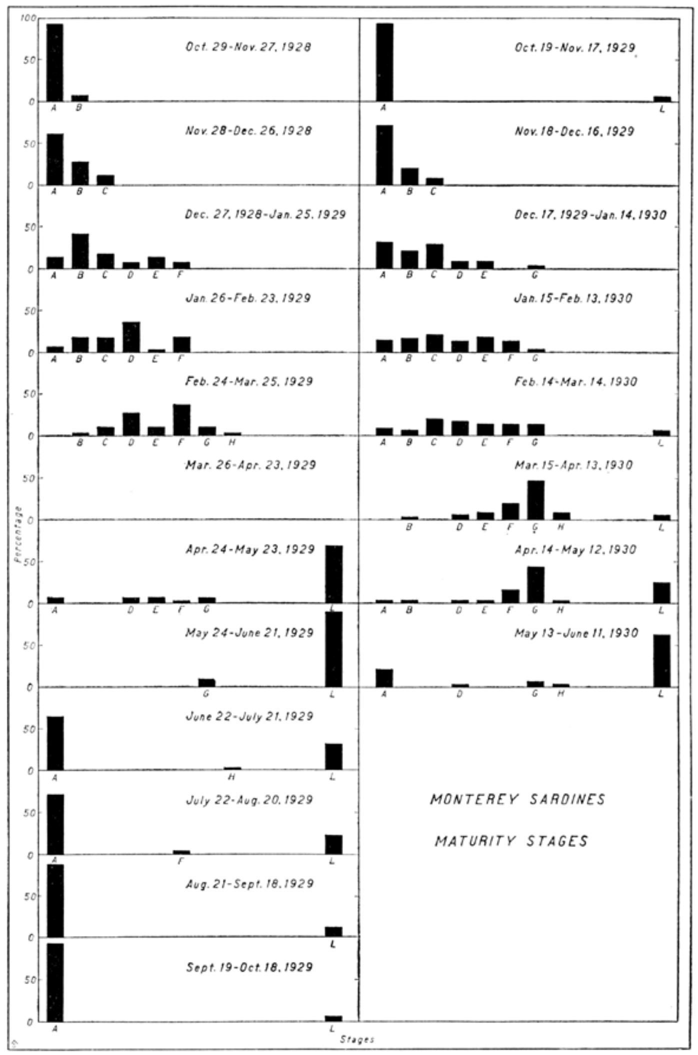

FIG. 9. Percentages of adult Monterey sardines in each stage of maturity. Data grouped by lunar months.

FIG. 9. Percentages of adult Monterey sardines in each stage of maturity. Data grouped by lunar months

From figures 3 and 4, it is evident that growth beyond G is more rapid than from C to G. The unit of slope of the straight line fitted to the data below 0.80 mm. (see Fig. 4) was 0.88 and for data above 0.80 mm., 0.42. This would imply that the growth rate from stage G to maturity is slightly more than twice as rapid as from C to G. These estimates of growth rates, however, would undoubtedly be modified if it were possible to measure the influence of complex biological changes taking place in the developing ova. Since the influence of these factors can not be determined, the calculations are here applied only in a general manner. The amount of growth, as expressed by diameter measurements, is approximately 0.5 mm. in both cases. Since the time required for eggs to grow from C to G can be determined with fair accuracy, from this rate of growth the time necessary for eggs to develop from G to maturity has been roughly estimated.

In the 1928–1929 season the first female in stage C was taken November 16 and in stage G, January 31. This suggests a lapse of 76 days between C and G. In 1929–1930, stage C first appeared November 20 and stage G, January 20, a lapse of 61 days. Although the small number of females sampled renders the accuracy of these dates questionable, the similarity of results for the two seasons furnishes a certain amount of justification in their use. The average time interval between C and G for the two seasons was 68.5 days, and probably slightly more than two months are necessary for eggs to grow from stage C to stage G. Finally, if growth from G to maturity is about twice as rapid as from C to G, approximately three or four weeks will elapse before females in stage G reach maturity. Since the first stage G fish were taken in late January spawning probably begins in late February and continues until September. The highest percentage of G fish were taken between mid-March and mid-April in 1928–1929 and with one exception also in 1929–1930. This suggests that the peak of the spawning occurred about one month later from the middle of April to the middle of May. For the San Pedro region, therefore, spawning occurs between February and August with the height of spawning in the last of April and early May.

of the 39 ripe or nearly ripe females observed in our studies 53 per cent were taken in April and May, 26 per cent in March and 13 per cent in June and July. This would seem to indicate that these scattered mature fish were not off-season spawners, as might be expected when ripe fish are so seldom taken in the sardine fishery.

7.2. Monterey

The Monterey spawning seasons differed somewhat from San Pedro and at the former port the 1929–1930 season did not correspond in detail to the 1928–1929 season. The percentage of adult fish (above 199 mm.) in each stage of maturity are given by lunar months for these two seasons in figure 9. Stage C was first taken December 20, 1928, and stage G, March 4, 1929, an interval of 74 days. Very few G fish were found at Monterey in the 1928–1929 season. Unfortunately, eggs from only 6 females were collected during the lunar month of March 26 to April 23, 1929. of these 6, only 3 were adults and 1 or 33 per cent was in stage G. This percentage can not be considered indicative

TABLE 8

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at Monterey in 1928, 1929, 1930, and 1931, Grouped by Lunar Months

Date	A		B		C		D		E		F		G		H		L		Total	
	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
1928—																				
X:29– XI:27	14	93	1	7															15	100
XI:28– XII:26	11	61	5	28	2	11													18	100
XII:27– I:25	4	14	12	41	5	17	2	7	4	14	2	7							29	100
1929—																				
I:26– II:23	2	7	5	18	5	18	10	36	1	3	5	18							28	100
II:24– III:25			1	3	3	10	8	27	3	10	11	37	3	10	1	3			30	100
III:26– IV:23	1	33									1	34	1	33					3	100
IV:24– V:23	2	7					2	7	2	7	1	3	2	7			20	69	29	100
V:24– VI:21													2	10			18	90	20	100
VI:22– VII:21	20	65													1	3	10	32	31	100
VII:22–VIII:20	15	71									1	5					5	24	21	100
VIII:21– IX:18	37	88															5	12	42	100
IX:19– X:18	32	94															2	6	34	100
X:19– XI:17	31	94															2	6	33	100
XI:18– XII:16	18	72	5	20	2	8													25	100
XII:17– I:14	12	31	8	21	11	29	3	8	3	8			1	3					38	100
1930—																				
I:15– II:13	8	14	9	16	12	21	7	13	10	18	8	14	2	4					56	100
II:14– III:14	3	9	2	6	7	20	6	17	5	14	5	14	5	14			2	6	35	100
III:15– IV:13			1	3			2	6	3	9	7	20	16	47	3	9	2	6	34	100
IV:14– V:12	1	3	1	3			1	3	1	3	5	16	14	44	1	3	8	25	32	100
V:13– VI:11	6	22					1	4					2	7	1	4	17	63	27	100
XII:6– I:4	21	57	7	19	5	14	2	5	2	5									37	100
1931—																				
I:5– II:3	16	37	8	19	10	23	7	17	1	2	1	2							43	100
II:4– III:4	2	6	8	22	11	30	7	19	5	14	1	3	2	6					36	100
III:5– IV:2							1	3	2	6	10	31	19	60					32	100
IV:3– V:2	1	4							1	3	2	7	20	69	5	17			29	100
V:3– V:31	10	31	1	3			1	3			1	3	2	7			17	53	32	100

TABLE 8

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at Monterey in 1928, 1929, 1930, and 1931, Grouped by Lunar Months

of the state of maturity for late March and April, but since in the previous lunar month and in the following two months not more than 10 per cent of the females were in stage G, probably at no time in the 1928–1929 season were more than 33 per cent of the fish in stage G. Spent fish first appeared in late April of this season and such fish dominated the catch through May and June. By July many females had apparently recovered after spawning, the degenerating eggs were all resorbed and the females were again in stage A. Some spent fish were taken, however, until October.

In the 1929–1930 season the first stage C fish appeared on November 25 and G fish on January 10, an interval of 46 days. Spent fish were

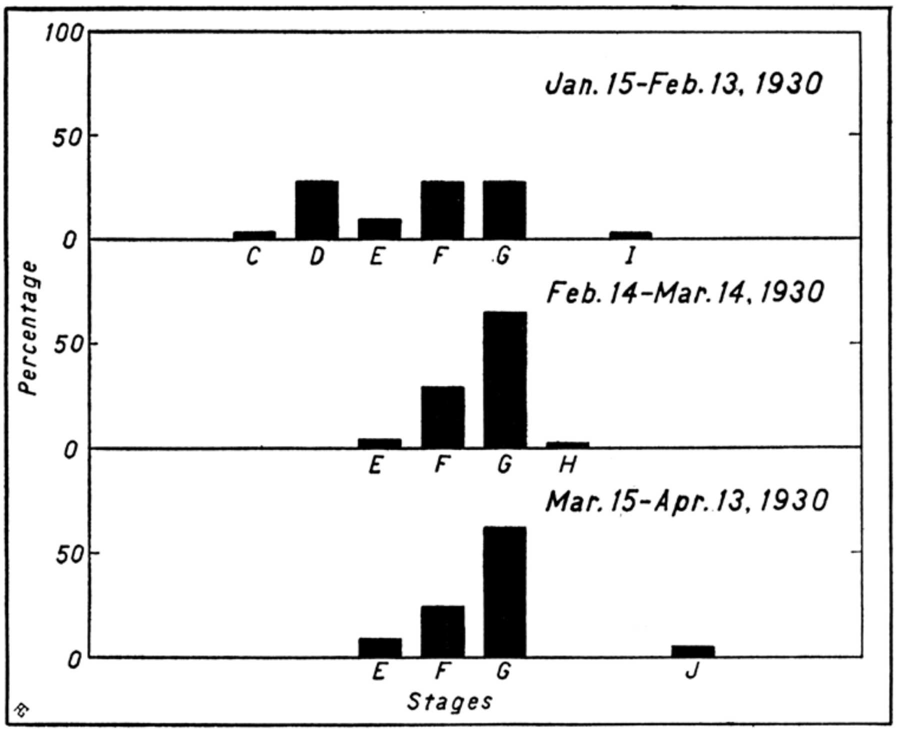

FIG. 10. Percentages of adult San Diego sardines in each stage of maturity. Data grouped by lunar months.

FIG. 10. Percentages of adult San Diego sardines in each stage of maturity. Data grouped by lunar months

first taken in early March, these increased in numbers in the next two lunar months, and dominated the catch in late May and early June. Stage G females were numerous from mid-March to mid-April and for two lunar months constituted over 40 per cent of the catch.

The average time interval between stages C and G for the two seasons at Monterey was 60 days, 8.5 days less than for San Pedro. But because of the inaccuracies of the collections and calculations, this can not be considered as indicative of a fundamental difference in the time required for eggs to grow from stages C to G. That the rate of growth in the two localities is the same seems much more probable. If we consider that at Monterey as at San Pedro about a month elapses between stage G and maturity, we may conclude that spawning occurs

TABLE 9

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Diego in 1930, Grouped by Lunar Months

Date	C		D		E		F		G		H		I		J		Total	
	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
1930—																		
I:15– II:13	1	3	8	28	3	10	8	28	8	28			1	3			29	100
II:14–III:14					2	4	14	29	32	65	1	2					49	100
III:15–IV:13					2	9	5	24	13	62					1	5	21	100

TABLE 9

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Diego in 1930, Grouped by Lunar Months

TABLE 10

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Francisco in 1930 and 1931, Grouped by Lunar Months

Date	A		B		C		D		E		F		G		L		Total	
	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
1929—																		
XI:18–XII:16	34	76	11	24													45	100
XII:17– I:14	31	70	9	20	4	10											44	100
1930—																		
I:15– II:13	18	41	13	29	10	23	2	5	1	2							44	100
IV:14– V:12	1	2			1	3	5	13	7	18	12	32	12	32			38	100
1931—																		
IV:3– V:2	4	14			2	7	3	10	1	3			15	52	4	14	29	100

TABLE 10

Number and Percentage of Adult Female Sardines in Each Stage of Maturity Taken at San Francisco in 1930 and 1931, Grouped by Lunar Months

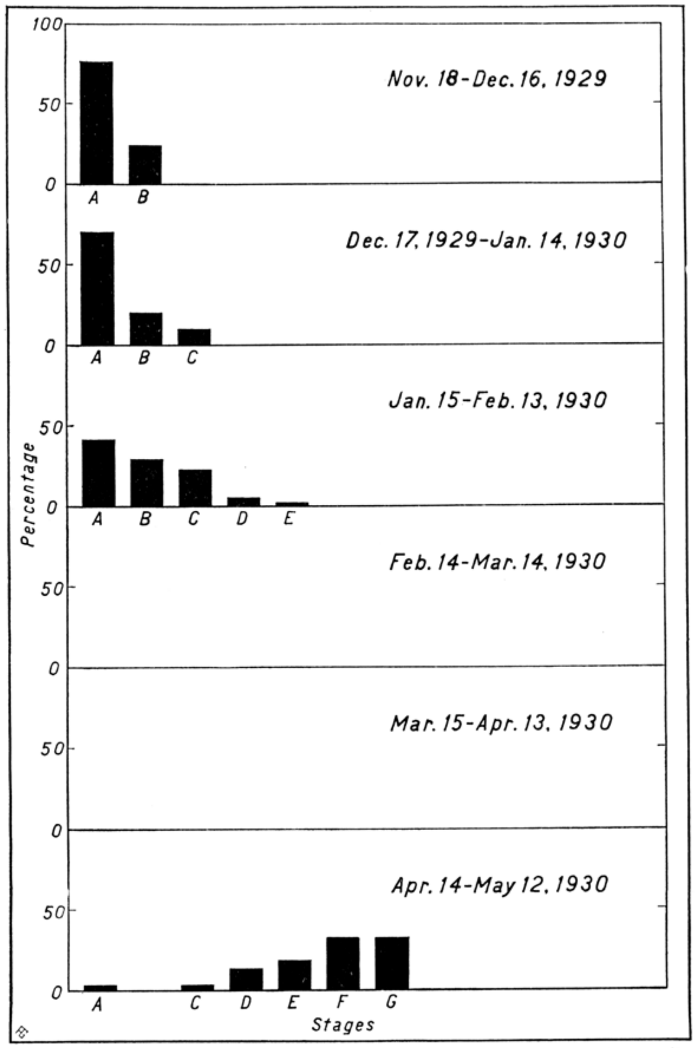

FIG. 11. Percentages of adult San Francisco sardines in each stage of maturity. Data grouped by lunar months.

FIG. 11. Percentages of adult San Francisco sardines in each stage of maturity. Data grouped by lunar months

at Monterey from February to July and the peak of spawning is from the middle of April to the middle of May.

7.3. San Diego

Data for studies on maturity of San Diego fish are very scanty. Collections were made during the 1929–1930 season, but since fishing for adult sardines is carried on in San Diego waters only from January to April (Godsil, 1931), measurements for but three lunar months are available. These data are presented for adult fish in figure 10. During these three lunar months no adult females were taken in stage A or B, and after the middle of February no C or D stage was found. San Diego was the only locality in which the I and J stages occurred in the regular samples, and at this port stage G far outnumbered the other stages. The spawning season at San Diego comprises the months from February to April at least, but the maximum limits can not be defined from the present data.

7.4. San Francisco

Collections from the San Francisco region also were confined to the 1929–1930 season. The cannery catch was sampled once in the middle of each lunar month from mid-November to mid-February, when the canning season closed. No more samples were obtained until April 23. On this date one sample was secured from the fresh fish markets of San Francisco. The percentages of adult fish in each stage of maturity (see Fig. 11) indicate that by the middle of February very few fish had progressed beyond stage C and no spawning could have occurred in this locality before March. The one sample in late April suggests that spawning may have taken place in April and May.

8. ESTIMATED AMOUNT OF SPAWNING IN EACH LOCALITY

8.1. Percentage of Stage G Fish

Although the dates of the maximum spawning period are similar for Monterey and San Pedro, a comparison of figures 8 and 9 indicates some differences in the amount and duration of spawning in these two localities. These differences are shown more clearly in figures 12 and 13. Because fish with egg diameters larger than stage G are seldom taken, no comparison of percentages of females in later stages of maturity could be made. In figure 12, therefore, the few individuals in later stages of development are grouped with stage G, and this figure compares the percentage of adult females in stage G in each locality in any lunar month for the three seasons of 1929, 1930 and 1931. Fish larger than 199 mm. have been classed as adults. Since females in this stage of maturity will spawn in at least three or four weeks, the assumption has been made that such fish would have spawned in or near the region where they were captured. A justification of this assumption is difficult and the only direct evidence we can offer here is the result of tow netting in Monterey Bay discussed in a later paragraph of this section.

In 1929 the maximum percentage of stage G fish at San Pedro occurred in April. In May and June this percentage decreased and again increased in July. The drop in the percentages in May and June does not indicate that fewer fish were spawning in this locality in these months but resulted from the method of sampling. Canning ceased after April and the material had to be collected from the fresh fish markets. During these two months it was not possible to get as adequate a representation of large fish as in the previous collections, and many of the smaller fish, maturing later, had not yet reached stage G.

At Monterey in March, 1929, 13 per cent of the females were in stage G or H. In April, of the 3 adult fish examined 1 or 33 per cent was in stage G, and the percentages decreased in the succeeding months. Unfortunately the numbers examined in April are wholly inadequate to give any measure of the possible amount of spawning in the Monterey region at this time, but since the percentages decreased in the later

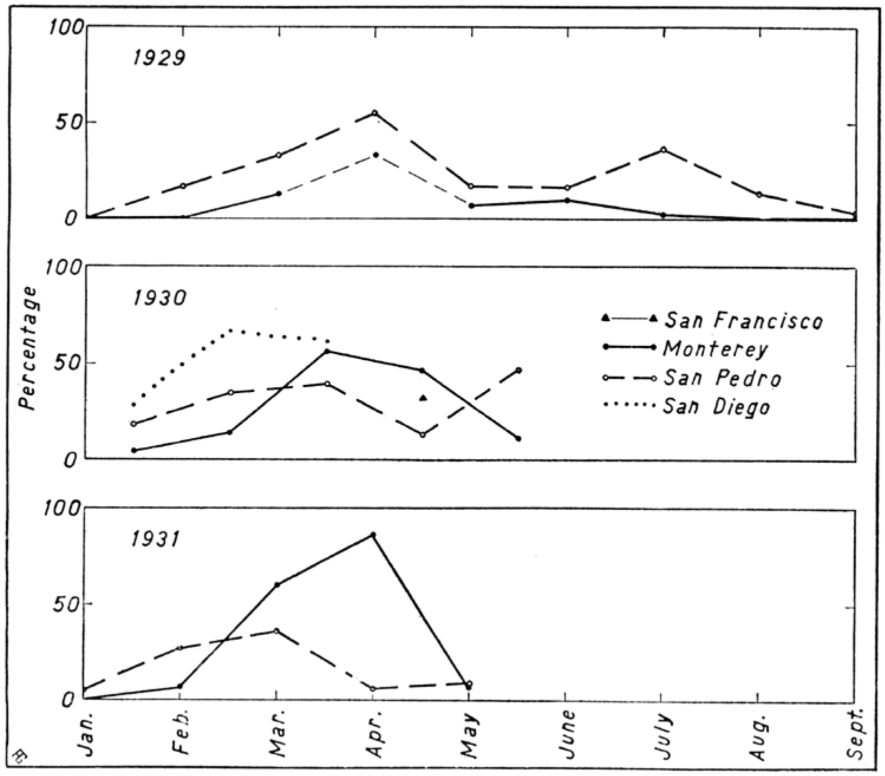

FIG. 12. Lunar month comparison by localities of the percentages of adult sardines in stage G, taken in the ova sample collections during the spawning seasons of 1929, 1930 and 1931.

FIG. 12. Lunar month comparison by localities of the percentages of adult sardines in stage G, taken in the ova sample collections during the spawning seasons of 1929, 1930 and 1931

months, it seems evident that at no period during 1929 did the amount of spawning in the Monterey region equal that at San Pedro. The drop in the percentages after April for Monterey resulted from the incoming of spent fish and not from the concentration of the collections on smaller sized and less mature fish as at San Pedro. (See Figs. 8 and 9.)

In 1930, collections were made at San Francisco, Monterey, San Pedro and San Diego. The highest percentage of stage G fish for any locality occurred at San Diego for the two lunar months of February and March. After March the San Diego collections were discontinued due to the close of the canning season. San Pedro percentages exceeded Monterey percentages except in March and April. The drop in percentages for San Pedro during April again resulted from the failure to secure large fish. The drop for Monterey in May resulted from the presence of spent fish in the samples. For two months of 1930 apparently as great a percentage of the Monterey sardine population spawned at Monterey as did the San Pedro population at San Pedro. As the San Pedro percentages did not differ greatly in the two seasons, this indicates a different spawning behavior for the Monterey sardines. More sardines appear to have spawned at Monterey in 1930 than in 1929. This evidence is further supported by the oceanographic collections of eggs and larvae made by E. C. Scofield and the Hopkins Marine Station on Monterey Bay. Although systematic and continued tow net hauls were made, no eggs or larvae were found in Monterey Bay in 1929, but in April and early May of 1930, abundant eggs were found at Monterey within the bay. On these findings we have based our conclusions that sardines in stage G would have spawned in or near the locality where they were caught. We would not interpret these results, however, as indicating that no fish spawned in Monterey Bay in 1929. Undoubtedly some fish spawned there in that season also but not in sufficient numbers to make the eggs and larvae numerous enough to be taken by the chance sampling of the tow nets. Collections for 1930 were discontinued after spent fish began to appear in the Monterey catch.

In 1931 percentages of stage G fish at Monterey again exceeded the percentages at San Pedro during March and April. Although the decrease in percentages at San Pedro in April and May once more resulted from the failure to obtain larger fish in the collections for these two months, presumably even had large fish been available the San Pedro percentages in April would not have exceeded those for Monterey. The percentages for Monterey in April were higher than for any other interval of the three years covered by the data for this port, thus probably indicating an unusually heavy spawning at Monterey for this month. During the first week in May, 1931, eggs and larvae were again found in the planktonic collections made by Scofield (1934) in Monterey Bay. When spent fish appeared at Monterey in May, the collections of ova samples were discontinued.

Incomplete collections made in 1922 indicated spawning conditions at Monterey and San Pedro similar to those for 1929. Very few stage G fish were taken at Monterey while the percentages for San Pedro did not differ greatly from those for the other three years studied. Table 11 gives the percentage of Monterey females in stages G and H examined during the months of March and April of 1922, 1929, 1930, and 1931.

TABLE 11

Number and Percentage of Adult Female Sardines in Stages G and H Examined at Monterey in March and April of 1922, 1929, 1930, and 1931

Season	Total number	Number in stages G and H	Percentages in stages G and H
1922	19	3	15.8
1929	33	5	15.2
1930	66	34	51.5
1931	61	44	72.1

TABLE 11

Number and Percentage of Adult Female Sardines in Stages G and H Examined at Monterey in March and April of 1922, 1929, 1930, and 1931

The percentage of the San Pedro population spawning in the San Pedro area, as interpreted from the numbers of stage G fish, seemingly differs but little from season to season. On the other hand, the percentages of the Monterey population spawning in the Monterey area varies considerably from year to year, but even for seasons when a high percentage of fish spawn in the Monterey region the duration of this spawning is much briefer than at San Pedro. At San Diego a still higher percentage of the fish spawn in the San Diego area. The significance of these varying percentages is discussed under the relation of these percentages to the movements of sardines.

8.2. Percentage of Spent Fish

In figure 13 are compared the percentages of spent fish, stage L, appearing at Monterey and San Pedro. Females of this stage were identified by the presence of degenerating eggs in the ovary. Andrews (MS.) made cytological studies of sardine ovaries in all stages of development and described the process of degeneration. Eggs were measured from the same group of ovaries that entered into Andrews' studies. Eggs from some of these ovaries appeared to be degenerating and such a condition was noted with an estimate of the approximate proportion of such eggs to the entire mass. These notes were checked with Andrews' observations and in no instance was there a disagreement. The use of gross microscopic observations to determine the presence of degenerating eggs was considered reliable, therefore, and has been used throughout this study.

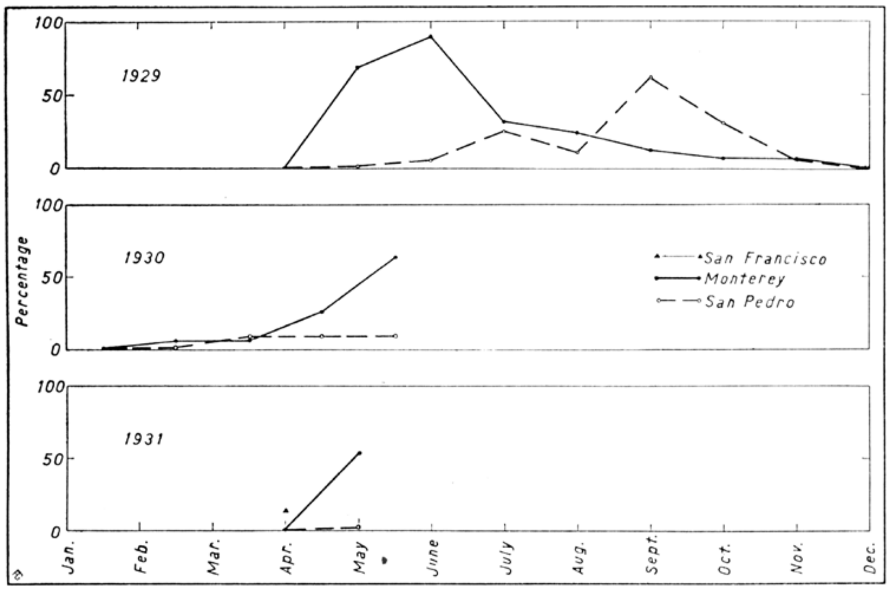

FIG. 13. Lunar month comparison by localities of the percentages of spent fish taken in the ova sample collections in 1929, 1930 and 1931.

FIG. 13. Lunar month comparison by localities of the percentages of spent fish taken in the ova sample collections in 1929, 1930 and 1931

Figure 13 indicates that spent fish appear earlier at Monterey than at San Pedro. The greatest numbers of these fish were present in the Monterey catch in May and June, while such fish did not dominate the

San Pedro fishery until September. Collections were made at San Pedro throughout the summer of 1928 and 1929 and in neither year did high percentages of spent fish appear before the late summer. For

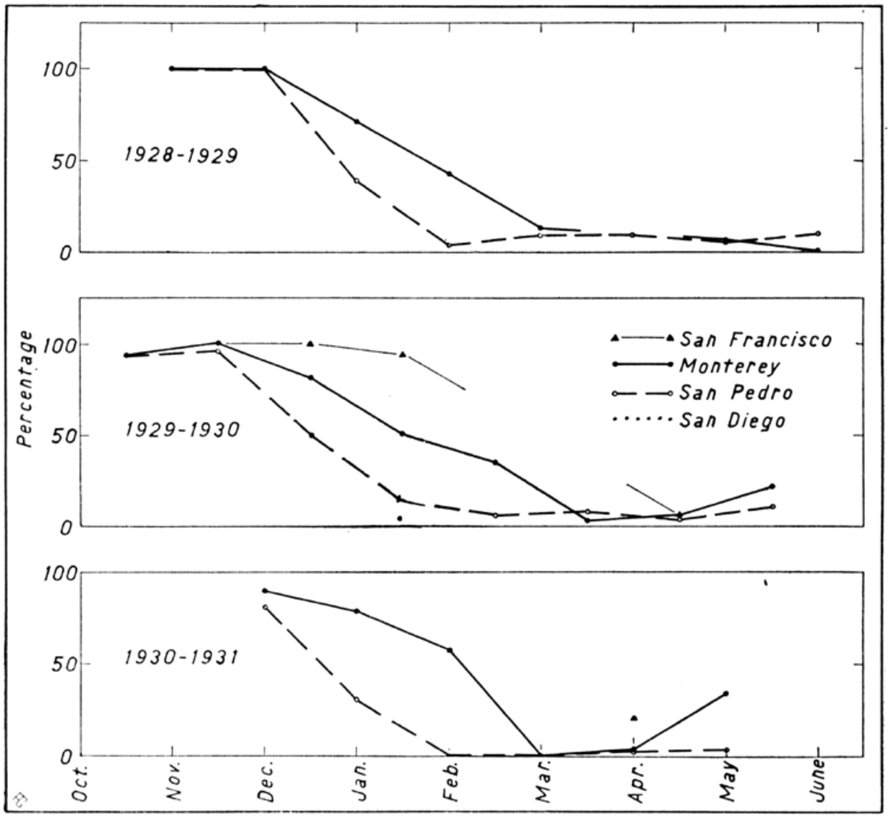

FIG. 14. Lunar month comparison by localities of the percentages of adult sardines in stages A, B and C, taken in the ova sample collections for the 1928–1929, 1929–1930 and 1930–1931 spawning seasons.

FIG. 14. Lunar month comparison by localities of the percentages of adult sardines in stages A, B and C, taken in the ova sample collections for the 1928–1929, 1929–1930 and 1930–1931 spawning seasons

1922, 1929, 1930, and 1931 at Monterey spent fish began to dominate the catch in May. After June the spent fish were replaced by stage A fish. (See Fig. 9.) We are justified in concluding, therefore, that few sardines spawn in the Monterey region except in April and May whereas at San Pedro spawning continues through July and into August.

8.3. Percentage of Stage A, B and C Fish

Adult females in stages A, B and C are fish which, at the onset of any spawning season, have not yet started to mature or are in the very early stages of maturity. The percentages of these fish, as shown by figure 14, differ in the three localities from which collections were secured. At San Francisco, Monterey and San Pedro through November and December practically the entire population was in stages A, B or C. By January the percentages differed for each locality. San Pedro had fewer fish in these stages, Monterey more than San Pedro and less than San Francisco, and in the latter locality practically the entire population was still in these early stages of maturity. In February at San Pedro almost all the adult females had developed beyond stage A, B or C; at Monterey the percentages were similar to the San Pedro January percentages, and at San Francisco the February percentages approximated those for Monterey in January. At Monterey in March most of the population had developed beyond stages A, B and C. No collections were made in San Francisco during this lunar month but in April very few females were found in these early maturity stages.

Figures 8, 9, 11, and 14 indicate that the onset of maturity occurs at approximately the same time at San Francisco, Monterey and San Pedro, but that the later maturity stages appear in greater numbers first in the south. San Francisco fish appear to lag behind Monterey fish about one month and Monterey fish have a corresponding lag when compared to San Pedro females. This retardation in development toward maturity at San Francisco and Monterey might be explained by the colder water in the north, except for the fact that the maximum amount of spawning occurs at Monterey and San Pedro at approximately the same time, April and May. The apparent retardation of maturing eggs at Monterey and San Francisco, therefore, must be only an apparent difference and not an actual one. Movements of the fish population offers the most satisfactory explanation of these differences. The populations at San Francisco and Monterey are evidently more transitory, than at San Pedro. As the individuals mature beyond stages B and C, they move out of these northern localities and are replaced by fish still in these earlier stages of maturity. The growth of the ova toward maturity, however, proceeds more rapidly than the movements of the fish and the percentages of the early stages gradually decrease and eventually stage G fish are found in all localities. The possible direction of these movements is discussed in the section dealing with the relation of stages of maturity to movements of sardines.

8.4. Relation of the Percentage of Stage G Fish to Temperature

Detailed water temperatures for the sardine fishing localities of California are difficult to obtain, but surface water temperatures near to shore have been recorded by the Scripps Institution of Oceanography for a period of years. Through the courtesy of this institution we have secured these temperatures and in figure 15 are presented the surface water temperatures averaged by lunar months for the four localities from October, 1928, to July, 1930. The San Francisco temperatures were taken off the Farallon Islands, Monterey temperatures in the bay at the Hopkins Marine Station, San Pedro temperatures represent an average of the temperatures taken at Hueneme and Balboa, and San Diego temperatures were recorded from the Scripps Institution pier at La Jolla.

For all four localities the temperatures for January to July of 1930 were higher than for the corresponding months in 1929. At Monterey from February through May of 1930 the temperatures equaled those for corresponding months of 1929 at San Pedro. This offers a possible explanation of the higher percentages of stage G fish at Monterey in 1930 than in 1929. Figure 16 compares the Monterey temperatures for 1922, 1929, 1930, and 1931. Again in 1931 during the spring months, the water temperatures were high at Monterey whereas in 1922 water temperatures at this port were low. These temperatures also correspond to the high percentage of stage G fish at Monterey in 1931 and the low percentage in 1922. Apparently in seasons when Monterey

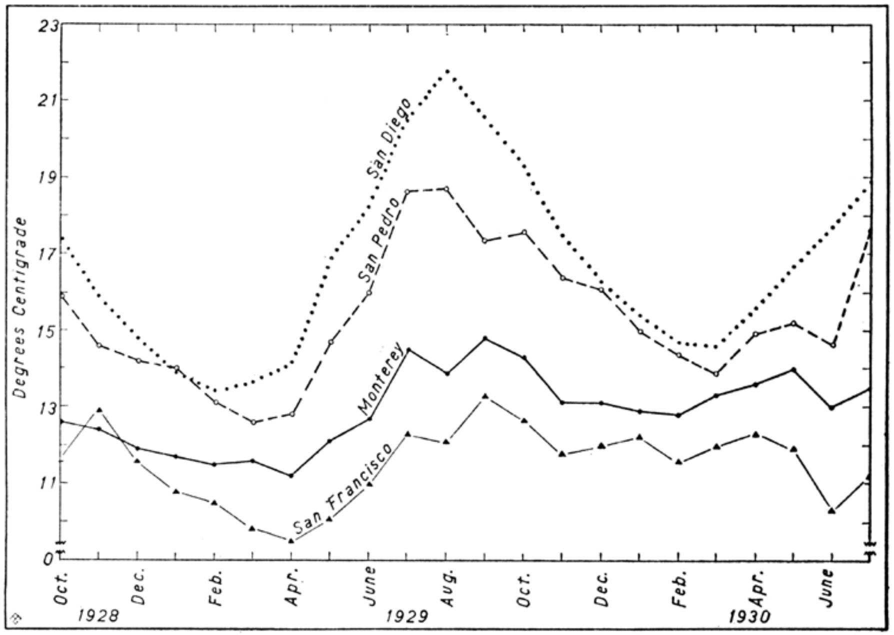

FIG. 15. Lunar month comparison by localities of the surface water temperatures from October, 1928, to July, 1930.

FIG. 15. Lunar month comparison by localities of the surface water temperatures from October, 1928, to July, 1930

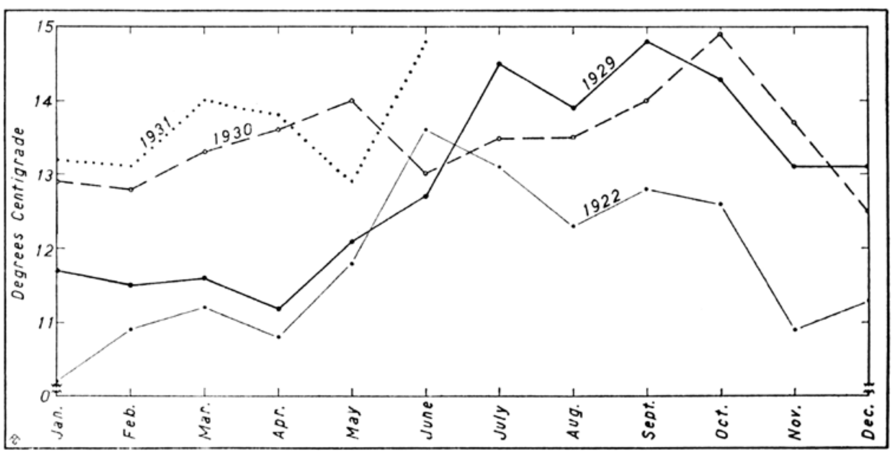

FIG. 16. Surface water temperatures at Monterey averaged by lunar months for the years 1922, 1929, 1930 and 1931.

FIG. 16. Surface water temperatures at Monterey averaged by lunar months for the years 1922, 1929, 1930 and 1931

surface water temperatures near to shore range between 13° and 15° C. from January to June, more sardines linger and spawn in this locality than in years when the temperatures do not rise to this height. The percentages of fish spawning in the San Pedro area are seemingly little affected by fluctuations in water temperatures. Even in the colder years presumably the temperatures at San Pedro and San Diego are sufficiently high to cause sardines to spawn in these localities, and in warmer seasons the temperatures are not too high to prevent spawning.

A similar comparison of stage G percentages with salinity records for the four localities was made but no relationship was evident.

8.5. Relation of the Percentage of the Maturity Stages to the Movements of Sardines

These comparisons of the percentages of the sardines in the various stages of maturity suggest a differential behavior of sardines in the various California localities. Stages A, B and C are taken over a longer time interval in the Monterey region than in the San Pedro area, stage G fish are not present in Monterey Bay for as many months as at San Pedro, and spent fish appear earlier at Monterey. On the basis that we are justified in our assumption that the percentages of these various stages can be used as an index of the behavior of the sardines we would interpret the above facts as follows: The longer duration of high percentages of stages A, B and C at Monterey indicates that the Monterey stock is continually moving away from the fishing grounds and being replaced by other fish less mature (see discussion in paragraphs dealing with these percentages); the presence of stage G fish for a shorter time at Monterey similarly suggests that there is a tendency for the more mature fish to move away from the Monterey area, whereas such fish tend to linger in the San Pedro region; and the earlier appearance of spent fish at Monterey indicates that such spawning as does take place at Monterey is confined to a shorter time interval than at San Pedro.

Since in warmer seasons more sardines apparently spawn in Monterey Bay that in colder seasons, the data suggest that these probable movements of the fish into and out of Monterey Bay are from the north toward the south, and are a part of a general tendency of the sardine population to move toward warmer waters to spawn. If this is true, the Monterey fish would presumably move toward the San Pedro region and the main spawning areas would be in the south, and the sardine population along our California coast would be relatively homogeneous.

There are, however, other explanations which can be advanced for the difference in maturity conditions in the Monterey and San Pedro localities. Such explanations are: an on- and off-shore movement in each locality, a tendency for mature sardines to remain in the same locality but to go to greater depths and thus not be available to the fishermen, or the possibility that the mature fish no longer congregate in schools and consequently are not taken by the fishermen.

A study of the egg measurements alone does not indicate which of these several explanations is correct, but in view of other facts known about the sardine the suggestion of a southward movement seems most favorable. Large fish which are taken each winter in the Monterey and San Pedro fishery appear about a month earlier at Monterey than at San Pedro (Clark, 1930), and within the Monterey fishing area these same large winter fish appear first in the northern part of the region, off San Francisco and Halfmoon Bay, and later in

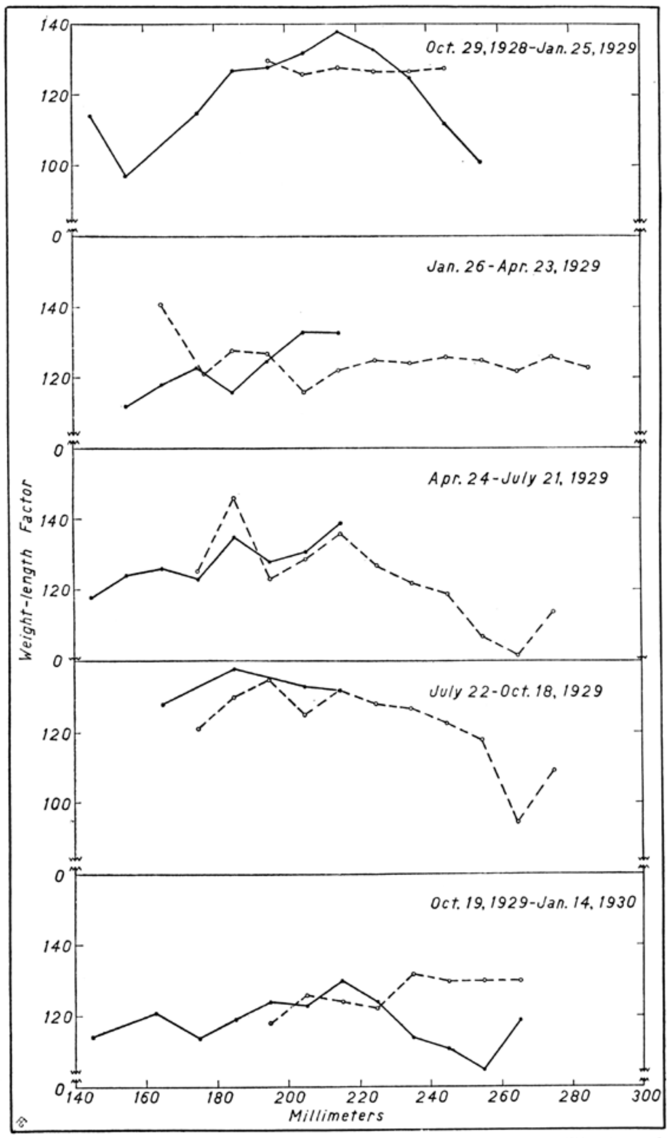

FIG. 17. Comparison of the weight-length factor in each ten millimeters of length of immature and maturing sardines. San Pedro data grouped by three-month intervals. —— Immature. ---- Maturing.

FIG. 17. Comparison of the weight-length factor in each ten millimeters of length of immature and maturing sardines. San Pedro data grouped by three-month intervals. — Immature. ---- Maturing

Monterey Bay itself. (Phillips, MS.) Also the same dominant size classes (Clark, 1931), suggesting a similarity in population characteristics, are found at both Monterey and San Pedro, and finally oceanographic investigations have demonstrated that the chief spawning center lies south of Point Conception. (Scofield, E. C., 1934.)

9. MATURITY AND THE CONDITION FACTOR

9.1. Changes in the Weight-Length Factor

In a previous study of the relationship between weight and length of sardines (Clark, 1928) fish smaller than 200 mm. were found to have a different seasonal change in weight than fish larger than 200 mm. The weight-length factors for larger fish decreased from December to May and for the smaller fish decreased from December to January or February and increased from February to May. This suggested that the seasonal cycle for young fish differed from that for adult fish and that the loss in weight of the larger fish resulted from spawning.

The present study of maturity has served to clarify this point. For the San Pedro data the weight-length factor, derived from the formula: $F = 1000W/L^3$ (where F is the factor; W, the weight; and L, the length), was calculated for each female and the resulting factors classified according to stage of maturity. These factors in each classification were then averaged at each length unit by lunar months. As the spawning season advanced the factors for large adult females decreased in value more rapidly than for small adult fish, and those for the small adults slightly more rapidly than for young fish.

To simplify the data further, stages of maturity A to C were grouped together and similarly stages D to K. Stages A to C were classified as immature, for, although B and C comprised fish that were starting to mature, maturity had not progressed far enough to affect the fat content and the weight-length factor. Stages D to K were termed maturing and as the spawning season advanced spent fish were also included in this category. Factors for three lunar months were then combined and averaged for each ten millimeters of length. The results of these combinations are presented in figure 17.

The five graphs of this figure embrace the following approximate time intervals: November to January, February to April, May to July, August to October, and again November to January. In the first graph the factors for immature fish increased in value for lengths from 150 to 220 mm. This size range presumably comprised fish which had spawned previously and fish which had never spawned. From 220 to 260 mm. the factors from immature females decreased in size. These factors were derived from fish which had spawned previously and the smaller factor values were undoubtedly explained by the fact that the fish had not yet increased in weight following the last spawning. The averages for these lengths were represented in the first two lunar months of this interval only. During the last month, corresponding to January, no large fish with low factor values were taken. The maturing fish for this interval, taken, however, in the last month only, had factor values of 0.0125 to 0.0130. By January adult fish apparently had attained their maximum weight and highest average factor values.

In the next three lunar months (February–April) maturing fish of all lengths had approximately the same factor values and all fish

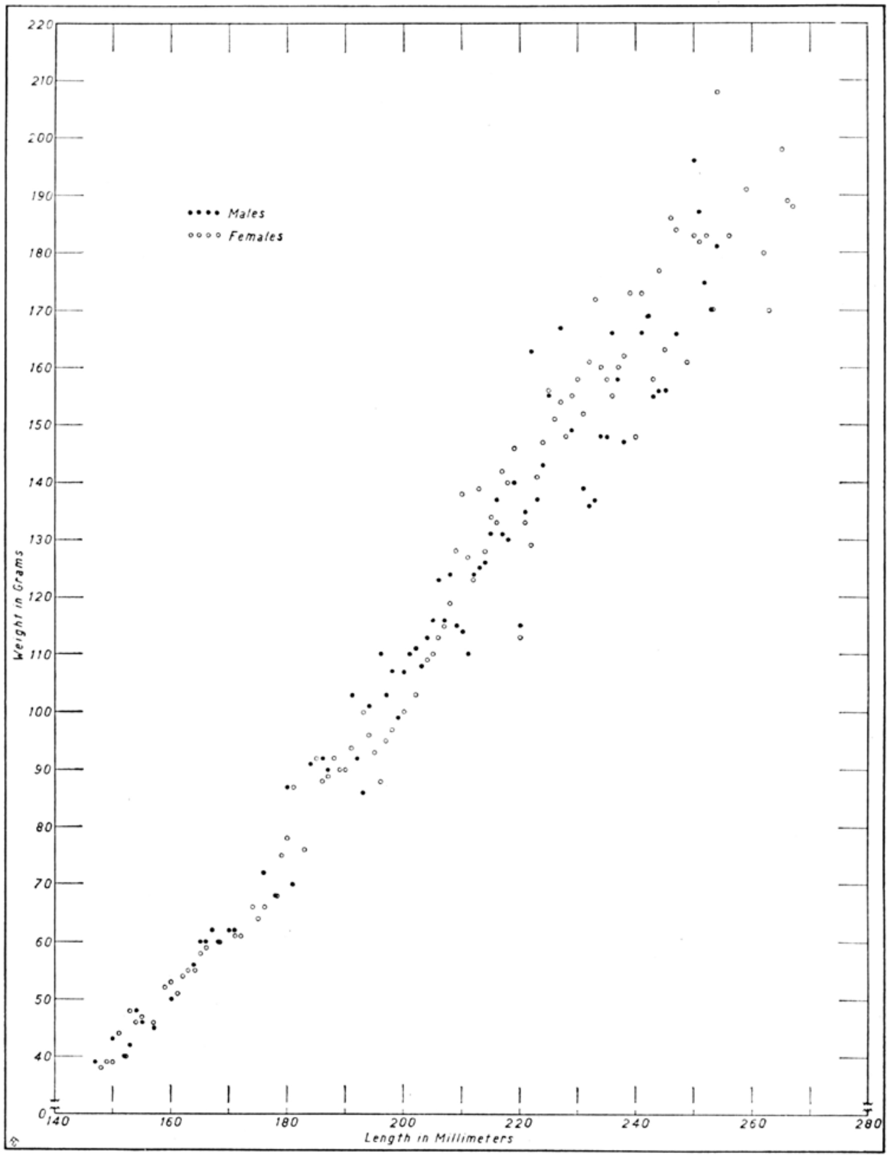

FIG. 18. Sexual comparison of the average weight at each millimeter of length for San Pedro sardines taken from May to October, 1929.

FIG. 18. Sexual comparison of the average weight at each millimeter of length for San Pedro sardines taken from May to October, 1929

larger than 220 mm. were maturing. Comparisons, therefore, between factor values for immature and maturing females can be made for smaller sizes only. From 160 to 200 mm., the maturing fish had larger values than the immature, but from 200 to 220 mm. the immature values were higher.

During the succeeding three months represented by the middle graph of figure 17, the factor values for the larger fish decreased and the maturing fish exceeded in fat content the immature only at lengths between 160 and 190 mm. The values for the smaller immature fish increased in size.

The fourth graph indicates that during the next three-month interval (August–October) little change occurred in the factor values for maturing fish but the values for immature females underwent a further size increase. The last graph represents the same seasonal time interval as the first and the factor values are very similar. Small immature fish had smaller factors than in the previous three-month interval and large immature fish about the same values. These again undoubtedly represent adult fish which had not recovered from the previous spawning. The maturing fish had higher factors and these presumably comprise adult fish which had recovered their fat content after spawning and had not yet been affected by the following spawning season.

This study of the seasonal changes in weight-length factors indicates that young sardines, smaller than 200 mm., have a minimum of fat in the early winter months, November to January, and that the fat content increases throughout the summer and reaches a maximum in the early fall, August to October. Adult breeding fish have a maximum weight in the fall and winter and experience a loss in fat throughout the summer as the spawning season progresses. The weight of large females is more seriously affected by the maturing of the sex products than that of smaller adults. This is probably explained by the fact that each individual spawns more than once during the breeding season. Since large fish mature more batches of eggs than do the smaller, younger adults, this accounts for the greater loss in fat content experienced by the larger fish. The different seasonal changes in the fat content of fish smaller than 200 mm. than of larger fish result, therefore, from the fact that young nonspawning fish gain in weight during the summer months and that small adult fish are not as greatly affected by the spawning as are larger adults.

9.2. Sexual Similarity in Weight

The above discussion of changes in the weight-length factor, based on data for females only, could not be considered applicable to sardines in general if males differed from females in their weight-length relationship. The previous study of winter fish only indicated no significant sexual differences in weight. A comparison of summer fish is made in figure 18. This figure gives the average weight at each millimeter of length for both males and females taken at San Pedro from May to October, 1929. No apparent differences in the weight of the two sexes are indicated in this figure.

The weight-length curves for each sex fitted to this data by the method of least squares with the formula, $W = FL^X$, differed so slightly that the differences could not be demonstrated graphically. For the males, F had a value of 0.0000289 and x, 2.8428. For the females, the values were 0.0000408 and 2.7767, respectively. This would seem to indicate that the males increased in weight slightly more rapidly than the females. But this difference resulted because the data comprised

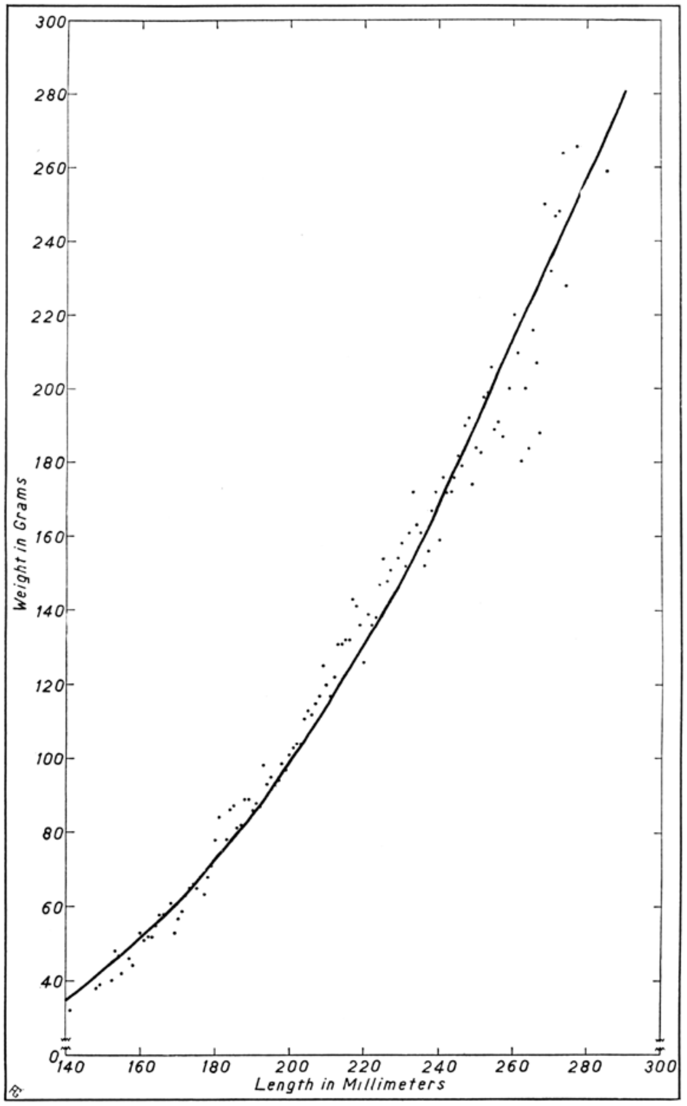

FIG. 19. **Weight-length curve** for San Pedro female sardines taken from October 29, 1928, to October 18, 1929. Curve fitted by the formula $W = 0.0000175\ L^{2.9353}$.

FIG. 19. Weight-length curve for San Pedro female sardines taken from October 29, 1928, to October 18, 1929. Curve fitted by the formula $W = 0.0000175\ L^{2.9353}$

larger females than males, and during the summer months the large fish have a smaller weight in proportion to their length than do smaller fish. No males larger than 255 mm. were taken. To make these sexes directly comparable, the value of F and x were calculated for the females, omitting all fish above 255 mm. These values were then found to be 0.0000233 and 2.8841.

TABLE 12

Weight Calculated at Each Tenth Millimeter of Length from the Formula $W=FL^x$ for San Pedro Sardines Taken from May to October, 1929

Body length, mm.	Weight in gm.		
	All females	Females smaller than 255 mm.	All males
140	37	37	37
150	45	44	44
160	54	53	53
170	64	63	64
180	75	74	75
190	87	87	87
200	100	101	101
210	114	116	116
220	130	132	132
230	148	151	150
240	167	171	169
250	186	192	190
260	207	215	212
270	230	239	236

TABLE 12

Weight Calculated at Each Tenth Millimeter of Length from the Formula $W=FL^x$ for San Pedro Sardines Taken from May to October, 1929

The calculated weights at each tenth millimeter are given for all females, for females smaller than 255 mm. and for males in table 12. For all females, fish larger than 200 mm. did not quite equal the males in weight, but even for the largest fish the difference was only 6 gm. The calculations based on females smaller than 255 mm. gave weights equal to the males for sizes as great as 220 mm. For the larger fish the females slightly exceeded the males, but the maximum difference was only 3 gm. These very slight differences and the fact that the two calculations for the females gave opposite results (weights both larger and smaller than the weights of the males), indicate that no significant sexual differences in weight occur in the San Pedro sardines.

9.3. Mathematical Relationship Between Weight and Length

In the study of the relationship between weight and length for the winter sardines, the weight was found to increase as the length to the 3.15047 power. In this study of the summer fish the weight for sexes combined increased as the length to the 2.7999 power. The data for the summer sardines, however, included no fish smaller than 150 mm. To make the weight increase for summer and winter fish directly comparable, fish smaller than 150 mm. must be omitted from the calculation for the winter fish. This gives a value for x of 3.0742. The increase in weight with length is therefore for the winter fish slightly greater than the cube of the length and for the summer fish somewhat less than the length cubed.

To determine the relationship throughout an entire year, calculations were made for females taken between October 29, 1928 and October 18, 1929. These dates included the fall and winter increase and summer decrease in fat content for the larger fish and the winter decrease and summer increase for smaller fish. Figure 19 gives the average weight at each millimeter of length and the weight-length curve fitted by the formula, $W = FL^x$. Since no sexual differences are demonstrable for the sardine, these data may be considered indicative of both sexes. The value of x from this calculation was 2.9353. If seasonal variations in weight are averaged out, the weight of the sardines may be said to increase at a rate slightly less than the cube of the length. But since the previous study on winter fish demonstrated yearly differences in fat content, undoubtedly if a study of the weight-length relationship was made for fish taken during a subsequent year, the value of x would differ from that obtained in 1928–1929. As it is obviously impossible to obtain a definite value for x in the weight-length formula, and since all calculations give results only slightly greater or less than 3, the cube of the length is the simplest and most satisfactory value to use to determine the changes in fat content as expressed by the fluctuations of F in this formula. But because the true value of x is not exactly 3, the values obtained for F from the formula, $F=WL^3$, must not be compared directly except at the same length units. As shown above, however, no consistent value of x can be obtained that will make these values directly comparable.

10. SUMMARY

To determine the dates of the spawning season and the size at first maturity of the California sardine, a study of the diameters of the ovarian eggs was necessary. This study has shown that:

Individual sardines spawn more than once during each spawning season.

Larger fish spawn more eggs at one time than do smaller fish and ripen more batches of eggs each season.

A few females mature for the first time at 160 to 170 mm., body length, 50 per cent of the females in the commercial catch mature at 180 to 190 mm., 90 per cent at 200 mm., and all females are mature at 220 mm.

Spawning occurs from February to August and the height of the spawning season is in April and May.

The estimated percentage of the San Pedro population spawning in the San Pedro area differed but little from season to season. The percentages for Monterey varied from year to year. When the water temperatures were high a greater percentage of the Monterey population spawned in Monterey than when water temperatures were lower. The percentage of spawning fish at San Pedro and San Diego was greater than at San Francisco and Monterey.

The difference between Monterey and San Pedro in the percentage of females in the early maturity stages and the amount of spawning in each locality, correlated with other sardine studies, has been interpreted as indicating that sardines are moving southward along the California coast during the winter months.

The maturing and spawning of the sexual products cause the sardines to lose weight in the spring and summer months. The weight of the larger fish is affected to a greater extent by spawning than is the weight of the smaller fish. This results in a different seasonal change in the weight-length relationship for fish larger than for fish smaller than 200 mm.

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