DISTRIBUTION AND ABUNDANCE OF EGG AND LARVAL POPULATIONS OF THE PACIFIC SARDINE

BY ELBERT H. AHLSTROM

FISHERY BULLETIN 93

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

A marked decrease in abundance of the Pacific sardine (*Sardinops caerulea*) in recent years led to the initiation in 1949 by the California Cooperative Oceanic Fisheries Investigations of continuing studies to determine the factors responsible for the fluctuations in abundance, distribution, and availability of this important species. The egg and larval populations are being sampled by means of quantitative plankton hauls made over an established pattern of stations occupied at regular intervals during the year.

Sardine spawning in 1950 and 1951 was mainly confined to two major spawning centers, one located off southern California and adjacent Baja California, the other off central Baja California. The latter was by far the more important center, supplying approximately 82 percent of the sardine eggs collected in 1950, and 94 percent of the eggs collected in 1951. Sardine eggs have been obtained during every month of the year off central Baja California, although in both 1950 and 1951 most spawning occurred during a 4-month period, February through May. In the more northern center, the season of spawning has been more sharply delimited, being mostly confined to the months of April, May, and June.

The estimated number of sardine eggs spawned in 1950 was 286,000 billion; in 1951 the total amounted to 611,000 billion. The survival from newly spawned eggs to the end of the planktonic phase of life was about 1 in 1,000 in both 1950 and 1951.

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DISTRIBUTION AND ABUNDANCE OF EGG AND LARVAL POPULATIONS OF THE PACIFIC SARDINE

By ELBERT H. AHLSTROM, *Fishery Research Biologist*

The population of the Pacific sardine, or pilchard (*Sardinops caerulea*), is subject to rather considerable fluctuations in abundance. In recent years there has been a marked decrease in abundance of the sardine over much of its range. To better understand the complex interrelationships responsible for fluctuations in population size, distribution, and availability, there has been an intensification of research on the sardine.

Investigation of the distribution and abundance of egg and larval populations of the Pacific sardine is one facet of the California Cooperative Oceanic Fisheries Investigations, a program sponsored by the Marine Research Committee and carried out cooperatively by the Scripps Institution of Oceanography of the University of California, the Bureau of Marine Fisheries of the California Department of Fish and Game, the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences. The oceanographic-biological survey program, commenced in March 1949 and continued since without interruption, is mainly the responsibility of the first three organizations.

A major line of research is directed toward determining the amount of spawn and the rate of larval survival in relation to environmental conditions. Inasmuch as the amount of spawn probably would be directly proportional to population numbers, this offers a means of estimating the size of the spawning population. The size of the larval population that survives to the postplanktonic stage may bear a direct relation to the subsequent number of individuals of the year class that reach commercial size. The larval studies are predicated on the assumption that such a relation exists. A correlation of the rate of larval survival with hydrographical, meteorological, and biological conditions may clarify the relation between survival rate and environmental conditions. Such information would have predictive value with regard to year-class size.

Personnel of the Scripps Institution of Oceanography and the California Department of Fish and Game cooperated in the collection of data at sea. Staff members of the South Pacific Fishery Investigations of the Fish and Wildlife Service contributed to this investigation, with the majority devoting full time to it. Suggestions of John C. Marr and Theodore Widrig were most helpful during preparation of the paper, and James R. Thrailkill and George Mattson prepared the figures and graphs.

RÉSUMÉ OF PREVIOUS RESEARCH

Eggs and larvae of the Pacific sardine, or pilchard *Sardinops caerulea* (Girard) 1854, were described by Scofield and Lindner (1930) from material collected off southern California in June 1929, during the first year of an investigation of the distribution of sardine spawning.

Results of 4 years (1929–32) of investigation of sardine spawning by the California Department of Fish and Game were reported by Scofield (1934). The surveys of 1929 and 1930 were preliminary. In 1929, both sardine eggs and larvae were taken in a number of hauls made off southern California in June, but neither eggs nor larvae were found in hauls made off central California during April and May. Sardine eggs were obtained in 7 out of 9 hauls made off central California during May and June 1930, a season in which "warmer water than average prevailed along the entire California coast" (ibid.: 19). As in 1929, the largest concentrations of eggs and larvae were obtained off southern California.

Unusually warm temperatures prevailed during the period of the 1931 survey. Scofield (ibid.: 11) noted that in March "warm water of 16° C. was found to be present north of Point Conception, and, as might have been expected, the eggs and larvae of sardine were found there in considerable numbers." The 1931 survey was more intensive and more extensive than earlier surveys. Furthermore, quantitative plankton sampling was initiated during this season and continued in 1932. As in previous years, most of the collections were made off southern and central California. Two survey cruises were made also along the coast of Baja California: The first, in April 1931, extended into the Gulf of California; the other, in February 1932, sampled as far south as Magdalena Bay. Although not many sardine eggs were taken on the southern survey cruises, large collections of sardine larvae were obtained off central Baja California during February 1932. Both the 1931 and 1932 year classes were outstandingly large, as measured by their representation in the commercial catches of the 1934–35 and 1935–36 seasons (Eckles 1954).

On the basis of 4 years of survey, Scofield (1934) concluded that the region of maximum spawning was a comparatively small area 200 miles long and 100 miles wide, situated off the coast of southern California between Point Conception and San Diego. General spawning was found to occur at least as far south as Magdalena Bay, Baja California, as far north as San Francisco, and offshore to a distance of more than 250 miles.

From a study of maturing ova in commercially landed fish, Clark (1934) determined that the spawning season for fish landed off southern California extended from February to August, with the height of the season in April and May. From fish landed at Monterey, she concluded that sardines from that area would probably spawn between February and July. Her data also led her to infer that the sardine spawned from 30,000 to 65,000 eggs in a batch, depending on size of the fish, and perhaps as many as 3 batches a season.

Tibby (1937) gathered together data on the relation between surface-water temperatures and the occurrence of sardine spawning. He based his analysis on data collected by Scofield in 1929–32 and on data obtained in 1936 on two trips along the coast of Baja California. Altogether, data were used from 81 collections, 62 from off California and 19 from Baja California waters. Tibby concluded that the minimum temperature at which sardine spawning would take place was approximately 13° C., that the optimum temperature for spawning was between 15° and 18° C., and that some spawning would occur at temperatures as high as 24° C. Subsequent investigations by us have confirmed the importance of 13° C. as a threshold temperature for spawning, but they have not substantiated the optimum temperature reported by Tibby. It must be taken into consideration that Tibby's data were heavily weighted by collections made during 1930 and 1931, years when water temperatures off California were unusually high. The five records of spawning at temperatures above 20° C. came from southern California in 1931.

Concerning the spawning off Baja California during 1936, Tibby (ibid.: 134) states, "Although no attempt was made at quantitative estimates, it was apparent that there was a sizable spawning in the Sebastian Viscaino Bay region and some localized spawnings were found as far south as Cape San Lucas. The importance of this southern spawning cannot as yet be told."

Clark (1938) records that 20 small sardines, 34 to 53 millimeters standard length, were taken off Oregon during September 1937. The sardines were obtained from the stomachs of albacore caught about 30 miles at sea off the mouth of the Columbia River. These juvenile sardines must have come from spawning in these northern waters; hence, this record constitutes a northerly extension of the known spawning grounds of the sardine.

Research on sardine recruitment through collections of eggs and larvae was undertaken in the spring of 1939, when the United States Fish and Wildlife Service entered into a collaborative program with the Scripps Institution of Oceanography to investigate sardine recruitment in conjunction with hydrographic conditions off the Pacific coast of the United States. The sea work was done on the research vessel *E. W. Scripps*, operated by the Scripps Institution of Oceanography. The investigation was continued through 1940 and 1941, after which it was discontinued because of war.

A primary purpose of the 1939 survey was to determine whether the entire spawning range of the sardine could be delimited. On a cruise of 2 months (*E. W. Scripps*, cruise 8), an area approximately 1,200 miles long by 300 miles wide was surveyed. Moderate numbers of sardine eggs were collected at several stations on the most northerly of the lines occupied. This line, off

Cascade Head, Oreg., was worked on May 22 to 25. The largest concentration of sardine eggs was encountered on a line off Monterey, worked on June 11 to 14. Sardine eggs were taken at eight contiguous stations on this line, the largest number occurring at a station located about 160 miles from shore. Most of the larvae were obtained on a line off Point Fermin in southern California, worked on June 16 to 23. Unfortunately, this cruise took place too late in the season to sample the southern spawning adequately. Sardine eggs were taken in only 1 of the 34 hauls made to the south of Point Conception between June 15 and July 10. Sardine eggs had been rather abundant in the area off southern California in April 1939, however, when a series of hauls was taken to develop sampling techniques.

Experience gained during the 1939 season indicated that the spawning range was too extensive to be surveyed adequately by one vessel. Consequently, during the following 2 years the investigation was confined to the more limited area off the coast of southern California previously shown by Scofield to be an area of abundant spawning. This concentration of effort served several purposes. It permitted continuation by the Scripps Institution of Oceanography of studies on the oceanography of the southern California area commenced in former years. Another consideration was that by surveying a limited area of abundant spawning, it should be possible to determine from the quantitative sampling of eggs and larvae the amount of spawning within the area and the rate of mortality during the planktonic existence of the sardine. Abundant spawning was found in the area in 1940 and 1941, and two papers dealing with the results of the spawning surveys have been published (Sette and Ahlstrom 1948; Ahlstrom 1948).

Godsil (1941) reported that in January and February 1940, sardine eggs and larvae were collected in the Gulf of California, and maturing fish also were taken there by the research vessel *N. B. Scofield.* This constitutes the first record of sardines spawning in the Gulf of California.

Moderate numbers of sardine eggs and larvae were taken in plankton hauls off San Francisco in June 1946 (Smith and Ahlstrom 1948), from the motorship *Pearl Harbor*, a purse-seine vessel chartered by the San Francisco Sardine Association to explore for sardines with echo-ranging and echo-sounding gear.

In February 1948, prior to the commissioning of the vessels to be used on the expanded oceanographic-biological surveys, a preliminary survey was made off central Baja California aboard the *E. W. Scripps* to obtain additional data on the amount of sardine spawning in that area. Effort was concentrated in the area between Point San Eugenio and Point Abreojos, and abundant spawning was found in a coastal strip about 50 miles wide.[1] This is the area that has proved, since 1949, to be the principal spawning ground of the sardine.

In brief, before the commencement of the California Cooperative Oceanic Fisheries Investigations, sardines were known to spawn over a very considerable area, from the Gulf of California in the south (Godsil 1941) to at least as far north as Cascade Head, Oreg. (Ahlstrom 1948). There was considerable evidence that during the very successful spawning season of 1939 some spawning had taken place as far north as British Columbia (Walford and Mosher 1941; Hart 1943). Within this range it was known that the area off southern California was a center of abundant spawning (Scofield 1934; Sette and Ahlstrom 1948), but it was not definitely known whether there were other important spawning areas.

Sardine eggs and larvae had been taken north of Point Conception during a number of seasons. Did spawning occur in these waters every year, or only during certain years when conditions were more favorable than usual? Scofield (1934) reported taking sardine eggs and larvae off central California in 1930 and 1931, but these were unusually warm years. He had not taken them in this area on cruises made during April and May in 1929 and again in 1932. Would he have taken them in these seasons if his sampling had extended over a longer portion of the year? In 1939, large numbers of sardine eggs had been taken on a line off Monterey, especially at a station located 160 miles from shore (Ahlstrom 1948), but 1939 may have been a season of unusually widespread spawning. Moderate numbers of sardine eggs and larvae had been taken off San Francisco in early June 1946 (Smith and Ahlstrom 1948). Evidence was accu-

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[1] Elbert H. Ahlstrom and J. L. McHugh, A record of Pacific sardine (*Sardinops caerulea*) and other fish eggs and larvae collected off central Baja California during February 1948. MS.

mulating that spawning did occur off central California during most years; however, we still did not know how important a segment of sardine spawning this constituted. There were only 2 seasons that sardine spawning to the north of California was definitely documented: off Oregon in 1937 (Clark 1938) and off Oregon (and probably Washington and British Columbia) in 1939 (Ahlstrom 1948; Walford and Mosher 1941; Hart 1943).

Information on the distribution and abundance of sardine spawning off Baja California was fragmentary. Scofield had visited this area only twice during the early period of survey, and on these cruises had taken few sardine eggs. He had made several large collections of sardine larvae off central Baja California, but had underestimated their importance. Tibby (1937: 134) reported making two additional cruises off Baja California in 1936, at which time he had found "sizable spawning in the Sebastian Viscaino Bay region." During 1939, sardine eggs or larvae were taken in only 2 out of 24 hauls off Baja California in late June and early July (Ahlstrom 1948); however, this cruise was made too late in the season to adequately sample the eggs or larvae off Baja California. Godsil (1941) reported taking eggs and larvae in the Gulf of California in January and February 1940. Our best evidence of the importance of central Baja California as a spawning center was obtained during the cruise of the *E. W. Scripps* in February 1948. Even this was fragmentary, being confined to a limited area off central Baja California during one cruise. Hence, nothing very definite was known concerning either the season of spawning, or the distribution and abundance of spawning off Baja California previous to the initiation of the investigations reported in this paper.

SARDINE SPAWNING SURVEYS, 1949–51

1949 SURVEY

Large-scale oceanographic-fishery survey cruises began in March 1949. The area surveyed at monthly intervals during 1949 was a strip of water approximately 400 miles wide and 1,320 miles long. It had its northern limit off the mouth of the Columbia River and its southern off Point San Eugenio, central Baja California. Within this area 12 lines of stations were spaced at intervals of 120 miles, the lines extending seaward normal to the general trend of the coastline. Along each line were 10 or 11 stations spaced at 40-mile intervals. Three vessels participated in the monthly coverage of the area.

The purpose of the initial year of survey, 1949, was exploratory, since information on place and time of sardine spawning as well as on the broad features of oceanic circulation and environment was needed.

Sardine eggs and larvae were collected by hauling a plankton net obliquely from about 70 meters below the surface to the surface. On taking a haul, the net was lowered on 100 meters of wire (¼-inch cable) at the rate of 50 meters a minute, and retrieved at the rate of 5 or 10 meters a minute. The actual depth reached by the net varied from haul to haul, depending on speed of the vessel and state of the sea. The nets used in 1949, and subsequently, measure 1.0 meter in diameter at the mouth, by about 5 meters in overall length. They are constructed of No. 30xxx grit gauze, a rugged grade of Swiss silk bolting cloth with mesh openings of about 0.7 millimeter when new but shrinking to about 0.55 millimeter on use.

To obtain a measure of the volume of water strained during a haul, an Atlas-type current meter was fastened in the center of the mouth of each net. The method used to standardize hauls was described by Ahlstrom (1948). This standard adjusts the number of eggs or larvae in a haul to the number in 10 cubic meters of water strained per meter of depth fished by the net. If the vertical range of the eggs or larvae has been completely traversed (as it has in the case of the sardine), this value is equivalent to the number of eggs or larvae under 10 square meters of sea surface. This area is referred to as a "standard area." For a more detailed discussion of the method of sampling sardine eggs and larvae see Ahlstrom (1948).

The 1949 collections were inadequate both for quantitative estimation of the amount of spawning and for determination of the rate of survival of larvae. Sardine eggs were taken in only 34 of the 924 hauls made during 1949; samples containing 100 or more eggs numbered only 7, and most of the eggs were collected at one station, the inner station on the southernmost line off Point San Eugenio. Sardine larvae were taken in 41 hauls, with 30 of the samples containing 5 or fewer larvae per haul, and only 3 having 100 or more larvae. The seasonal distributions of sardine eggs and larvae taken in 1949 are shown in figure 1.

Despite the quantitative inadequacy of the 1949 collections, the results of the survey were of considerable value in planning a more intensive coverage of the sardine spawning centers. They established the importance of the spawning center off central Baja California and the need for more thorough coverage of it. The area off southern California was again observed to be an important spawning center, and it was found that spawning in this area sometimes occurred at a considerable distance from shore. Some spawning was found along the length of the California coast and, judging from the number of larvae taken off Point Sur, considerable spawning must have occurred off central California.

The results obtained in 1949 also indicated a northward progression of spawning as the season advanced. During March and April the only large collection of eggs and all hauls containing larvae were obtained off central Baja California (tables 1 and 2). The height of spawning occurred in the southern California area during May. By the following month, spawning had spread to central California (off Point Sur), while still occurring in a continuous belt south to Point San Eugenio. On the July cruise, all sardine eggs

TABLE 1.—*Stations at which sardine eggs were collected, 1949*

[Number per standard haul]

Station	March (cruise 1)	April (cruise 2)	May (cruise 3)	June (cruise 4)	July (cruise 5)	August (cruise 6)	September (cruise 7)	Total
401	------	0	0	0	0	26	0	26
601	0	0	------	0	210	0	0	210
701	0	0	0	14	1	0	0	15
801	0	0	0	5	0	0	0	5
901	1	3	0	47	0	0	0	51
902	0	0	0	38	0	0	0	38
903	0	1	1,810	17	172	0	0	2,000
904	0	0	15	0	0	0	0	15
905	0	7	121	0	0	0	0	128
908	0	0	1	0	0	0	0	1
1001	0	88	1,119	9	0	0	0	1,216
1002	0	0	79	0	0	0	0	79
1004	0	1	0	0	0	0	0	1
1101	1	2	4	0	0	0	0	7
1102	0	0	14	0	0	0	0	14
1104	0	5	0	0	0	0	0	5
1105	6	0	0	0	0	0	0	6
1106	0	3	0	0	0	0	0	3
1201	------	20,421	67	1,264	0	0	0	21,752
1202	0	0	7	0	0	0	0	7
1203	0	32	0	0	0	0	0	32
Total	8	20,563	3,237	1,394	383	26	0	25,611

TABLE 2.—*Stations at which sardine larvae were collected, 1949*

[Number per standard haul]

Station	March (cruise 1)	April (cruise 2)	May (cruise 3)	June (cruise 4)	July (cruise 5)	August (cruise 6)	September (cruise 7)	Total
203	------	------	0	------	0	0	0.8	0.8
601	0	0	------	0	0	3.7	0	3.7
701	0	0	0	0	261.7	0	0	261.7
702	0	0	0	------	15.5	------	0	15.5
803	0	0	0	0	4.8	0	0	4.8
901	0	0	0	1.0	2.6	0	0	3.6
903	0	0	0	14.6	16.3	0	0	30.9
904	0	0	1.1	11.0	1.8	0	0	13.9
905	0	0	1.5	2.7	0	0	0	4.2
906	0	0	5.4	1.4	0	0	0	6.8
907	0	0	0.4	0	0	0	0	0.4
1001	0	0	3.6	4.4	0	0	0	8.0
1002	0	0	0	9.0	0	0	0	9.0
1003	0	0	0.8	0	0	0	0	0.8
1007	0	0	1.4	0	0	0	0	1.4
1101	2.7	379.8	0.9	2.1	0	0	0	385.5
1102	1.6	0	0	30.1	0	0	0	31.7
1103	0.5	0	0	0	0	0	0	0.5
1107	0	0.4	0	0	0	0	0	0.4
1201	------	105.0	1.5	7.7	0	0	0	114.2
1202	3.0	0	0.7	0	0	0	0	3.7
1203	1.0	0	0.6	0	0	0	0	1.6
1204	1.3	0	0	0	0	1.8	0	3.1
1205	0	3.9	0	0	0	0	0	3.9
1206	0	3.8	0	0	0	0	0	3.8
Total	10.1	492.9	17.9	84.0	302.7	5.5	.8	913.9

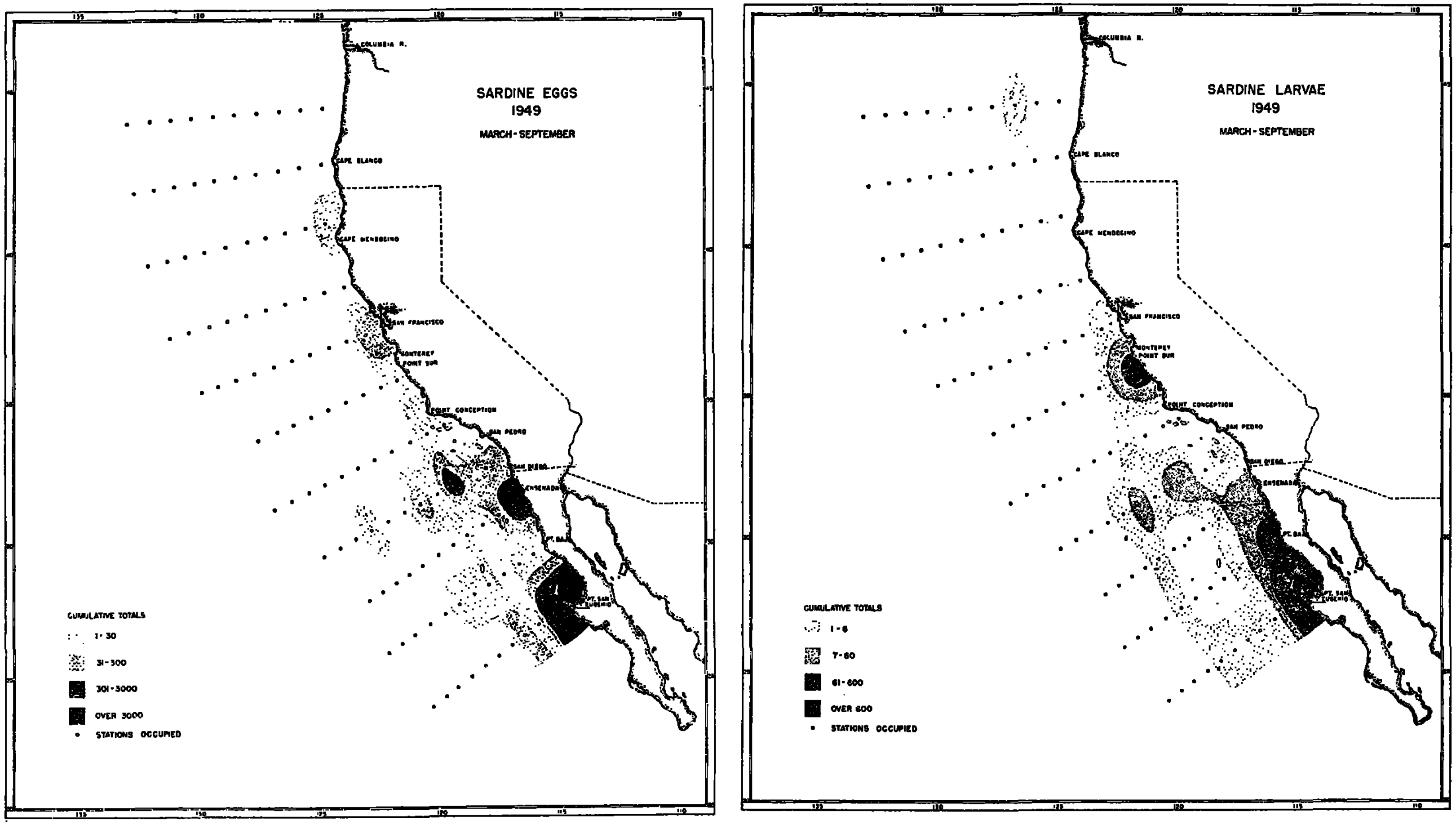

FIGURE 1.—Distribution and abundance of sardine eggs and sardine larvae, March through September, 1949.

and larvae obtained were taken off central and southern California; moderately heavy spawning was sampled off San Francisco, and a large collection of larvae was obtained off Point Sur. Few eggs or larvae were taken in August, but a collection of eggs was obtained off Cape Mendocino, indicating that some spawning occurred off northern California. A single larva was collected off Oregon in September.

A relation between water temperature and the occurrence of sardine spawning was indicated, as almost all of the sardine eggs were found in water with temperatures between 13° and 16° C. (figs. 2–3). Although we subsequently found that the temperature relation is neither as simple nor as clear cut as it appears from the 1949 data, the limiting effect of low temperatures on spawning seems to be an important factor. Only a negligible amount of spawning has been found at any time in waters below 13° C.

1950 SURVEY

The survey was intensified during the 1950 season in the two areas known to be important sardine spawning centers. Four lines of stations were added in the area between Point Conception and Ensenada, Baja California; consequently, the distance between lines in this area was reduced to 40 miles, a distance equivalent to the spacing of stations on the lines. To more adequately sample the spawning off central Baja California, 3 short lines of stations were added to the south of the area covered in 1949. These lines, spaced 40 miles apart, extended the survey area south from Point San Eugenio to Point Abreojos. Inshore stations were added between the remaining station lines. A fairly extensive coverage was maintained to the north of Point Conception during 1950 to sample any important sardine spawning that might occur in this area. The cruises routinely extended as far north as the Oregon-California border, and in August and September they were extended northward to Oregon waters. The stations regularly occupied on the 1950 survey cruises are shown in figure 4. The same sampling procedures were followed as in 1949. The average depth reached by the net was 68 meters.

Two of the 1950 cruises were extended to areas not routinely sampled. During cruise 18 (September), lines 70 and 90 were extended for an additional 600 miles seaward. No sardine eggs or larvae were taken on these lines. During cruise 20 (November) two vessels occupied stations off central and southern Baja California, between Point San Eugenio and Cape San Lucas. Thirty of the stations occupied on this cruise had been regularly occupied on routine survey cruises, and 60 stations were added. This cruise was made for a twofold purpose: (1) to extend the coverage in order to obtain a better understanding of the oceanic circulation off Baja California, and (2) to determine the amount and extent of sardine spawning off central and southern Baja California during this season. Regarding the latter, results were almost entirely negative: sardine larvae were obtained in only one haul, off Magdalena Bay, and no sardine eggs were taken during the entire cruise. It has been learned since that off-season spawning (i. e., fall spawning) is often close inshore, and more positive results might have been obtained had additional stations been occupied inshore.

In place of the regular survey cruise in October, three stations on line 70 were occupied repeatedly to obtain data on short-period variations in physical, chemical, and biological properties, especially those of a periodic nature. Six other stations on line 70 were occupied once. Sardine eggs and larvae were not found in any of the 185 plankton hauls made during this cruise.

The month-by-month coverage during 1950 in different parts of the survey area is summarized in table 3. Omitted from this tabulation are stations occupied only on the September or November cruises. The stations worked repeatedly during October are recorded in the table as if each had been occupied but once. With these deletions, the number of station occupancies in 1950 was 964. The largest number of hauls, 376, was obtained to the north of Point Conception; 358 samples were obtained between Point Conception and Ensenada, Baja California; and 230 hauls were made off central Baja California.

Location and importance of the spawning center off central Baja California were definitely established by the 1950 survey cruises. The center of abundant spawning was found to lie within about 50 miles of the coast between Point San Eugenio (off line 120) and Point Abreojos (off line 130). Approximately 82 percent of the sardine eggs and 70 percent of the larvae collected during 1950 were taken in this area. Most of the remainder were taken in the spawning center off

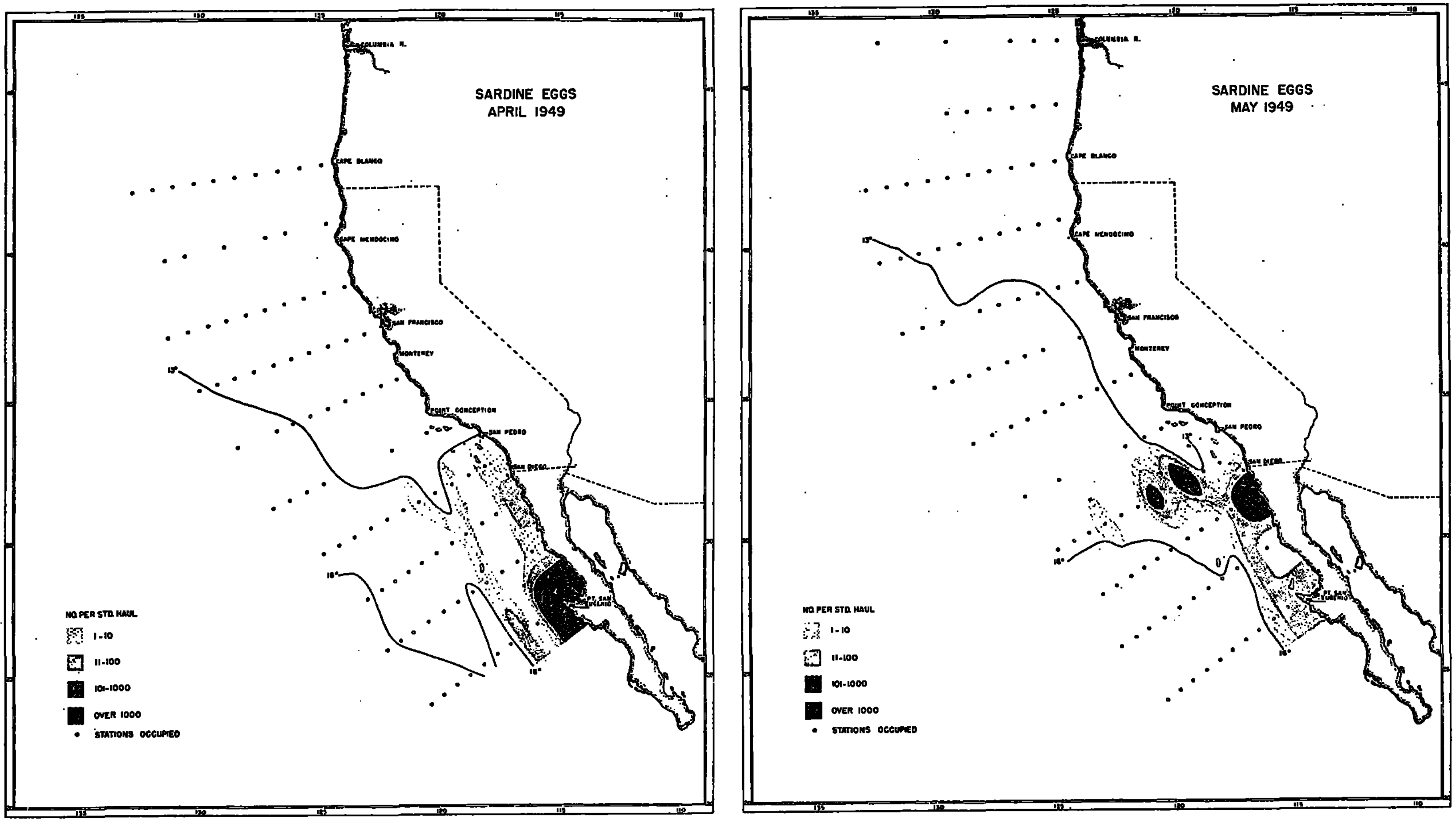

FIGURE 2.—Monthly distribution of sardine eggs in relation to temperature (at the 15-meter level), April and May 1949. The 13° and 16° C. isotherms are shown.

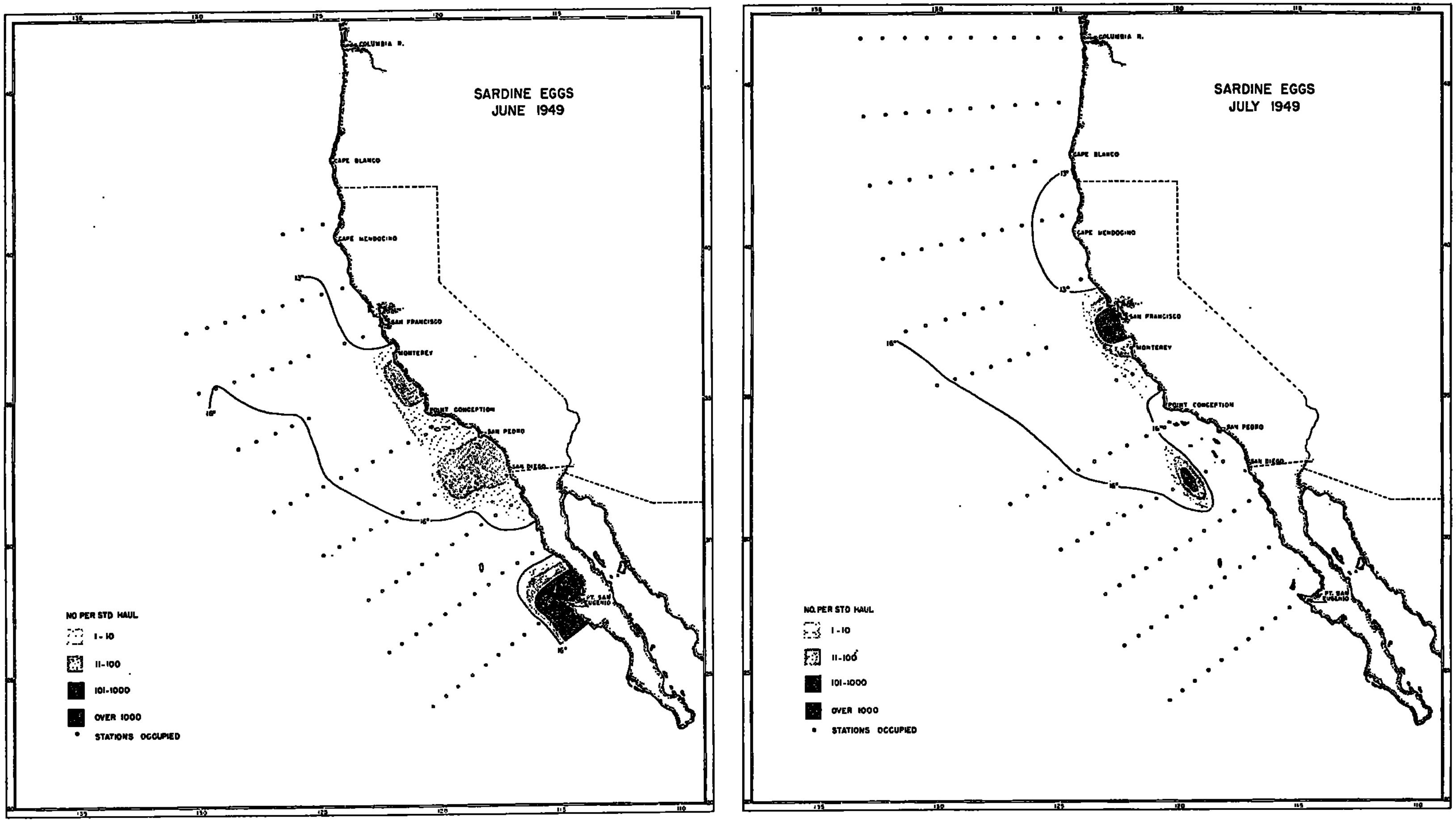

FIGURE 3.—Monthly distribution of sardine eggs in relation to temperature (at the 15-meter level), June and July 1949. The 13° and 16° C. isotherms are shown.

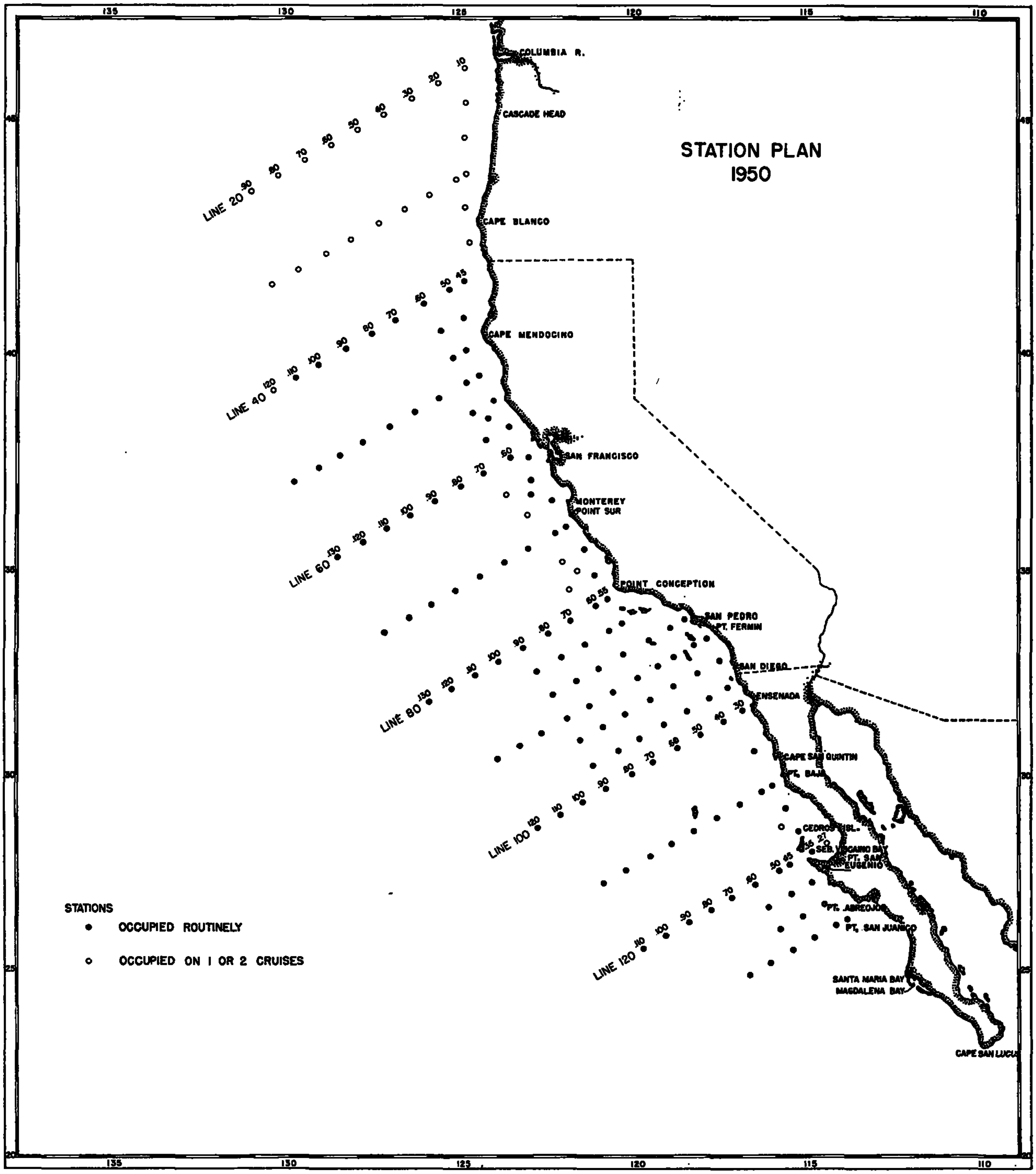

Figure 4.—Location of stations occupied during the regular survey cruises of 1950.

TABLE 3.—*Number of stations occupied monthly during survey cruises, 1950*

	February (cruise 11)	March (cruise 12)	April (cruise 13)	May (cruise 14)	June (cruise 15)	July (cruise 16)	August (cruise 17)	September (cruise 18)	October (cruise 19)	November (cruise 20)	Total
Lines 20–37	0	0	0	0	0	0	22	11	0	0	33
Lines 40–57	10	22	22	21	18	25	24	26	0	0	168
Lines 60–77	17	19	19	19	26	26	22	[1] 18	9	0	175
Lines 80–87	21	15	20	21	20	21	14	0	0	4	136
Lines 90–97	24	12	21	25	24	25	11	[1] 11	0	1	154
Lines 100–105	11	11	11	11	2	11	0	10	0	1	68
Lines 110–117	10	11	11	11	3	11	0	11	0	3	71
Lines 120–127	15	15	15	15	10	15	0	14	0	15	114
Line 130	6	6	6	6	3	6	0	6	0	6	45
Total	114	111	125	129	106	140	93	107	9	30	964

[1] Totals for cruise 18 do not include stations occupied on the seaward extension of lines 70 and 90.

southern California and adjacent Baja California. Less than 1 percent of the eggs and larvae were taken to the north of Point Conception (see table 4). The number (standard haul totals) of sardine eggs and larvae taken at each station occupied in 1950 is given in Ahlstrom (1952).

Although sardine eggs and/or larvae were taken off central Baja California on every cruise made in this area in 1950, most of them were collected during a 3-month period, March through May. In the spawning center off southern California and adjacent Baja California, over 99 percent of the sardine eggs and larvae were collected during April, May, and June. To the north of Point Conception eggs and larvae were obtained in June, July, and August. The season of occurrence in different parts of the spawning range was quite similar to that found in 1949.

The relation between temperature and distribution of sardine eggs was similar to that found in 1949. Approximately 98.5 percent of the sardine eggs were taken within a 3.5 degree temperature range, 12.5° to 16.0° C.

1951 SURVEY

During 1951, additional lines of stations were added within the spawning areas off Baja California, both in the area between Ensenada and Point San Eugenio and to the south of Point Abreojos. In all, 6 lines of stations were added, bringing to 18 the number of lines routinely occupied between Point Conception and central Baja California, all of which were spaced 40 miles apart.

Because of more intensive work south of Point Conception, the survey off northern California was less extensive than in 1949 and 1950. Stations were occupied to the north of San Francisco only on the July and August cruises, the time of year spawning had occurred in this area in previous surveys; however, the work between San Francisco and Point Conception was about as

TABLE 4.—*Occurrence and abundance of eggs and larvae, by month and area, in hauls made during 1950*

[Based on standard haul totals]

	Central California (lines 40–77)				Southern California (lines 80–93)				Northern Baja California (lines 97–105)				Central Baja California (lines 110–130)				All areas combined			
	Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae	
	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number
January	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
February	0	0	0	0	0	0	0	0	0	0	0	0	4	1,193	6	349	4	1,193	6	349
March	0	0	0	0	0	0	1	1	0	0	0	0	9	5,887	14	327	9	5,887	15	328
April	0	0	0	0	4	173	0	0	6	1,998	5	139	12	25,487	13	1,947	22	27,658	18	2,086
May	0	0	0	0	7	855	6	353	5	136	14	734	8	5,149	11	3,321	20	6,140	31	4,408
June	6	378	4	15	9	5,733	15	1,007	0	0	6	288	5	249	5	10	20	6,360	30	1,320
July	1	2	5	20	1	22	5	19	0	0	1	3	3	379	3	27	5	403	14	69
August	1	3	2	15	0	0	0	0	-----	-----	-----	-----	-----	-----	-----	-----	1	3	2	15
September	0	0	0	0	0	0	0	0	0	0	0	0	1	59	3	16	1	59	3	16
October	0	0	0	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0	0	0	0
November	-----	-----	-----	-----	-----	-----	-----	-----	0	0	0	0	0	0	0	0	0	0	0	0
December	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Total	8	383	11	50	21	6,783	27	1,380	11	2,134	26	1,164	42	38,403	55	5,997	82	47,703	119	8,591

intensive as previously. No stations were occupied off Oregon.

Beginning with the August cruise a number of inshore stations were added, and as a result, offshore work was somewhat reduced. At the same time, routine investigation of shore temperatures between San Francisco and central Baja California was begun. The additional inshore stations have proved exceedingly valuable for sampling off-season sardine spawning, especially off central Baja California. During three cruises of 1951, spaced at 3-month intervals, coverage was extended to Cape San Lucas. The stations occupied during 1951 are illustrated in figure 5.

The month-by-month coverage in different parts of the survey area is summarized in table 5. Including the tows made at 29 nonroutine stations occupied off central California during both September and October, 1,440 plankton hauls were made at stations in 1951. Of these, 288 were taken north of Point Conception, 597 between Point Conception and Cape San Quintin, 466 off central Baja California, and 89 off southern Baja California.

TABLE 5.—*Stations occupied monthly during survey cruises, 1951*

	January (cruise 21)	February (cruise 22)	March (cruise 23)	April (cruise 24)	May (cruise 25)	June (cruise 26)	July (cruise 27)	August [1] (cruise 28)	September [1] (cruise 29)	October [1] (cruise 30)	November [1] (cruise 31)	December [1] (cruise 32)	Total
Lines 20–30	0	0	0	0	0	0	0	0	0	0	0	0	0
Lines 40–57	0	0	0	0	0	0	23	22	0	0	0	0	45
Lines 60–77	15	0	0	22	21	26	24	20	[2] 41	[2] 40	20	14	243
Lines 80–87	16	13	14	21	11	19	8	12	11	13	12	9	159
Lines 90–97	25	25	25	25	25	24	22	24	15	15	14	12	251
Lines 100–107	21	14	20	22	22	18	7	11	14	14	12	12	187
Lines 110–117	19	18	19	19	19	19	2	10	9	9	9	9	161
Lines 120–127	15	14	15	15	15	15	13	17	12	15	13	9	168
Lines 130–137	14	14	14	14	14	15	10	13	10	10	9	0	137
Lines 140–157	0	0	30	0	0	34	0	0	25	0	0	0	89
Total	125	98	137	138	127	170	109	129	137	116	89	65	1,440

[1] Totals for cruises 28 through 32 include 17 to 24 additional inshore stations added to the regular grid pattern beginning with cruise 28.

[2] Included in the total of lines 60–77 on cruises 29 and 30 are 29 closely spaced inshore stations, not a part of the regular grid pattern.

A greater depth stratum was sampled in oblique net hauls made during 1951 than in preceding years. Where depth of water permitted, the net was lowered with 200 meters of wire out, instead of 100 meters as had been routinely used on earlier cruises. The actual depth reached by the net averaged approximately 130 meters. One of the chief reasons for increasing the depth of the hauls was to be certain of sampling completely the mixed layer above the thermocline on offshore stations. The deeper hauls also provided better sampling of the general plankton, and of the larvae of a number of species of fish, including hake and anchovy.

It was definitely established in 1951 that sardine spawning took place in every month of the year off central Baja California (see table 6). Off-season

TABLE 6.—*Occurrence and abundance of eggs and larvae, by month and area, in hauls made during 1951*

[Based on standard haul totals]

	Central California (lines 40–77)				Southern California (lines 80–93)				Northern Baja California (lines 97–107)				Central Baja California (lines 110–137)				All areas combined			
	Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae		Eggs		Larvae	
	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number	Occurrence	Number
January	0	0	0	0	0	0	0	0	0	0	0	0	5	3,005	2	82	5	3,005	2	82
February	------	------	------	------	1	32	1	7	0	0	1	2	5	10,465	6	297	6	10,497	8	306
March	------	------	------	------	2	22	3	6	3	23	2	4	13	61,226	10	871	18	61,271	15	881
April	0	0	0	0	6	72	7	148	6	491	7	98	14	16,729	16	1,543	26	17,292	30	1,789
May	0	0	0	0	4	2,265	3	55	8	598	8	531	12	18,163	20	2,930	24	21,026	31	3,516
June	1	4	1	2	6	827	6	73	7	2,182	8	125	3	34	13	1,483	17	3,047	28	1,683
July	0	0	0	0	3	56	3	24	0	0	0	0	3	1,855	5	67	6	1,911	8	91
August	0	0	0	0	0	0	0	0	1	26	0	0	5	2,044	12	1,279	6	2,070	12	1,279
September	0	0	0	0	0	0	0	0	0	0	0	0	2	89	8	84	2	89	8	84
October	0	0	0	0	0	0	0	0	0	0	0	0	3	4,652	4	139	3	4,652	4	139
November	0	0	0	0	0	0	0	0	0	0	0	0	2	1,248	5	729	2	1,248	5	729
December	0	0	0	0	0	0	0	0	0	0	0	0	4	330	9	416	4	330	9	416
Total	1	4	1	2	22	3,274	23	313	25	3,320	26	760	71	119,840	110	9,920	119	126,438	160	10,995

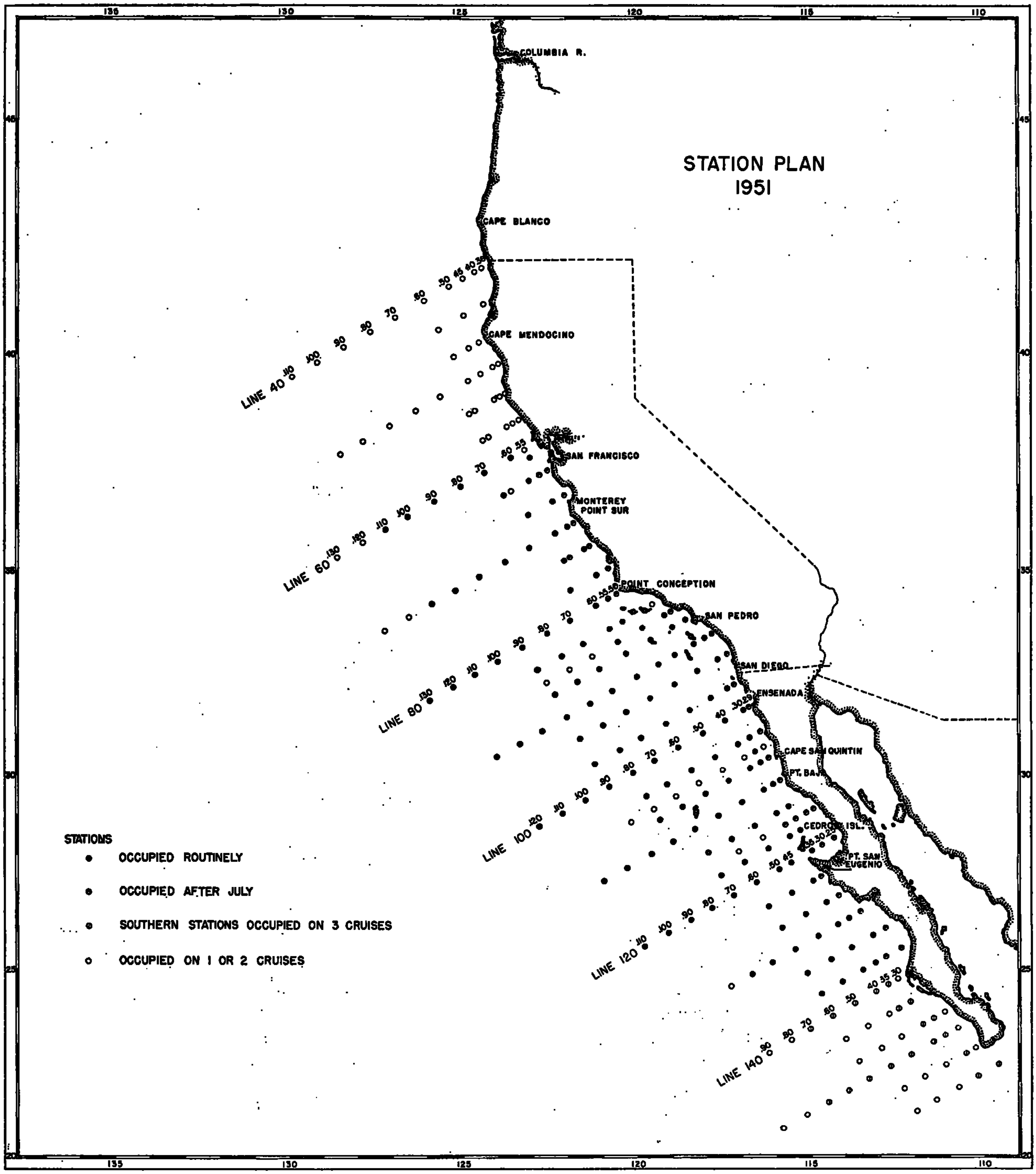

FIGURE 5.—Location of stations occupied during survey cruises made in 1951.

spawning was found to be confined mainly to Sebastian Viscaino Bay.

As in previous years, spawning was mostly confined to two centers: the more important, off central Baja California, the other, off southern California and adjacent Baja California. The latter had declined in importance since 1950. Practically no spawning was found to the north of Point Conception, and very little off southern Baja California. The number (standard haul total) of sardine eggs and larvae taken at each station occupied in 1951 is given in Ahlstrom (1953).

The relation between temperature and spawning was found to be more complex than previously supposed. During the first 6 months of 1951, approximately 98.7 percent of the sardine eggs were taken within a 3-degree temperature range, 13.5° to 16.5° C., but in the off-season, spawning occurred at much higher temperatures, mostly over 19° C.

ESTIMATING ABUNDANCE OF SARDINE EGGS, 1950 AND 1951

Enumeration of the total number of eggs spawned each season is prerequisite to the objectives of our research on the sardine, and the information is of value in several phases of the research. An estimate of the number of eggs spawned is one of the values needed in determining survival rate of larvae during the period of their planktonic existence. It can be used in conjunction with data on fecundity to obtain an estimate of the size of the spawning stock. The distribution of sardine eggs affords, at present, the only reliable information on the distribution of the sardine spawning stock during the spawning period.

It is possible that the extent of the area over which sardine spawning takes place may have an important bearing on the success or failure of year classes of sardines. The 1939 year class, an exceptionally large one, is known to have resulted from very widespread spawning. It is likely that spawning was equally widespread during the warm year of 1931 (*cf.* Hart 1943: 59), a season that produced another successful year class. The sardine spawning area has been contracting each year during the recent survey period, and the year classes have been below average.

The egg, or embryonic stage, is only the first of several stages concerning which information is needed in studying the rate of replenishment of the sardine stock through its productive processes. Others include larval and juvenile stages. Our research is presently limited to those stages that can be sampled by quantitative plankton techniques, i. e., eggs and larvae. Surveys of the distribution and abundance of juveniles are being conducted by the Bureau of Marine Fisheries of the California Department of Fish and Game (Phillips and Radovich 1952).

The methods used to obtain an estimate of the number of sardine eggs spawned in a year have been discussed in detail by Sette and Ahlstrom (1948). The basic data have been obtained from systematic sampling at regular time intervals at a number of stations distributed rather evenly through space. The data from each cruise have been treated as a problem of integration over space, and the combining of the data from the monthly cruises as a problem of integration on time. Two important assumptions underlie this method of treatment: (1) The distribution of egg concentrations through space and through time are continuous, and (2) the egg concentration gradients between points in space and time are linear. A number of special studies have been made in the past 2 years to test the validity of these assumptions. As the material is still under study, the findings are not available for inclusion in this paper. It appears unlikely that the results will materially alter our methods of estimation; rather, they should aid us in assigning values to the reliability of our estimates.

DEFINITION OF SYMBOLS

For consistency, I have used wherever possible the symbols used by Sette and Ahlstrom (1948); it was necessary to make several changes in the definitions of symbols, and to add several symbols.

c_i—Any of several estimates of the number of sardine eggs spawned per day in a standard area representing 10 square meters of sea surface at the *i*th station.

c'_i—The total number of sardine eggs in a standard haul or standard area at the *i*th station.

c''_i—The total number of sardine eggs in a standard haul at the *i*th station belonging to "complete" age categories, i. e., c'_i less incomplete age categories.

$\bar{c}'_i$—Any of several estimates of c_i, derived by dividing c'_i by the number of days' eggs represented in the haul at the *i*th station.

$\bar{c}_i''$—An estimate of c_i, derived by dividing c_i'' by the number of complete age categories.

$\bar{c}_{id}'$—An estimate of c_i, derived by dividing c_i' by d.

$\bar{c}_{ig}'$—An estimate of c_i, derived by dividing c_i' by g.

d_i—An estimate for each station of the time in days from spawning to hatching, determined from the relation between rate of development and temperature at the 10-meter level.

g_i—The total number of age categories, complete or incomplete, represented in a standard haul at the ith station.

t_i—The time weighting given to the ith station, equal to one-half the time elapsing since the preceding occupancy plus one-half the time elapsing prior to the succeeding occupancy.

w_i—The weighting factor for space, in standard areas, that is proportional to the area of the polygon assumed to be presented by the ith station on a given cruise.

C—The estimated number of eggs spawned over the complete survey area during the period of a cruise, according to

$$C=\Sigma(c_i w_i t_i)$$

C_s—The estimated number of eggs in the survey area during the period of survey; i. e., the sum of C for all cruises.

C_S—The estimated number of eggs spawned over the complete survey area during the spawning season.

The steps followed in obtaining the monthly and yearly estimates of egg numbers will be briefly described.

DETERMINING NUMBER OF EGGS SPAWNED PER DAY

The number of eggs taken in any given haul has been made comparable with the numbers from other samples by referring all collections to a common basis—the number of eggs under a standard area of 10 square meters. The number of eggs taken under a standard area may represent an accumulation of eggs from as many as 4 days' spawning or as few as 2 (occasionally 1 day's), depending on the water temperature at which they have been developing. Incubation is slower at lower temperatures, more rapid at higher temperatures (Ahlstrom 1943), hence it is necessary to determine for each collection the number of eggs spawned per day.

Two methods have been employed in estimating the number of eggs spawned per day, and estimates based on both methods will be given. The simpler of the two methods is to divide the total number of eggs in a standardized sample by the estimated number of days from spawning to hatching, as determined from the relation between rate of development and temperature. In previous studies (Ahlstrom 1943), the temperature at the 15-meter level was used in determining the relation between temperature and rate of development of sardine eggs. Temperature determination at this level, being an interpolated value, is not always readily available, but temperatures at the 10-meter level, measured directly from reversing thermometers, are available soon after the completion of each cruise. The 10-meter temperatures are now being used, and for most stations they are quite similar to the temperatures at 15 meters. The original choice of the 15-meter level had been based on the results of several series of horizontal hauls made with closing nets (*cf.* Silliman 1943). Most sardine eggs had been found to occur above a depth of 20 meters, usually between 10 and 20 meters, although in several series the largest concentration occurred within the upper 10 meters. Hence, there is as much justification for using the temperature at 10 meters as at 15 meters.

Estimates of the duration of the incubation period (time from spawning to hatching) are approximations. It is difficult to determine the exact duration of this period since embryos seldom are obtained in the act of hatching; however, our collections contain abundant material of eggs in the stage of development immediately preceding hatching. A determination has been made of the relation between water temperature at the 10-meter level and the rate of development of eggs to this stage. I have utilized data from 7 years of survey that met the following requirements: (1) At least 5 late-stage eggs in the sample, and (2) a nearly uniform temperature throughout the upper 20-meter stratum (difference between surface, 10- and 20-meter depths should not exceed 0.5° C.). Consequently, the determination is relevant not only for the 10-meter level, but for the upper 20-meter depth range. The regression line shown in figure 6 is very similar to that given for this stage by Ahlstrom (1943: fig. 1).

The incubation period was estimated from the regression line by adding 1½ to 4 hours, depending on the temperature. Several independent means of checking the accuracy of these estimates have been used. Miller (1952) reported that the majority of artificially fertilized sardine eggs,

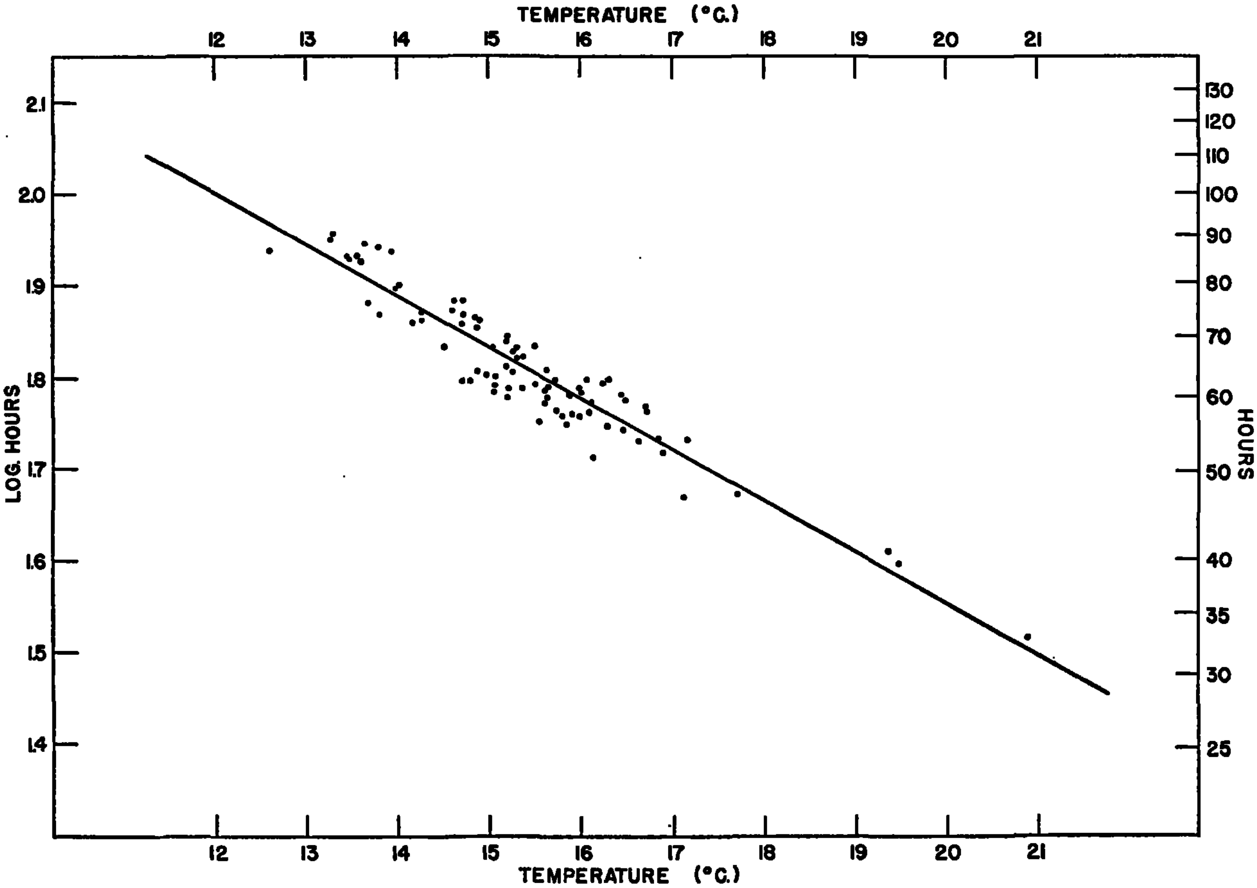

FIGURE 6.—Regression diagram showing influence of temperature (°C.) on time of development (log hours) of sardine eggs to the stage of development immediately preceding hatching. The linear-regression line was fitted to the scatter of points by the method of least squares. Data for the linear-regression line, based on the formula $y=a+bx$: $\bar{x}=15.40$, $\bar{y}=1.809$, $a=2.67$, $b=-0.0558$, s (standard error of estimate) $=0.0258$.

reared at a constant temperature of 16.8° C., hatched between 54 and 56 hours after fertilization. My estimate for incubation at this temperature is 54 hours. A comparison was made of the average incubation period for sardine eggs as estimated from temperature data and the average number of age categories represented in the same hauls for the 1950 and 1951 seasons. The agreement is very close.

Average accumulation of eggs (in days):	*1950*	*1951*
Determined from regression of time of development on temperature	3.20	2.685
Determined from age categories	3.16	2.760
Ratio	1.013	0.972

The alternative method of determining the number of eggs spawned per day requires separation of the eggs in each sample into the several age categories represented. Although time consuming, the separation seldom presents any difficulty, even when one or more of the categories are represented by "zero" abundance. To obtain the average number of eggs spawned per day, the standard haul total is divided by the number of age categories involved. In practice, complicating features arise, owing to some collections having been made while spawning or hatching was actively taking place. There are two alternatives for dealing with this problem, either use all age categories whether complete or incomplete, or set up criteria for identifying incomplete age categories, and eliminate these from consideration when determining the per-day spawning at a station.

An age category may be incomplete because a haul was made while spawning was taking place.

Based on the time of collection of newly spawned eggs, spawning was found to be confined mostly to the 4-hour period from 8 p. m. to midnight (Ahlstrom 1943). Nevertheless, the most recent day's eggs are underrepresented in the collections, not only during these hours, but between midnight and 6 a. m. as well (*cf.* Sette and Ahlstrom 1948: 520). Although the reason for this underrepresenation cannot be given, it is too marked to be ignored. Consequently, the youngest age category collected between 8 p. m. and 6 a. m. has been designated "incomplete."

It is more difficult to determine when an age category is incomplete because a portion of the oldest age group has hatched. A criterion, admittedly somewhat arbitrary, has been established: If over 80 percent of the eggs of the oldest age category are in the stage immediately preceding hatching, some of the eggs of the category would have hatched already, and the category should be judged incomplete.

The question may be asked, Why use two different methods for determining the number of eggs spawned per day? Why not standardize on a single method of determining c_i? The reason is that no one method is entirely satisfactory. Determination based on age categories would be satisfactory were it not for the problem of incomplete age categories. A strict adherence to the criteria established for eliminating incomplete age categories results, at times, in a "zero" estimate for a station at which a considerable number of eggs were collected. Furthermore, it is less than satisfactory in dealing with collections of sardine eggs that have developed at temperatures above 17° C. In such samples, because of the rapidity of development at higher temperatures, only 1 or 2 age categories are present and, too often, 1 or occasionally both have to be classed as incomplete.

Because of the complication arising from incomplete age categories, it seemed desirable to make estimates using all age categories to determine how serious an underrepresentation would result. For purposes of this study, the spawning day was assumed to begin at midnight. Newly spawned eggs obtained between 8 p. m. and midnight were not considered; otherwise, all categories were used.

Determination of per-day spawning using $\overline{c}_{id}$ is a much less direct method than that based on age categories. Based on the relation between rate of development and temperature, it introduces another variable, temperature, into every determination. Incorrect temperature values for a given station would result in an inaccurate estimate of c_i for that station. Occasionally we lack any temperature data for a haul, and for such samples this method is inapplicable. Furthermore, if egg concentrations at any given station occur at a different level than 10 meters, and if the temperature at that level is higher or lower than at the 10-meter level, the estimate will be inaccurate by the amount of this difference. Also, the temperature at the time of collection may not represent the temperature during the entire period of development. Another defect in this method of estimating per-day spawning is that the value for any individual determination is not as reliable as the estimate based on age categories.

DETERMINING THE AREA OF STATIONS

There are various methods of accomplishing a linear integration over space. Isometric lines commonly are employed to define areas of equal abundance. I have used this technique for illustrating distribution, but only occasionally for estimating total quantities. The objection to this method as a tool for estimating abundance is twofold: (1) There is some subjectivity in drawing the lines, with the result that the linear interpolation is approximate rather than precise, and (2) the method is time consuming.

A more precise method of integration over space, presented by Sette and Ahlstrom (1948), involves a concept which we have termed "area of station." A basic assumption of this procedure is that the catch at a particular station is not only an estimate of abundance at that point, but representative of the abundance over a larger area. To define this area for any particular station, a polygon is constructed, the sides of which are the perpendicular bisectors of lines drawn from that station to all surrounding stations. The result is a unique polygon surrounding each station (except peripheral ones). If the concentration at each station is then weighted to the area of the polygons and the values are summed, the resulting total value will be identical to that obtained by linear interpolation between stations. Because of the regularity in our spacing of stations and station lines, the polygon for most stations is a square, 40 miles on a side.

This has greatly simplified the determination of the area represented by each station. There has been no problem in assigning an area to peripheral stations. The boundary of an outer station on a line is defined as if there were another outlying station at the regular spacing of 40 miles. For delimiting the area of the stations on the most northerly line occupied during a cruise, the stations are treated as if the next adjacent line to the north had been occupied; similarly for the most southerly line. An advantage of this method of integration over space is that the sum of the weights given to the stations equals the area surveyed. It has the added advantage of being completely objective.

DETERMINING TIME WEIGHTING TO BE APPLIED TO A STATION

The concentration found at a station is assumed to represent the concentration for an adjacent period of time. The survey cruises are spaced at monthly intervals, hence the time interval represented by each cruise approximates 30 days; however, the time interval between successive occupancies of any given station is somewhat irregular. An individual time-weighting factor has been applied to each haul made at a station, which is equal to one-half the total time elapsing between the previous and succeeding occupancies of the station. By this method of weighting for time, a value is obtained that is exactly equivalent to a linear interpolation in time.

ESTIMATING EGG ABUNDANCE

An estimate of the number of sardine eggs spawned during each cruise (= month), was obtained from

$$C=\Sigma(c_i w_i t_i)$$

The seasonal total is a summation of the monthly estimates of egg numbers. Three estimates of abundance of sardine eggs are given for each season. All estimates make use of the same weighting factors for area and time, but differ in the method of determining c_i. These estimates, summarized by month and season, are given in table 7.

TABLE 7.—*Comparison of estimates of the number of sardine eggs, 1950 and 1951*

[In billions of eggs. Estimate based on formula $C=\Sigma(c_i w_i t_i)$]

Month	1950				1951			
	Estimate using—			Average	Estimate using—			Average
	$\bar{c}_i''$	$\bar{c}_{ig}'$	$\bar{c}_{id}'$		$\bar{c}_i''$	$\bar{c}_{ig}'$	$\bar{c}_{id}'$	
January	----------	----------	----------	----------	11,436	15,388	18,352	15,058
February	10,488	10,596	10,929	10,671	69,598	67,151	53,163	63,304
March	36,916	41,625	44,886	41,142	265,277	253,378	285,752	268,136
April	150,118	132,759	152,768	145,215	65,368	73,995	82,592	73,985
May	53,020	51,551	52,407	52,326	100,935	92,319	95,573	96,275
June	28,745	29,909	32,339	30,331	18,054	14,452	16,040	16,182
July	5,951	5,037	5,505	5,498	30,525	29,105	40,615	33,415
August	16	16	16	16	9,663	12,545	15,458	12,555
September	423	605	786	605	353	345	408	369
October	----------	----------	----------	----------	30,736	30,736	38,361	33,278
November	0	0	0	0	6,932	6,041	8,492	7,155
December	----------	----------	----------	----------	1,971	2,116	2,530	2,206
Total	285,677	272,098	299,636	285,804	610,848	597,571	657,336	621,918

For both years, the estimate using $\bar{c}_{ig}'$ for determining per-day spawning is the lowest; the estimate using $\bar{c}_i''$ (per-day abundance based on complete age categories only) is intermediate; while the estimate based on $\bar{c}_{id}'$ is highest. For the 1950 season, the lowest estimate is 90.8 percent of the highest; for the 1951 season, the lowest is 90.9 percent of the highest.

How do estimates based on $\bar{c}_{ig}'$, where use is made of all age categories, compare with estimates based on $\bar{c}_i''$, where per-day spawning is determined from complete age categories only? For 1950, the estimate using $\bar{c}_{ig}'$ is 95.2 percent as high as that based on $\bar{c}_i''$; for 1951, it is 97.8 percent as high as the estimate based on complete age categories. Hence the underestimation resulting from the inclusion of incomplete age categories is not particularly important in either the 1950 or the 1951 determinations.

It undoubtedly is due to chance that the estimates of egg abundance using $\bar{c}_{id}'$ are larger than estimates otherwise obtained for 1950 and 1951. This is evident if a comparison is made of estimates of egg abundance based on this method with those based on complete age categories for two different periods, as shown in the following tabulation:

Year and area	Estimate using $\bar{c}'_{id}$	Estimate using $\bar{c}''_i$	Ratio $\bar{c}'_{id}/\bar{c}''_i$	Difference $\bar{c}'_{id}$ from $\bar{c}''_i$
				Percent
1940 (southern California)	179,943	190,026	0.947	−5.3
1941 (southern California)	150,728	163,689	0.921	−7.9
1950 (all areas)	299,636	285,677	1.049	+4.9
1951 (all areas)	657,336	610,848	1.076	+7.6

Estimates obtained by this method are about as much lower than estimates based on complete age categories for 1940 and 1941 as they are higher than those for 1950 and 1951.

RELIABILITY OF ESTIMATES

An extended discussion of the reliability of estimates of egg abundance, determined in the manner previously outlined, is given by Sette and Ahlstrom (1948). Three sources of variability are of particular concern: Sampling variability of hauls, mortality during the incubation period, and errors introduced by interpolations.

Sampling variability of hauls.—To obtain information on sampling variability, duplicate hauls were taken at most stations occupied during 1940. The two hauls were taken successively, not simultaneously, but in an identical manner. In his analysis of variability in the numbers of sardine eggs in a set of 24 paired hauls, Silliman (1946) was able to separate the variability due to real differences in egg concentrations at different stations (time-place of hauls) from the sampling variability between the two hauls at a station. He found that differences in concentration between stations roughly accounted for 90 percent of the total variability. In regard to sampling variability between paired hauls at a station, he concluded that the number of eggs in one haul could not be considered significantly different (at the level $P=0.05$) from the number in the other unless it was about one-half or double.

Using Silliman's data as a basis for further analyses, Sette and Ahlstrom (1948) found that sampling variability became moderate for the sum of all hauls made during a season, amounting to about 5 percent at the one standard-deviation limit. The conclusion was reached that this source of error was not important enough to warrant attempting further refinements aimed at decreasing haul variability.

Inasmuch as routine sampling procedures have been improved during recent years, there is no reason to suppose that the variability from this source can introduce a significant error in determinations.

Mortality during the incubation period.—It takes one to several days for sardine eggs to develop from spawning to hatching. During this period some mortality is inevitable. Because of this mortality, one would expect to find a decrease in abundance of older stages as compared with younger. Contrary to expectation, the youngest age group of eggs is not much more abundant than the next older age category, as the following table illustrates:

Year	Number of eggs aged—	
	8–32 hours	32.1–56 hours
	c_a	c_b
1940	55,923	54,263
1941	30,586	33,980
1950	12,596	12,645
1951	28,986	26,588
Total	128,091	127,476

To ensure that only complete age categories were used in this tabulation, newly spawned eggs collected between 8 p. m. and 6 a. m. were omitted. Hence the youngest age group includes eggs collected between 6 a. m. and 6 a. m. estimated to be between 8 to 32 hours old, while the group a day older is estimated to be between 32.1 and 56 hours old. In determining the age of sardine eggs, the hour of 10 p. m. was selected as the "zero" point, as it represents the midpoint of spawning, which has been shown to be confined mostly to the 4-hour period, 8 p. m. to midnight (Ahlstrom 1943: 4). Age categories with eggs 56.1 to 80 hours old were not included in the tabulation, inasmuch as they would be "completely" represented in only a fraction of the hauls. The largest haul made during 1951 was omitted from the totals for that year. If included, the value for c_a for 1951 would be 34,805, for c_b, 47,880. This unusually rich haul, containing twice as many eggs as any other ever obtained on a regular survey cruise, would unduly influence the total. Otherwise the two age groups are about equally abundant, hence it may be assumed that mortality during the embryonic period is negligible.

Errors introduced by interpolation.—Of greater consequence than the preceding sources of variability are the errors introduced by interpolations over space and time. As stated earlier, a basic assumption of the method followed is that each of the egg concentrations sampled has a linear continuity in space and time. As Sette and Ahlstrom (1948) pointed out, this assumption would tend toward validity as the spacing of stations in space and time became infinitesimally small. Hence the question arises whether the rather wide spacing of stations in space and time introduces too great a variability in our estimates.

Unfortunately, no definite answer to this problem is possible from routine survey data. The problem must be approached through a study of the distribution of sardine eggs in a limited area where stations can be closely spaced, and frequently occupied. Several such studies have been made during the past 2 years, but the data are only partly processed. Even these studies will afford only partial answers, but when supplemented by additional studies, they will permit a fairly precise evaluation of the variability introduced by interpolations.

GEOGRAPHICAL DISTRIBUTION OF SARDINE EGGS, 1950 AND 1951

Quantitative estimates of the number of sardine eggs taken monthly in different parts of the spawning range are given in table 8 for 1950 and in table 9 for 1951. The estimates are summarized by station lines. These are grouped into the following five areas:

1. Area north of Point Conception: Includes all stations occupied to the north of line 80. Lines 40–77 were routinely occupied during 1950, lines 60–77 during 1951.
2. Southern California area: From Point Conception to San Diego (lines 80–93). This area includes the region surveyed during 1940–41.
3. Northern Baja California area: From the International Border south to Point San Quintin (lines 97–107). The southern California and northern Baja California areas together make up one of the two major sardine spawning centers.
4. Central Baja California area: From Point Baja to Point San Juanico (lines 110–137). This constitutes the other major sardine spawning center.
5. Southern Baja California area: From Point San Juanico to Cape San Lucas (lines 140–157). This area is not routinely covered; however, it

TABLE 8.—*Estimated number of sardine eggs in survey areas, 1950*

[In billions. Estimate based on formula $C=\Sigma\,(\bar{c}_i''\,w_i t_i)$]

	February (cruise 11)	March (cruise 12)	April (cruise 13)	May (cruise 14)	June (cruise 15)	July (cruise 16)	August (cruise 17)	September (cruise 18)	Total	Percent of total
Area north of Point Conception:										
Lines 40–57	0	0	0	0	0	0	16	0	16	----------
Lines 60–77	0	0	0	0	2,278	12	0	0	2,290	----------
Total	0	0	0	0	2,278	12	16	0	2,306	0.8
Southern California area:										
Line 80	0	0	0	0	570	0	0	----------	570	----------
Line 83	0	0	0	331	0	0	0	----------	331	----------
Line 87	0	0	36	0	23,345	0	0	----------	23,381	----------
Line 90	0	0	0	15	402	137	0	0	554	----------
Line 93	0	0	768	6,612	507	0	----------	----------	7,887	----------
Total	0	0	804	6,958	24,824	137	0	0	32,723	11.4
Northern Baja California area:										
Line 97	0	----------	1,707	145	0	0	----------	----------	1,852	----------
Line 100	0	0	14,475	0	----------	0	----------	0	14,475	----------
Sta. 105.35	0	0	61	54	0	0	----------	0	115	----------
Total	0	0	16,243	199	0	0	----------	0	16,442	5.8
Central Baja California area:										
Lines 110–117	0	50	7,319	710	418	0	----------	0	8,497	----------
Line 120	10,468	4,122	5,466	40,184	0	5,802	----------	0	66,042	----------
Line 123	0	1,338	73,921	3,568	72	0	----------	0	78,899	----------
Line 127	0	0	937	0	0	0	----------	0	937	----------
Line 130	20	31,406	45,428	1,401	1.153	0	----------	423	79,831	----------
Total	10,488	36,916	133,071	45,863	1,643	5,802	----------	423	234,206	82.0
Grand total	10,488	36,916	150,118	53,020	28,745	5,951	16	423	285,677	100.0
Percent	3.7	12.9	52.5	18.6	10.1	2.1	0	0.1	100.0	----------

TABLE 9.—*Estimated number of sardine eggs in survey areas, 1951*

[In billions. Estimate based on formula $C = \Sigma (\bar{c}_i'' w_i t_i)$]

	January (cruise 21)	February (cruise 22)	March (cruise 23)	April (cruise 24)	May (cruise 25)	June (cruise 26)	July (cruise 27)	August (cruise 28)	September (cruise 29)	October (cruise 30)	November (cruise 31)	December (cruise 32)	Total	Percent of total
Area north of Point Conception:														
Lines 40-57	-------	-------	-------	-------	-------	-------	0	0	-------	-------	-------	-------	0	-------
Lines 60-77	0	-------	-------	0	0	0	0	0	0	0	0	0	0	-------
Total	0	-------	-------	0	0	0	0	0	0	0	0	0	0	0.0
Southern California area:														
Line 80	0	0	28	0	0	219	0	0	0	0	0	0	247	-------
Line 83	0	0	0	0	0	0	0	0	0	0	0	0	0	-------
Line 87	0	0	0	99	0	2,240	0	0	0	0	0	0	2,339	-------
Line 90	0	0	183	45	8,023	1,606	315	0	0	0	0	0	10,172	-------
Line 93	0	0	0	58	2,904	0	0	0	0	0	0	0	2,962	-------
Total	0	0	211	202	10,927	4,065	315	0	0	0	0	0	15,720	2.6
Northern Baja California area:														
Line 97	0	0	0	2,338	711	8,736	0	42	0	0	0	0	11,827	-------
Line 100	0	0	11	52	1,015	18	0	0	0	0	0	0	1,096	-------
Line 103	0	0	50	285	615	4,792	0	0	0	0	0	0	5,742	-------
Line 107	0	0	0	0	14	0	0	0	0	0	0	0	14	-------
Total	0	0	61	2,675	2,355	13,546	0	42	0	0	0	0	18,679	3.1
Central Baja California area:														
Line 110	0	0	0	15	558	0	0	0	0	0	0	0	573	-------
Line 113	0	0	2,953	4,569	51	0	-------	-------	-------	-------	-------	-------	7,573	-------
Line 115	-------	-------	-------	-------	-------	-------	-------	0	0	28,922	0	0	28,922	-------
Line 117	0	0	9,129	31	138	34	-------	-------	-------	-------	-------	-------	9,332	-------
Line 120	1,026	52,336	75,122	18,189	18,744	359	26,396	6,916	306	1,814	6,932	1,933	210,073	-------
Line 123	9,897	17,262	177,177	24,718	40,784	0	0	162	47	0	0	38	270,085	-------
Line 127	130	0	257	11,330	27,344	0	0	0	0	0	0	-------	39,061	-------
Line 130	383	0	367	3,639	34	0	0	2,543	0	0	0	-------	6,966	-------
Line 133	0	0	0	0	0	0	3,814	0	0	0	0	-------	3,814	-------
Line 137	0	0	0	0	0	0	0	0	0	0	0	-------	0	-------
Total	11,436	69,598	265,005	62,491	87,653	393	30,210	9,621	353	30,736	6,932	1,971	576,399	94.4
Southern Baja California area:														
Line 140	-------	-------	0	-------	-------	0	-------	-------	0	-------	-------	-------	0	-------
Line 143	-------	-------	0	-------	-------	50	-------	-------	0	-------	-------	-------	50	-------
Line 147	-------	-------	0	-------	-------	0	-------	-------	0	-------	-------	-------	0	-------
Line 150	-------	-------	0	-------	-------	0	-------	-------	0	-------	-------	-------	0	-------
Line 153	-------	-------	0	-------	-------	0	-------	-------	0	-------	-------	-------	0	-------
Line 157	-------	-------	0	-------	-------	0	-------	-------	0	-------	-------	-------	0	-------
Total	-------	-------	0	-------	-------	50	-------	-------	0	-------	-------	-------	50	0.0
Grand total	11,436	69,598	265,277	65,368	100,935	18,054	30,525	9,663	353	30,736	6,932	1,971	610,848	100.1
Percent	1.9	11.4	43.4	10.7	16.5	3.0	5.0	1.6	0.1	5.0	1.1	0.3	100.0	-------

was occupied during the November cruise of 1950, and during the March, June, and September cruises of 1951.

The distribution of sardine eggs as determined from the 1950 survey cruises is illustrated in figure 7. The concentrations shown at each station are cumulative totals for 8 monthly cruises made February through September. To facilitate comparison, the distribution of sardine larvae during 1950 is shown in an adjacent chart.

Similar charts for the 1951 survey period are shown in figure 8. To emphasize the restricted distribution of sardine spawning during the off-season, the location of sardine eggs during the latter part of the year, August through December, is shown as an inset, while the distribution during the main spawning period, January through July, is shown in the full-sized chart. For ready comparison, the distribution of sardine larvae during 1951 is given in a companion chart.

Estimates of the abundance of sardine eggs in different parts of the spawning range in 1950 and 1951 were as follows:

Areas	1950		1951	
	Number of eggs	Percent of total	Number of eggs	Percent of total
	Billions		*Billions*	
Area north of Point Conception	2,306	0.8	0	0
Southern California area	32,723	11.4	15,720	2.6
Northern Baja California area	16,442	5.8	18,679	3.1
Central Baja California area	234,206	82.0	576,399	94.4
Southern Baja California area	0	0	50	0
Total	285,677	100.0	610,848	100.1

Area north of Point Conception.—Sardine spawning off central and northern California has decreased each year during the period of survey. In 1949, there was evidence of fairly extensive spawning to the north of Point Conception. Sardine

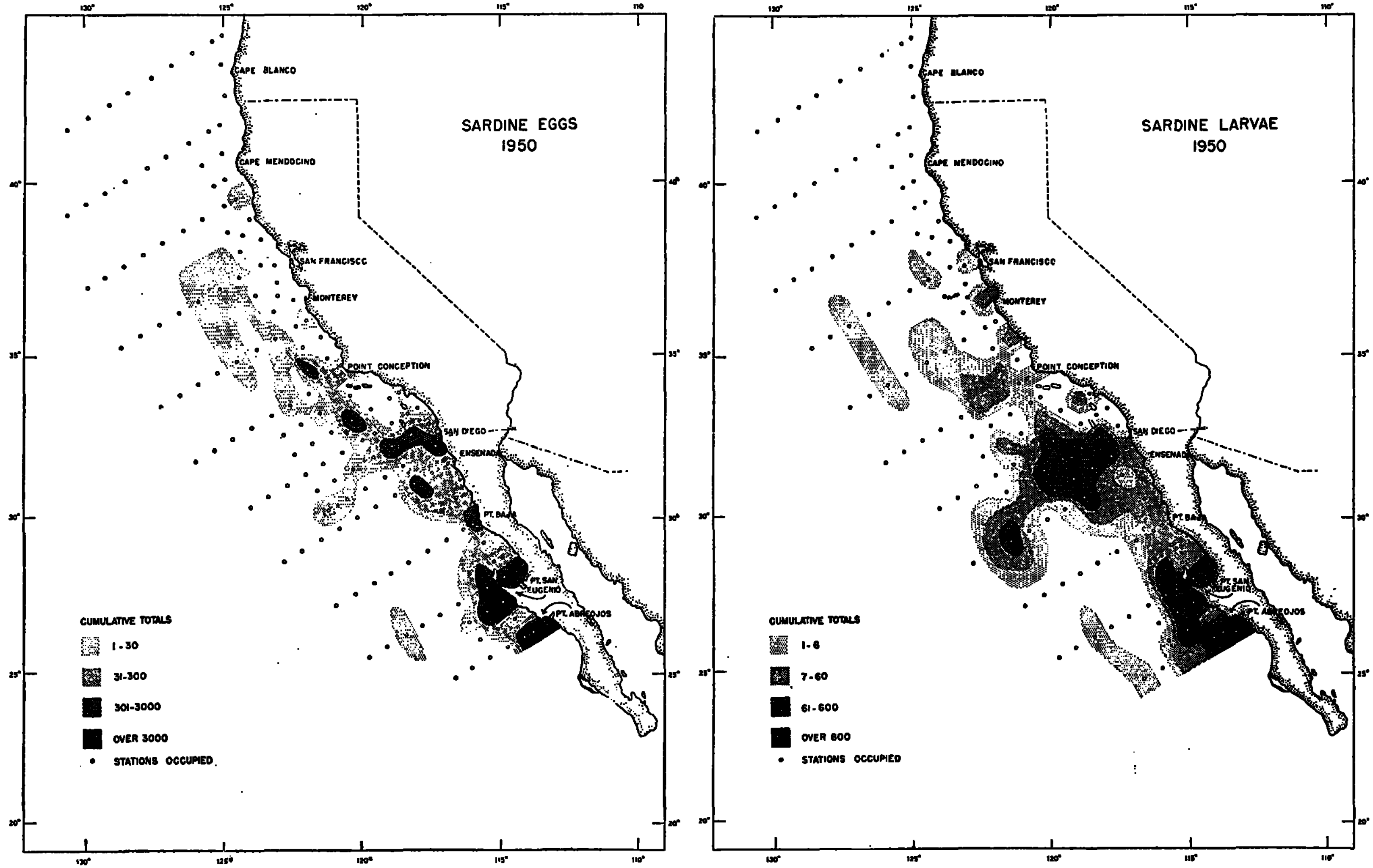

FIGURE 7.—Distribution and abundance of sardine eggs and sardine larvae during 8-month period, February through September, 1950.

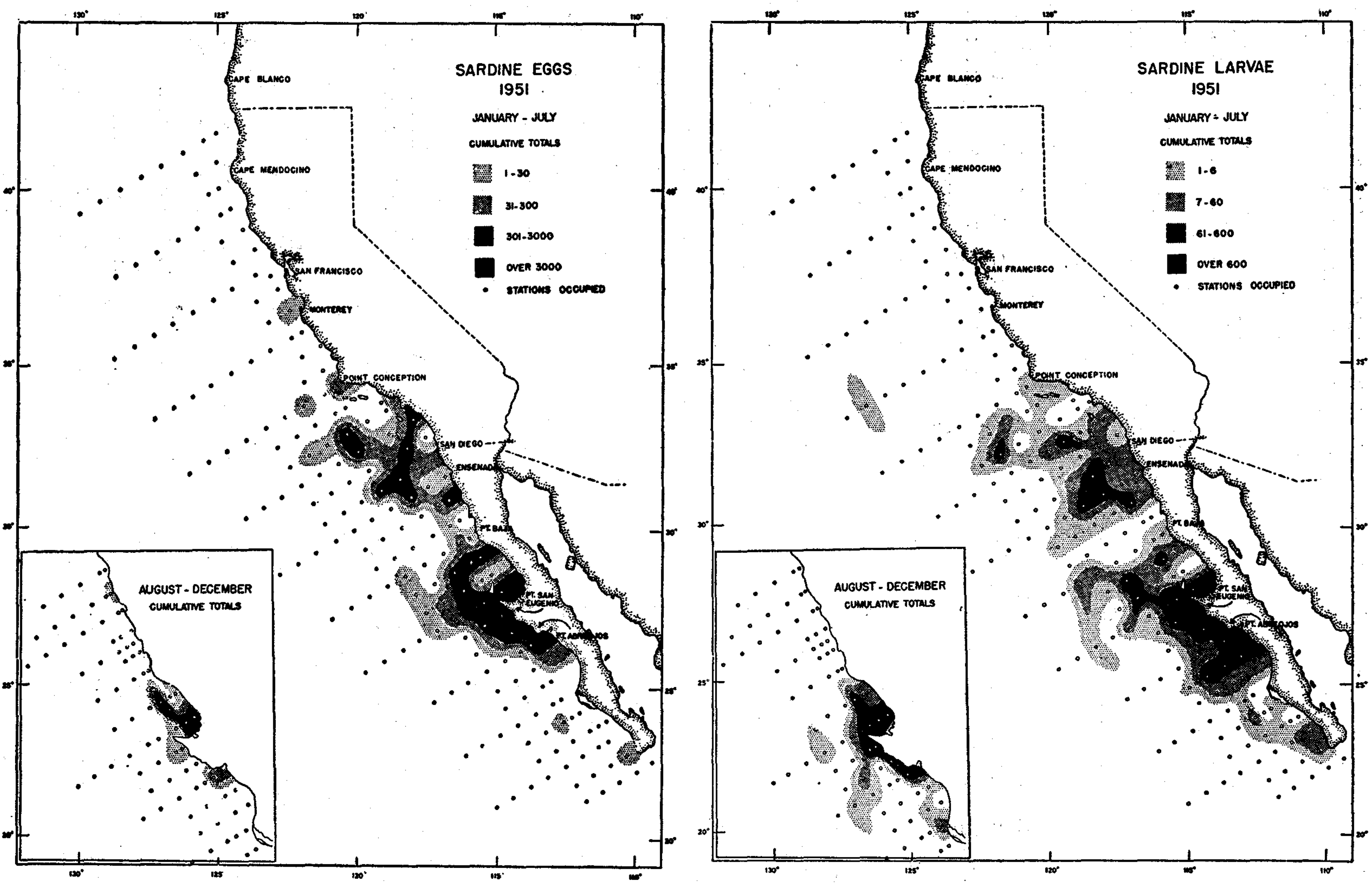

FIGURE 8.—Distribution and abundance of sardine eggs and sardine larvae during 1951. Distributions during the main spawning period, January through July, are shown in the main charts, while distributions during remainder of the year, August through December, are shown in the insets.

eggs were taken as far north as Cape Mendocino and one larva was taken off Oregon. A large number of sardine larvae were taken in a haul made off Point Sur. During 1950, there was evidence of widespread but light spawning off central California. Sardine spawning was almost absent from this area in 1951; only one egg and one larva were taken in hauls made to the north of Point Conception.

Southern California and northern Baja California areas.—Although the contributions of southern California and adjacent Baja California have been segregated in tables 8 and 9, the distribution of sardine spawning is continuous between these areas, and together they constitute one of the major centers of sardine spawning.

The importance of southern California as a sardine spawning area has been known for many years. Scofield (1934) first called attention to it, and the United States Fish and Wildlife Service conducted systematic surveys over a portion of the area during 1940 and 1941. In a subsequent report, the results obtained then will be compared with findings in this area during current surveys.

Spawning off southern California and adjacent Baja California may occur at considerable distances from shore. Sardine eggs have been collected about 250 miles offshore, and larvae at even greater distances; but large concentrations of eggs are seldom taken farther from shore than 150 miles.

Spawning in this center was less abundant in 1951 than in 1950, and a larger part of it occurred off northern Baja California. Decline for the center as a whole was about 33 percent in actual numbers of eggs taken. When expressed as a percentage of the total eggs taken throughout the spawning range, the decline appears more precipitous, the drop being from 17.21 percent to 5.63 percent.

Central Baja California area.—In recent years, this area has been the major sardine spawning center. The heaviest concentrations of sardine eggs have been taken between Cedros Island and Point Abreojos. During the 1950 season there were two areas of heavy spawning; one was located within a radius of 50 miles of Point San Eugenio, the other offshore from Point Abreojos. During 1951, heavy spawning was concentrated in the vicinity of Point San Eugenio. Egg estimates are not decreasing in amount in this area, as is the case in more northerly waters. As a consequence, the percentage contribution of this area has been increasing; in 1950 it amounted to 82 percent, while in 1951 it was over 94 percent.

Southern Baja California area.—Although this area has not been routinely covered, it was surveyed 4 times between November 1950 and September 1951. Sardine eggs were taken in only two hauls. If these collections were representative of the spawning off southern Baja California, this area is unimportant as a spawning center. Sardine eggs and larvae have been taken in most hauls made in Magdalena and Santa Maria Bays, however, and it is likely that sardines spawn there during much of the year. These bay areas are not included in the regular survey pattern.

DISTRIBUTION OF SPAWNING IN TIME, 1950 AND 1951

The seasonal abundance of sardine eggs in different parts of the spawning range is summarized in table 10, and is illustrated by a series of charts showing the monthly distribution of sardine eggs and larvae during 1950 and 1951 (figs. 9–28).

Area north of Point Conception.—Since 1949, sardine eggs have been collected off central and northern California during the 3-month period, June through August. In 1949, eggs were taken off Point Sur in June, off San Francisco in July, and off Cape Mendocino in August, suggesting a northward progression of spawning even within this area. In 1950, sardine eggs were taken as far north as San Francisco in June; however, the few eggs collected off northern California were obtained in August, as in 1949. The only haul containing sardine eggs from this area in 1951 was obtained in June.

Spawning had been found in this area as early as March, in the unusually warm year of 1931 (Scofield 1934). Hence, it is likely that spawning in this area will be early or late, depending on whether water temperatures are warmer or colder than usual. In recent years they have been colder.

Southern California and northern Baja California areas.—In recent years most of the sardine spawning in this center has been confined to a 3-month period, April through June. In 1950, 99.7 percent of sardine eggs were taken during these months; in 1951 over 98 percent. The 1950 and 1951 seasons appear to have been a month

TABLE 10.—*Abundance of sardine eggs, by month and area, 1950 and 1951*

[In billions. Estimate based on formula $C=\Sigma\,(\bar{c}_i'' w_i t_i)$]

Month	Area north of Point Conception				Southern California and northern Baja California areas				Central Baja California area			
	1950		1951		1950		1951		1950		1951	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
January	-----	-----	0	0	-----	-----	0	0	-----	-----	11,436	2.0
February	0	0	-----	-----	0	0	(1)	0	10,488	4.5	69,598	12.1
March	0	0	-----	-----	0	0	272	0.8	36,916	15.8	265,005	46.0
April	0	0	0	0	17,047	34.7	2,877	8.4	133,071	56.8	62,491	10.8
May	0	0	0	0	7,157	14.6	13,282	38.6	45,863	19.6	87,653	15.2
June	2,278	98.8	(1)	0	24,824	50.5	17,611	51.2	1,643	0.7	393	0.1
July	12	0.5	0	0	137	0.3	315	0.9	5,802	2.5	30,210	5.2
August	16	0.7	0	0	0	0	42	0.1	-----	-----	9,621	1.7
September	0	0	0	0	0	0	0	0	423	0.2	353	0.1
October	-----	-----	0	0	-----	-----	0	0	-----	-----	30,736	5.3
November	-----	-----	0	0	-----	-----	0	0	0	0	6,932	1.2
December	-----	-----	0	0	-----	-----	0	0	-----	-----	1,971	0.3
Total	2,306	100.0	0	0	49,165	100.1	34,399	100.0	234,206	100.1	576,399	100.0

[1] Sardine eggs were collected, but when estimates were based on the formula $C=\Sigma\,(\bar{c}_i'' w_i t_i)$, no values were obtained.

later than the spawning seasons of 1940 and 1941. This will be discussed in more detail in a subsequent report. Some spawning occurred off southern California from February to August in 1951.

Central Baja California area.—Sardine eggs have been collected off central Baja California in every month of the year; however, in 1950, the majority of sardine eggs were taken during a 3-month period, March through May. In 1951, the main spawning in this area was from February through May. The peak of spawning in 1951 was somewhat earlier than in 1950. The off-season spawning, especially that occurring from August through December, was largely confined to Sebastian Viscaino Bay. The off-season spawning was not adequately sampled in 1950.

Southern Baja California area.—This area has been surveyed too infrequently to permit an adequate determination of the season of spawning. In bays, such as Magdalena Bay, spawning probably occurs throughout the year.

DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF SARDINE LARVAE, 1950 AND 1951

A basic reason for conducting sardine larval studies is to test the widely held assumption that the early postembryonic period is one of the most critical periods, if indeed it is not the most critical period, in the life of a pelagic fish in regard to mortality. Infant mortality is high and it is variable. It is assumed that the success or failure of year classes of sardines and other fishes probably is determined during this period.

Theoretical considerations appear to justify this assumption. It is known, from a study of a number of fisheries, that there is considerable variation in the success of year classes. Good year classes have been recorded that were 50 times as large as poor ones (e. g., herring and cod). The sardine is more at the mercy of its environment during its planktonic existence than at any other period of its life. On hatching, the larva is small and defenseless. It lacks a functional mouth, pigmented eyes for vision, or fins for locomotion. It must develop in an environment where there is sufficient food of the right kind that it can obtain as soon as its yolk supply is depleted, or it will perish.

Studies on food requirements of the young sardine larva have shown that its initial food is composed almost entirely of copepod eggs and nauplii. The larva is severely restricted in the size of food it can utilize, and at first it is limited to food smaller than 80 microns in length.[2]

In addition to rigid food requirements, the small larva is at the mercy of a much larger group of predators than at any other period of life. Not only is it preyed on by many of the larger filter-feeding animals—fish, crustacea, and molluscs—but even by many organisms in the

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[2] The food requirements of sardine larvae are being investigated by David Arthur, of Scripps Institution of Oceanography. Results were reported upon briefly in California Cooperative Sardine Research Program Progress Report, 1 January 1951 to 30 June 1952.

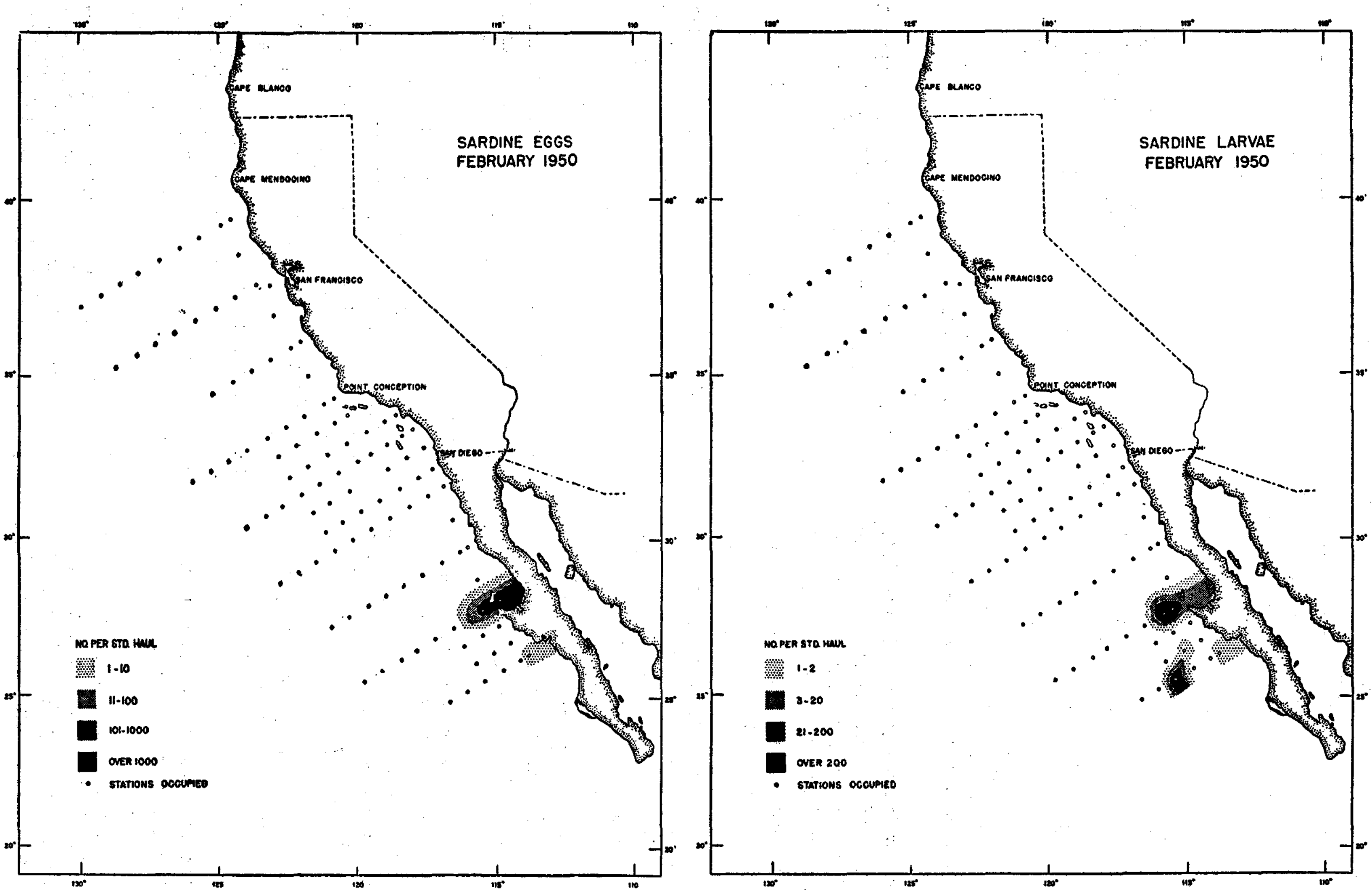

FIGURE 9.—Distribution and abundance of sardine eggs and larvae, February 1950.

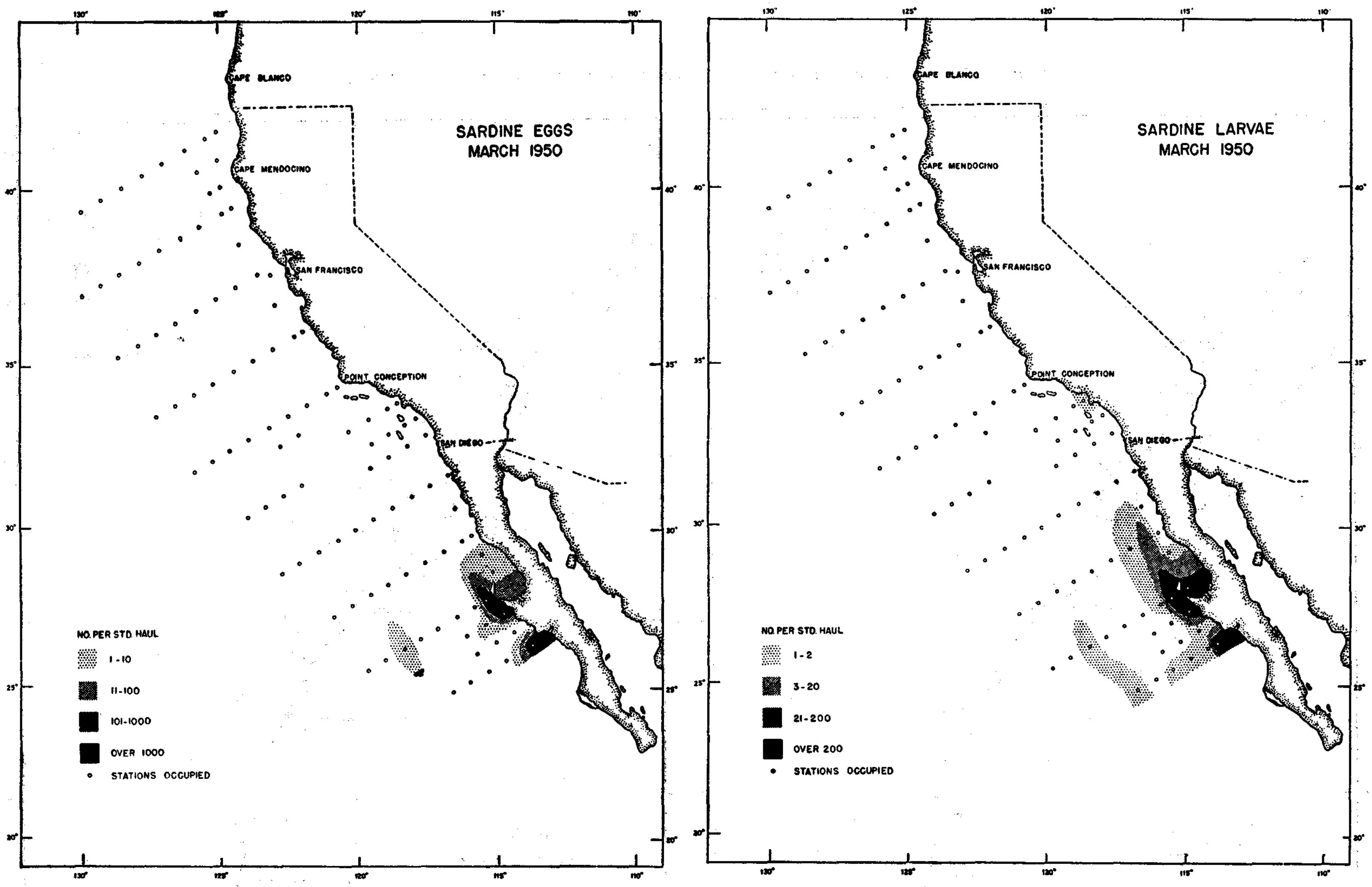

Figure 10.—Distribution and abundance of sardine eggs and larvae, March 1950.

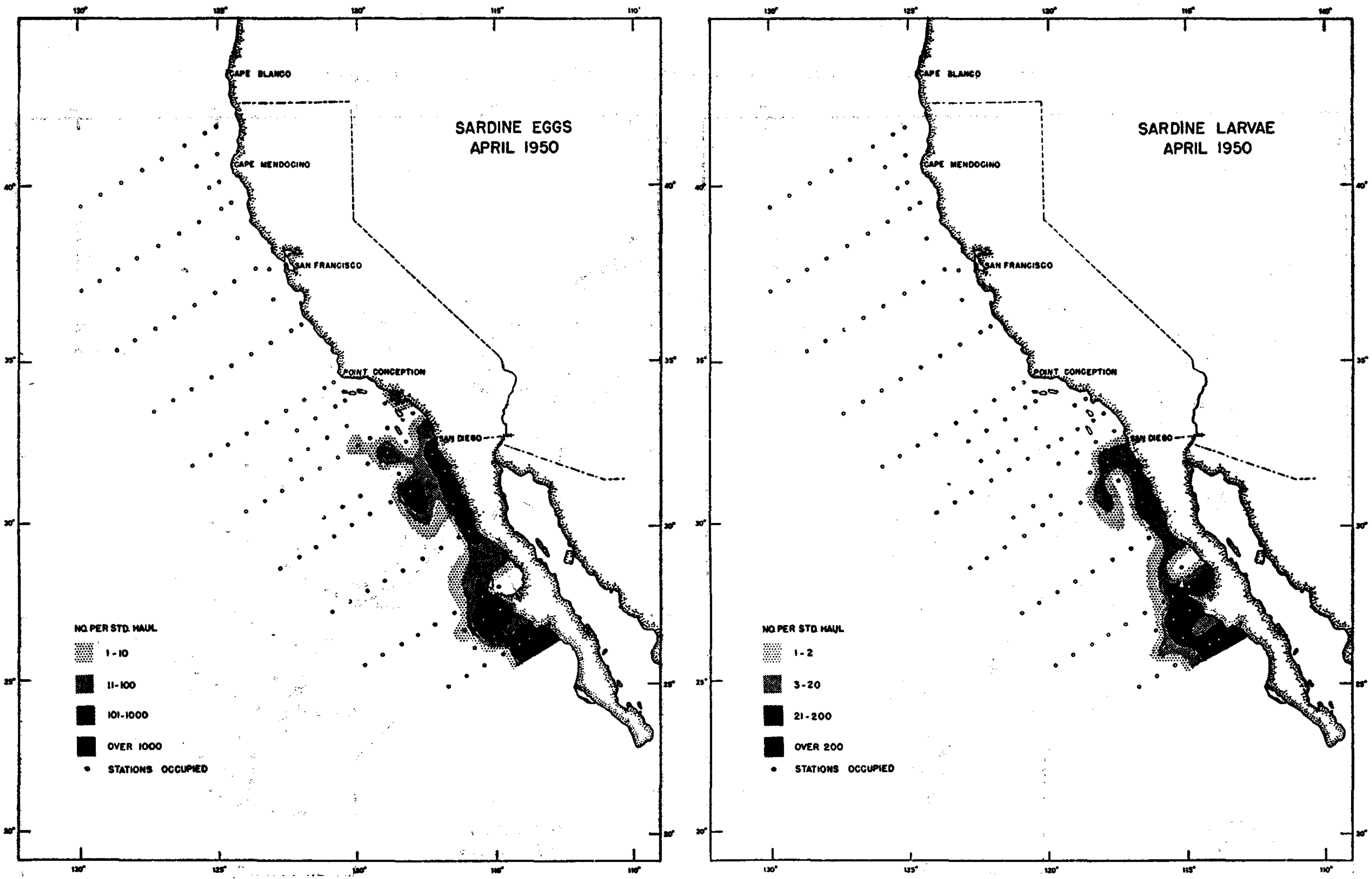

FIGURE 11.—Distribution and abundance of sardine eggs and larvae, April 1950.

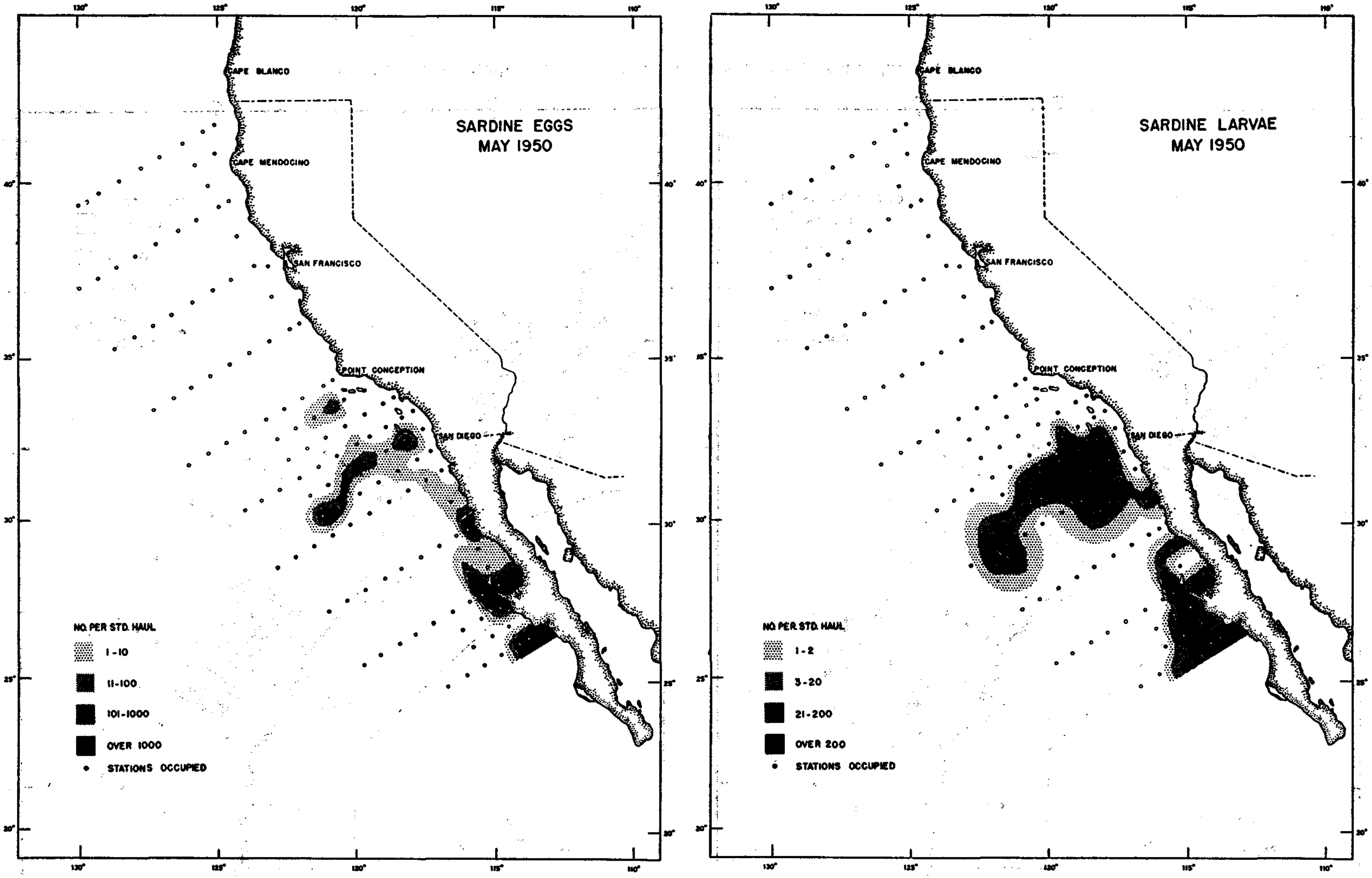

Figure 12.—Distribution and abundance of sardine eggs and larvae, May 1950.

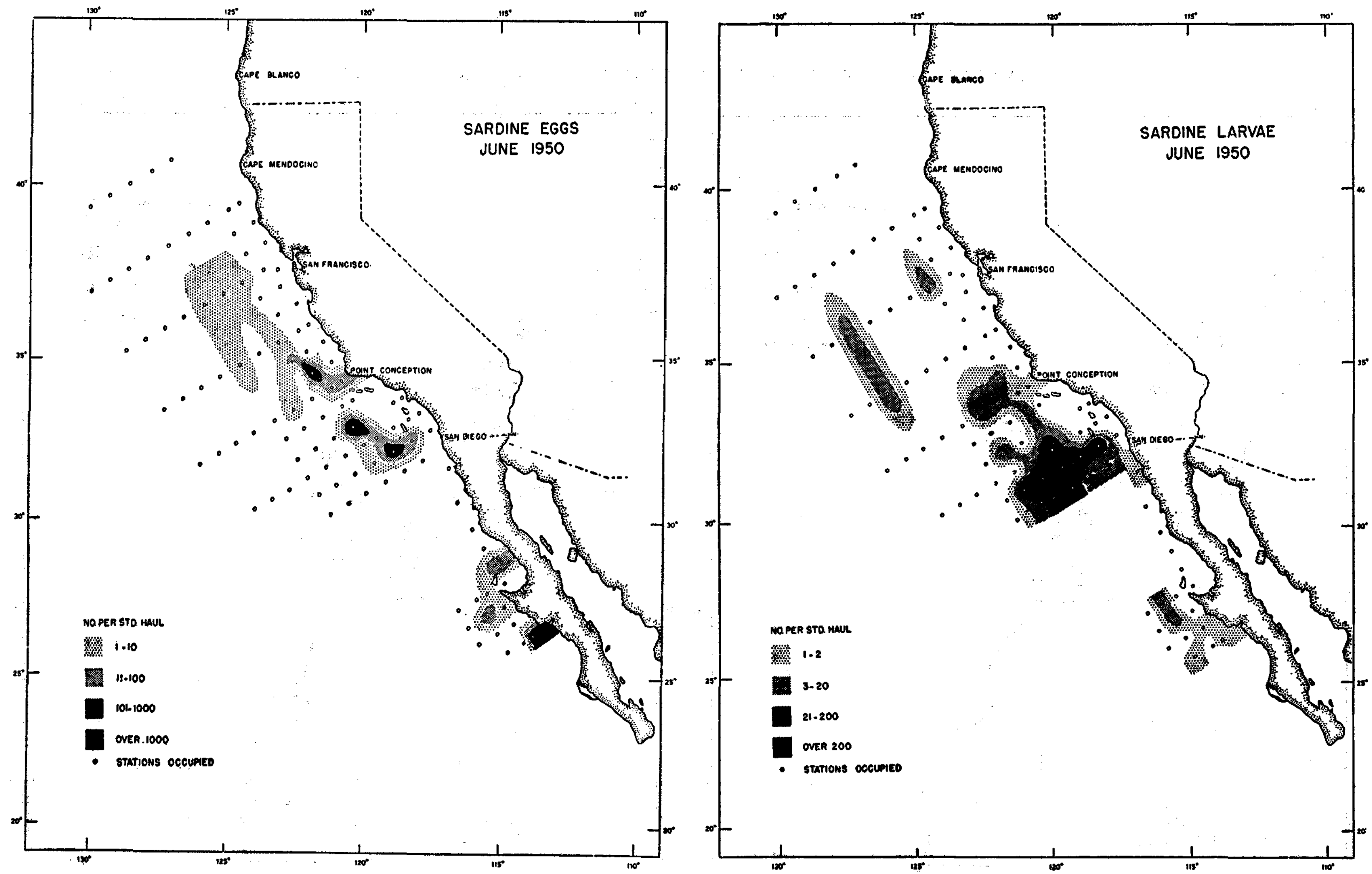

FIGURE 13.—Distribution and abundance of sardine eggs and larvae, June 1950.

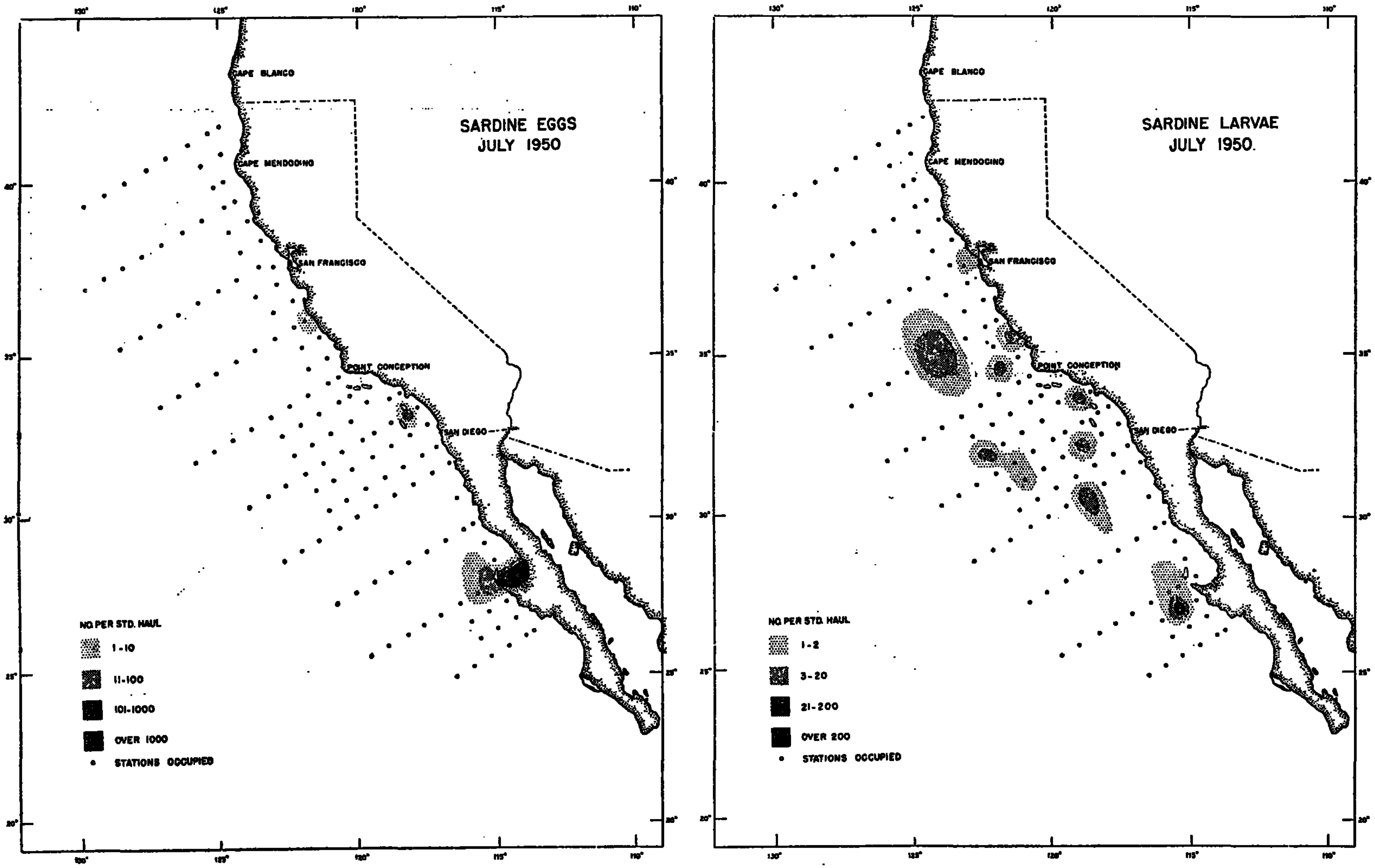

FIGURE 14.—Distribution and abundance of sardine eggs and larvae, July 1950.

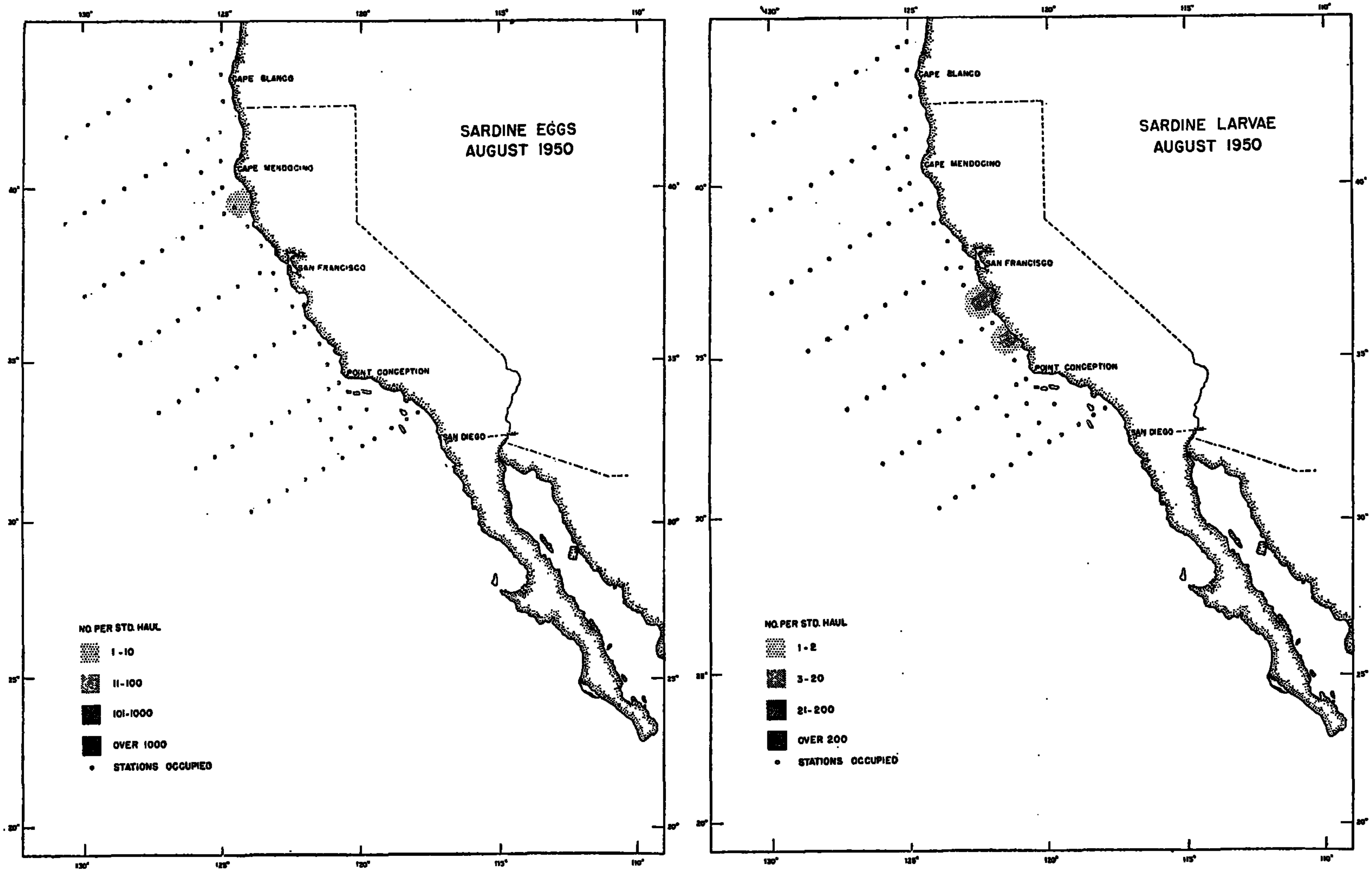

Figure 15.—Distribution and abundance of sardine eggs and larvae, August 1950.

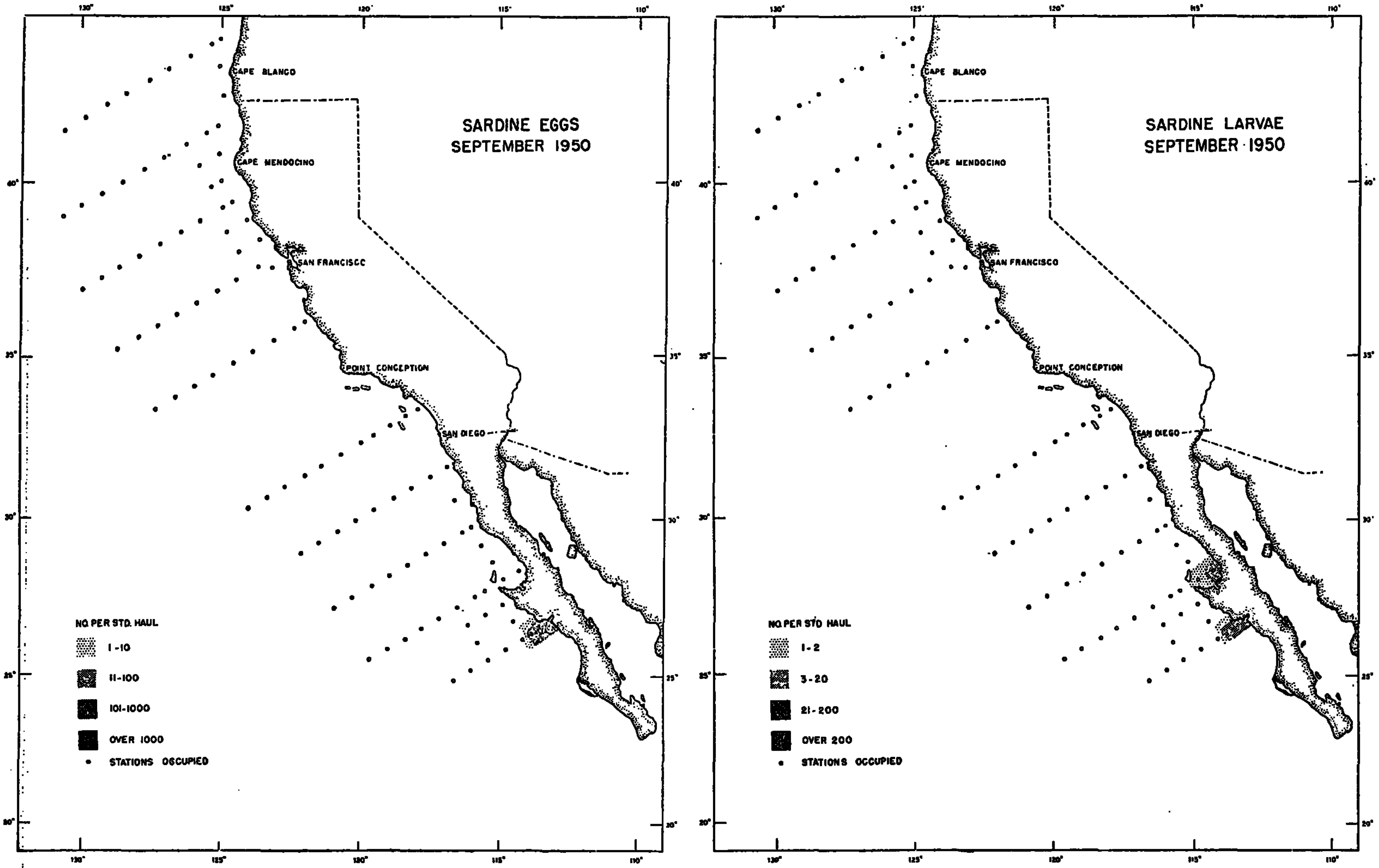

FIGURE 16.—Distribution and abundance of sardine eggs and larvae, September 1950.

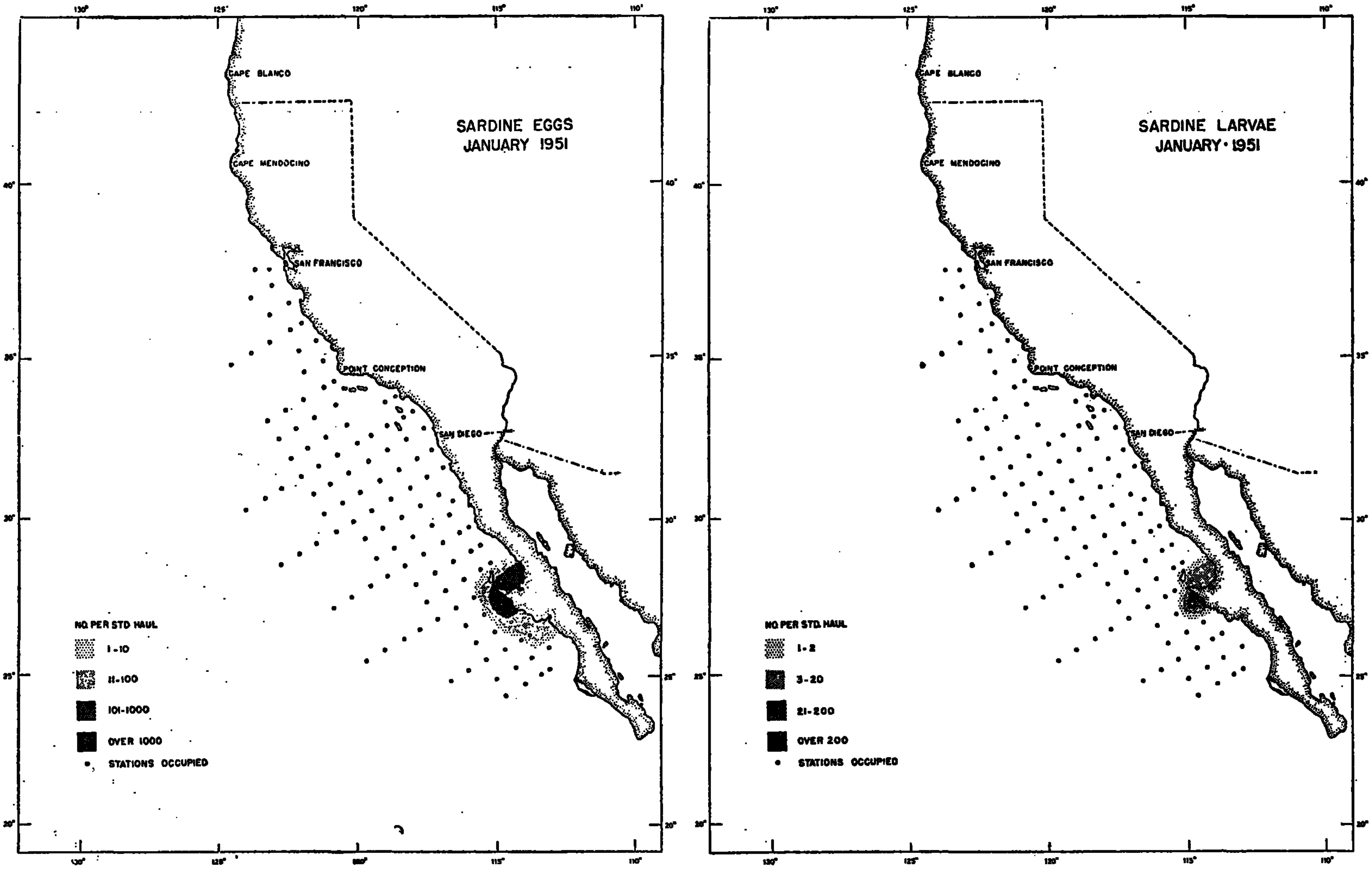

FIGURE 17.—Distribution and abundance of sardine eggs and larvae, January 1951.

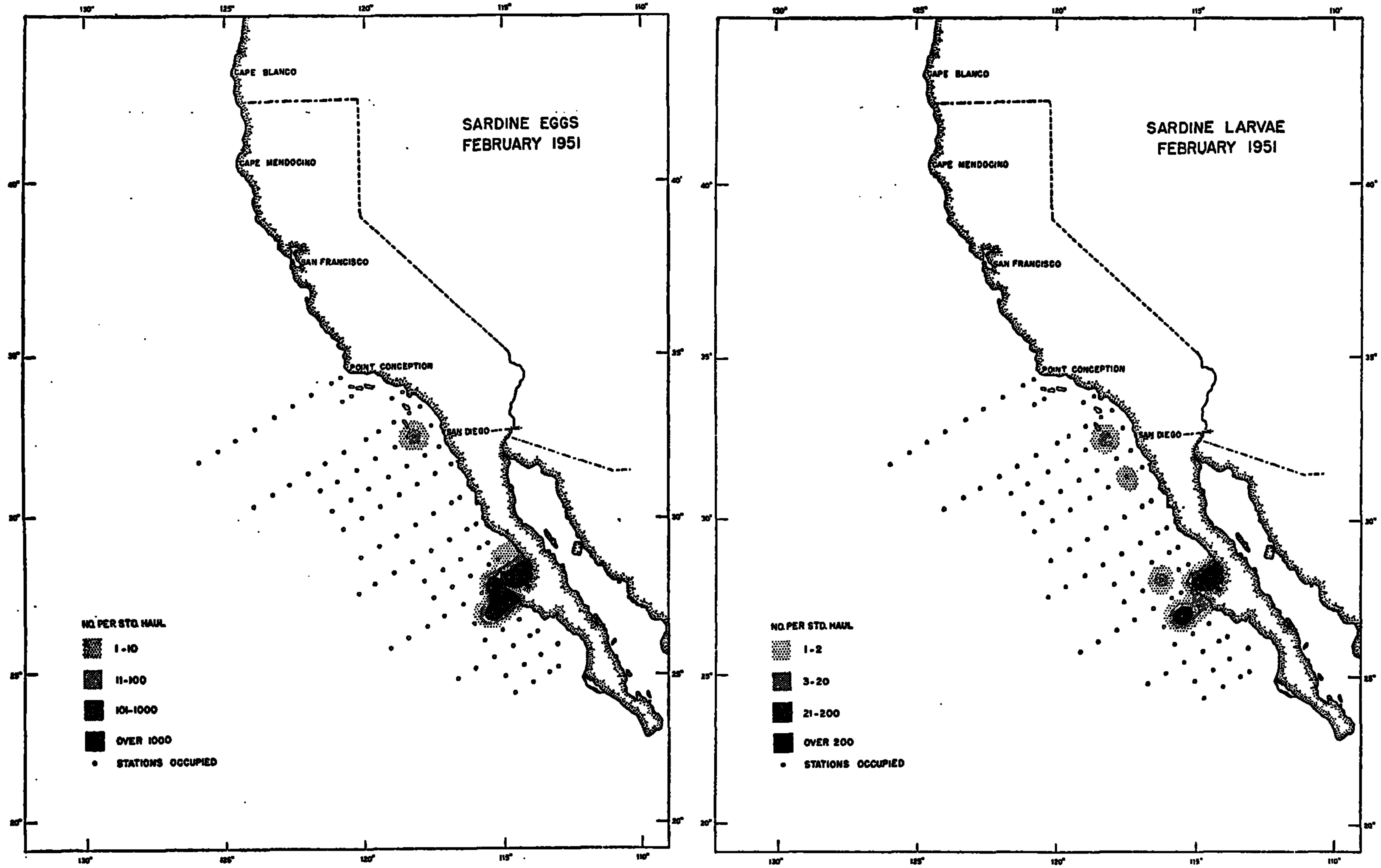

FIGURE 18.—Distribution and abundance of sardine eggs and larvae, February 1951.

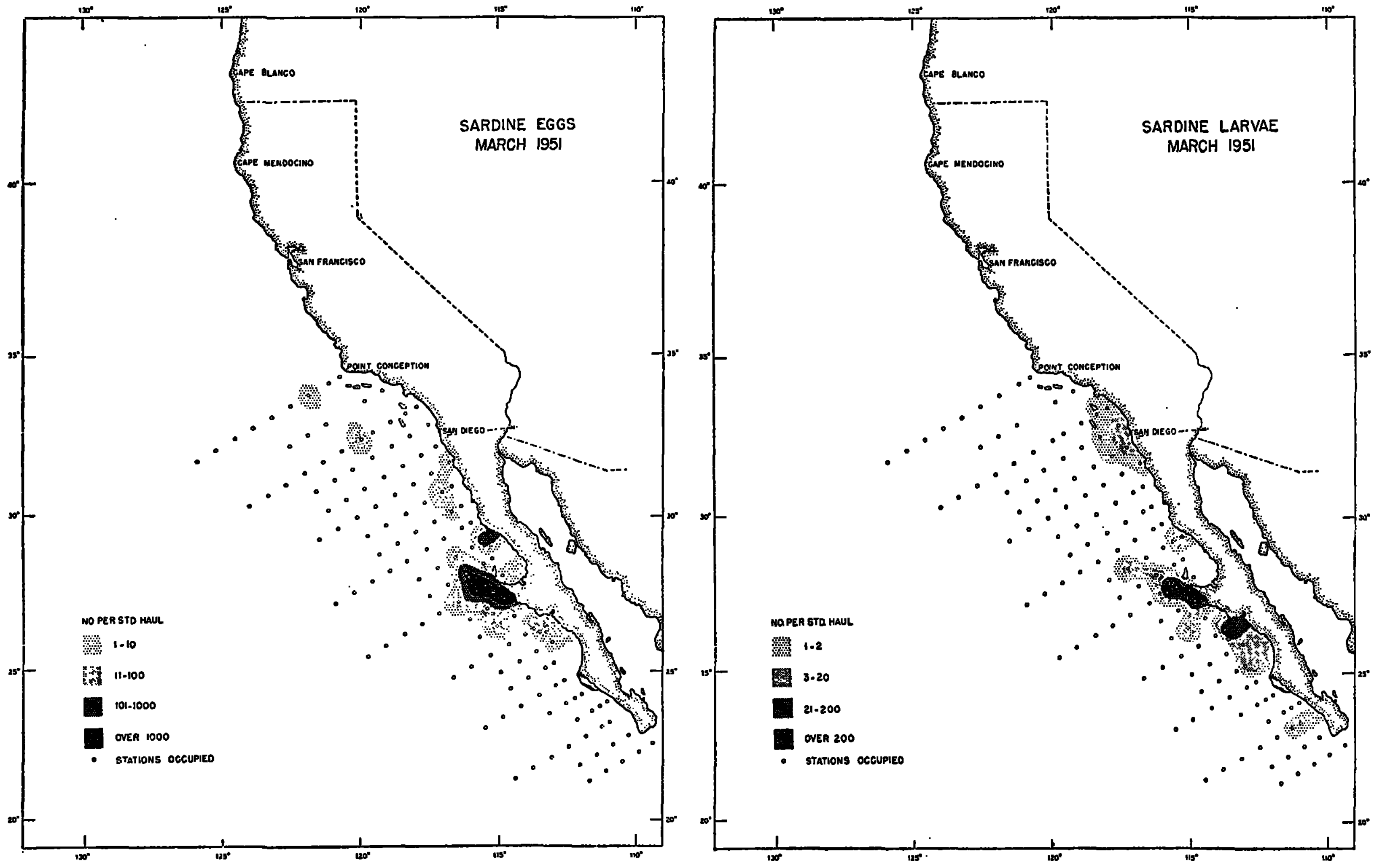

FIGURE 19.—Distribution and abundance of sardine eggs and larvae, March 1951.

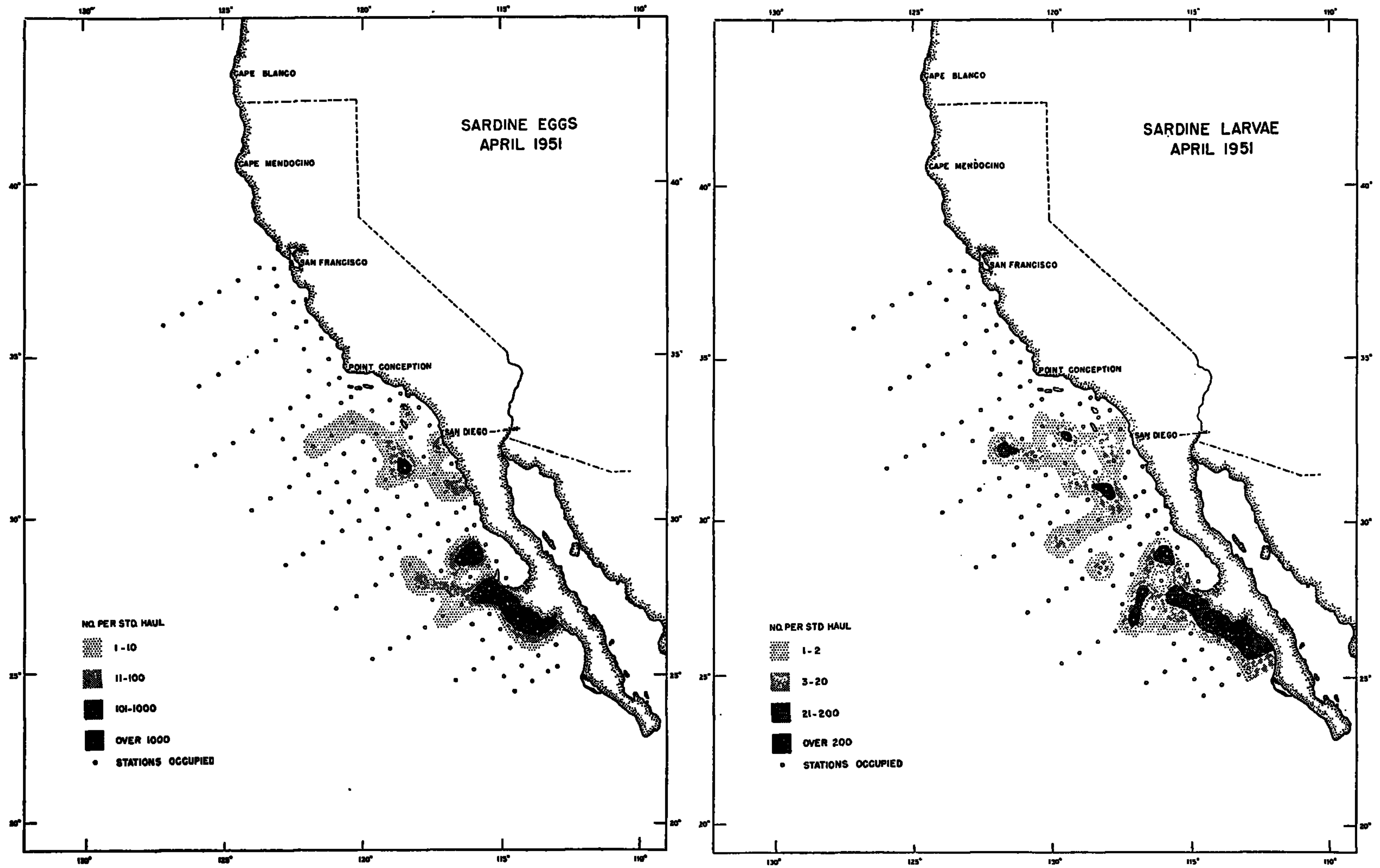

FIGURE 20.—Distribution and abundance of sardine eggs and larvae, April 1951.

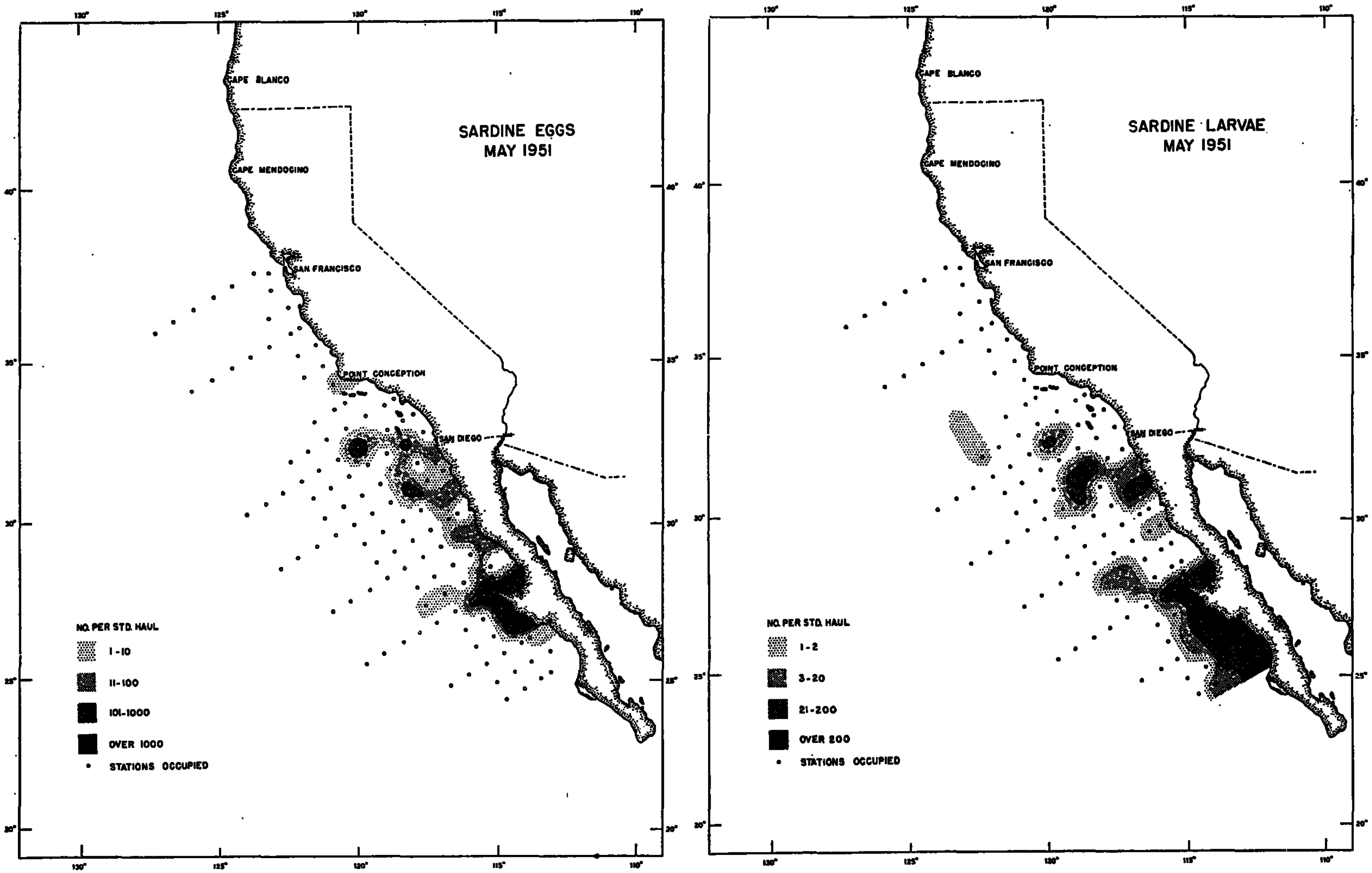

Figure 21.—Distribution and abundance of sardine eggs and larvae, May 1951.

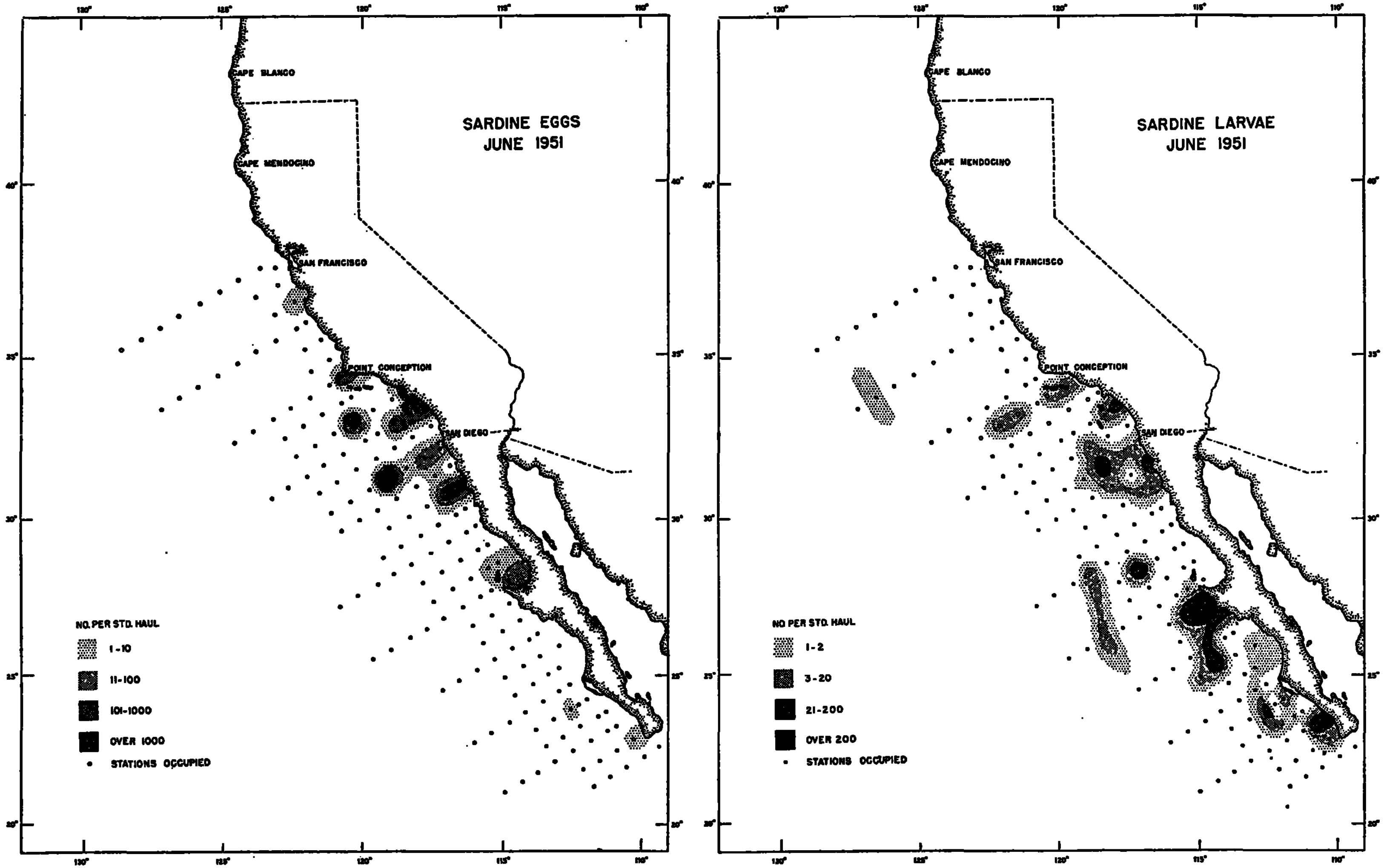

FIGURE 22.—Distribution and abundance of sardine eggs and larvae, June 1951.

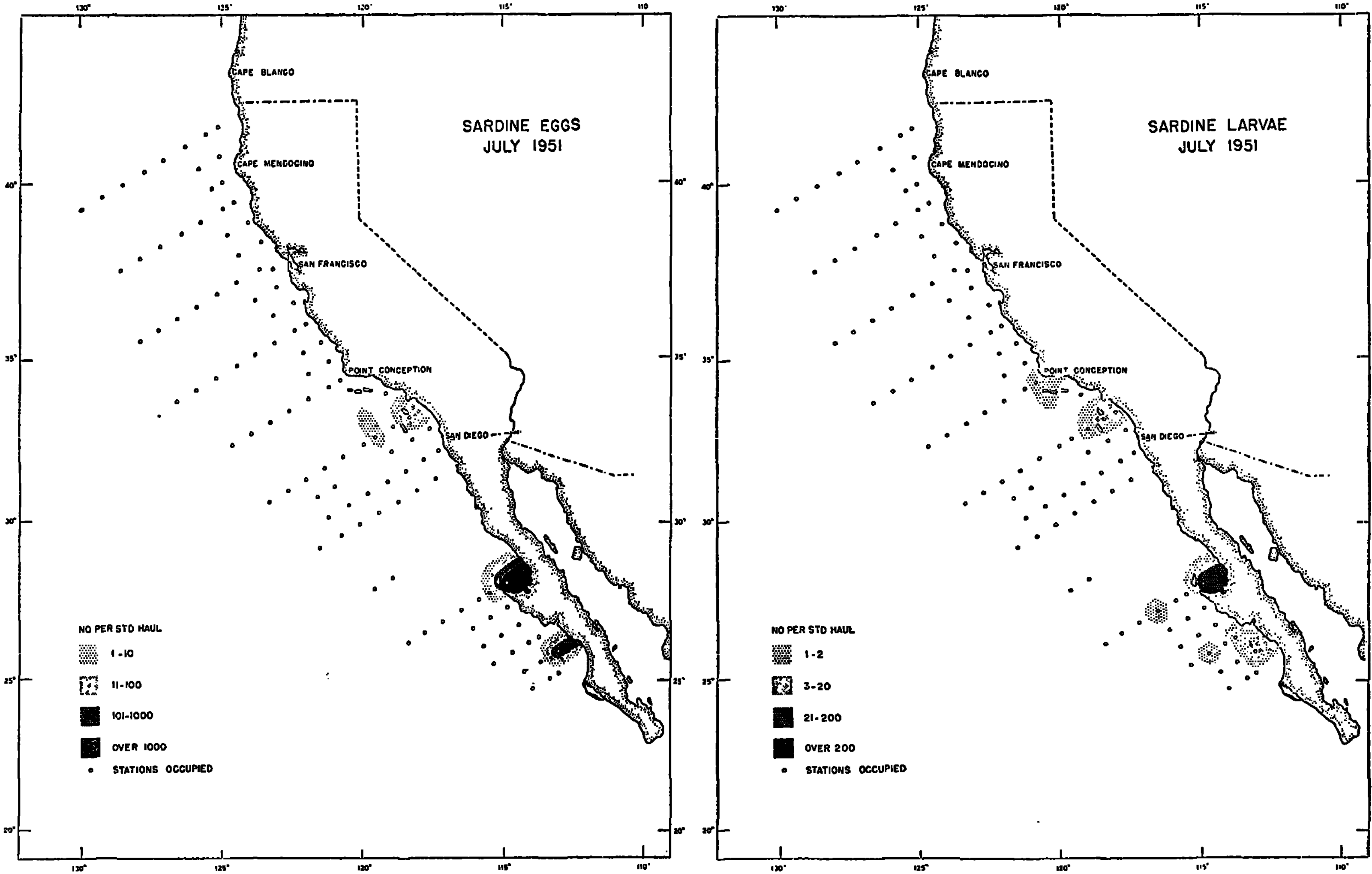

FIGURE 23.—Distribution and abundance of sardine eggs and larvae, July 1951.

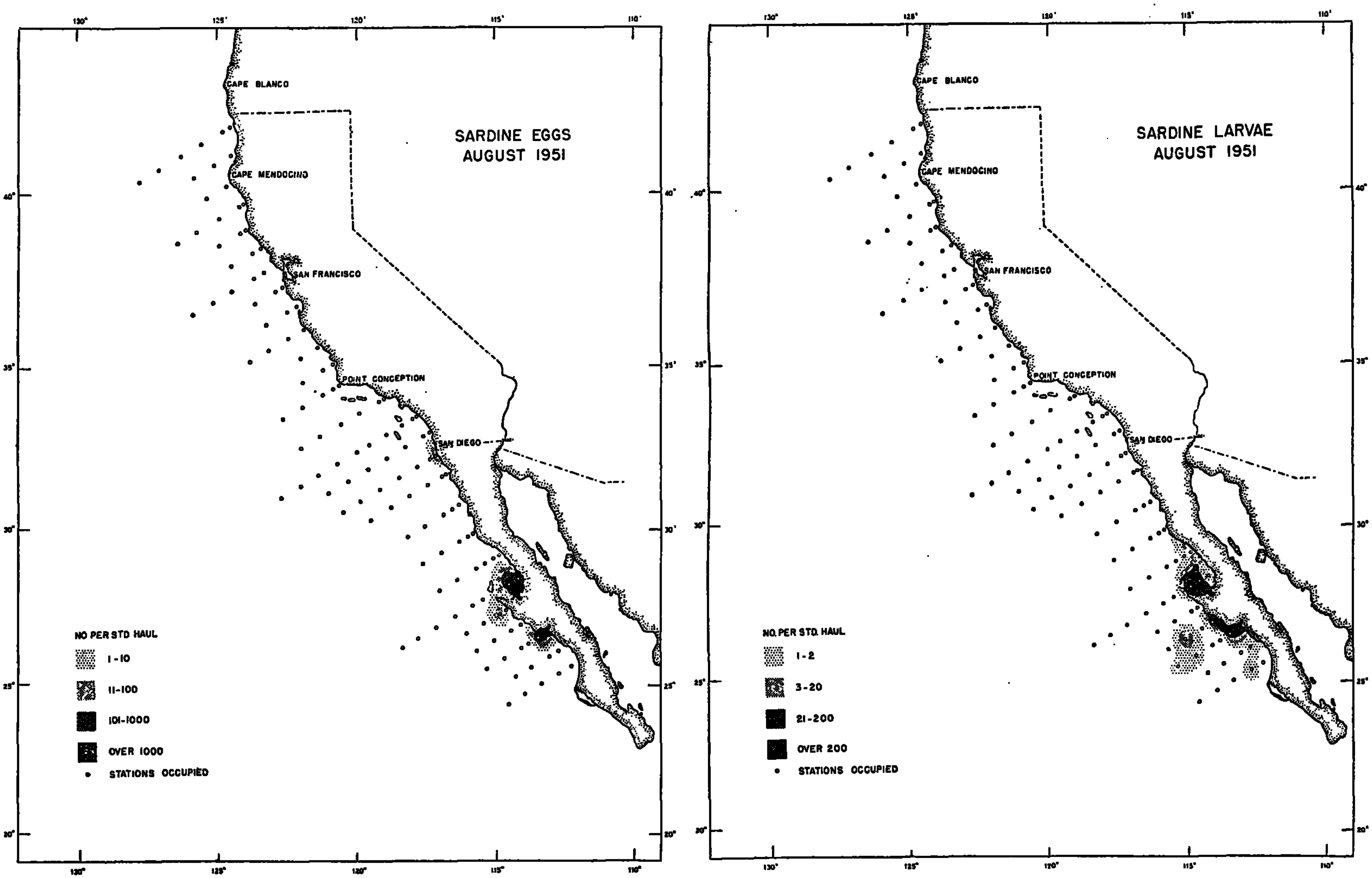

FIGURE 24.—Distribution and abundance of sardine eggs and larvae, August 1951.

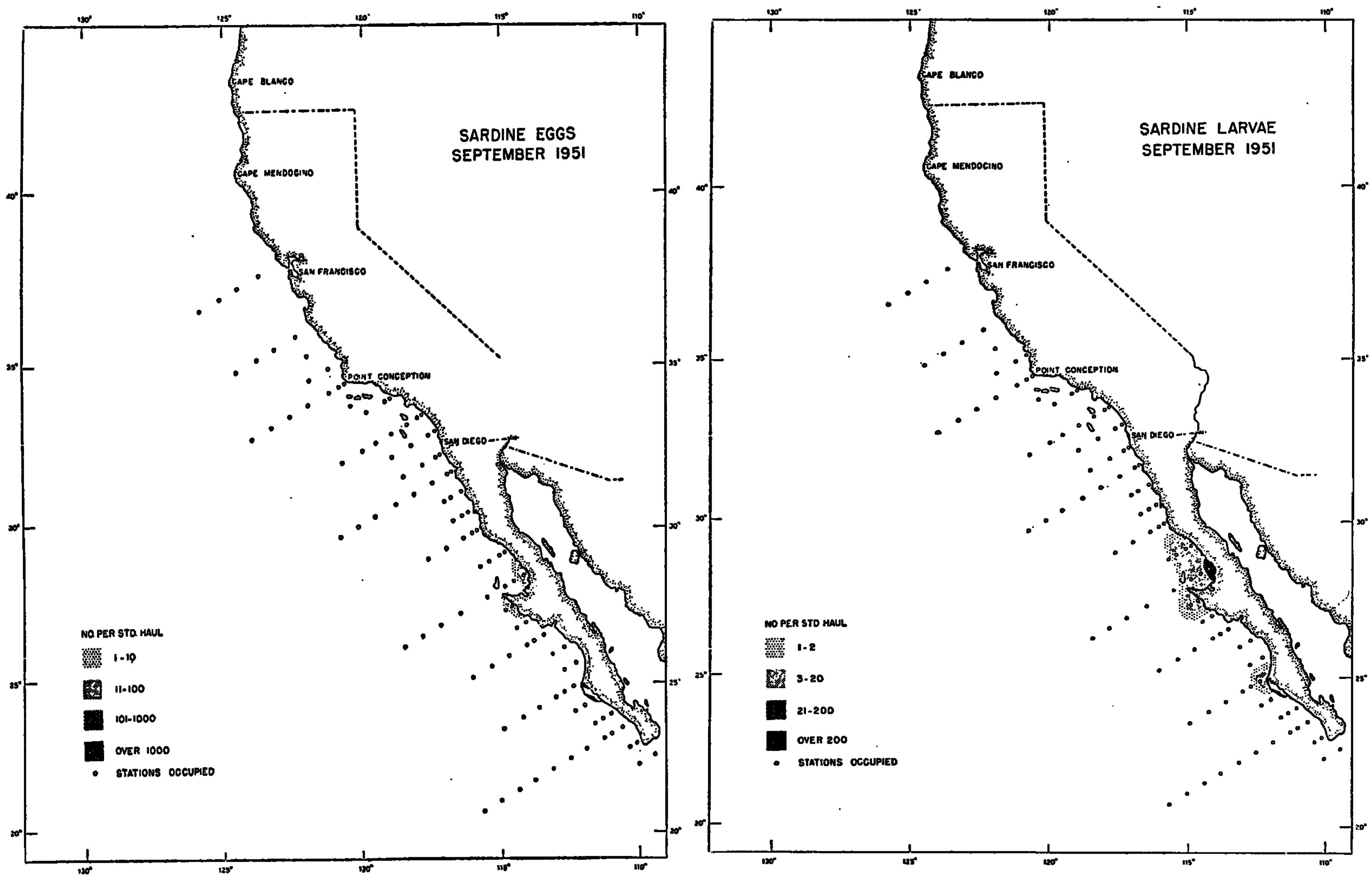

Figure 25.—Distribution and abundance of sardine eggs and larvae, September 1951.

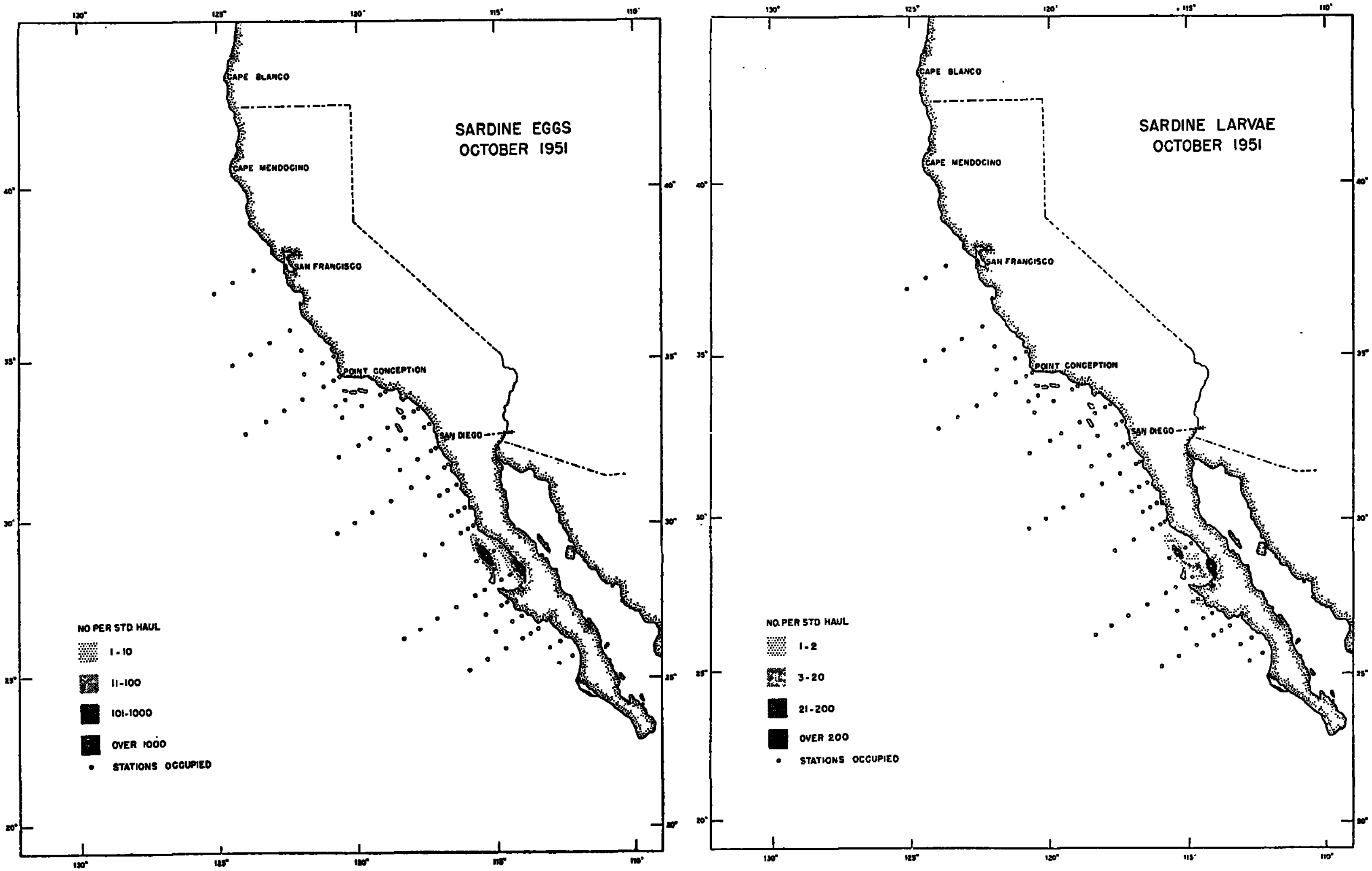

FIGURE 26.—Distribution and abundance of sardine eggs and larvae, October 1951.

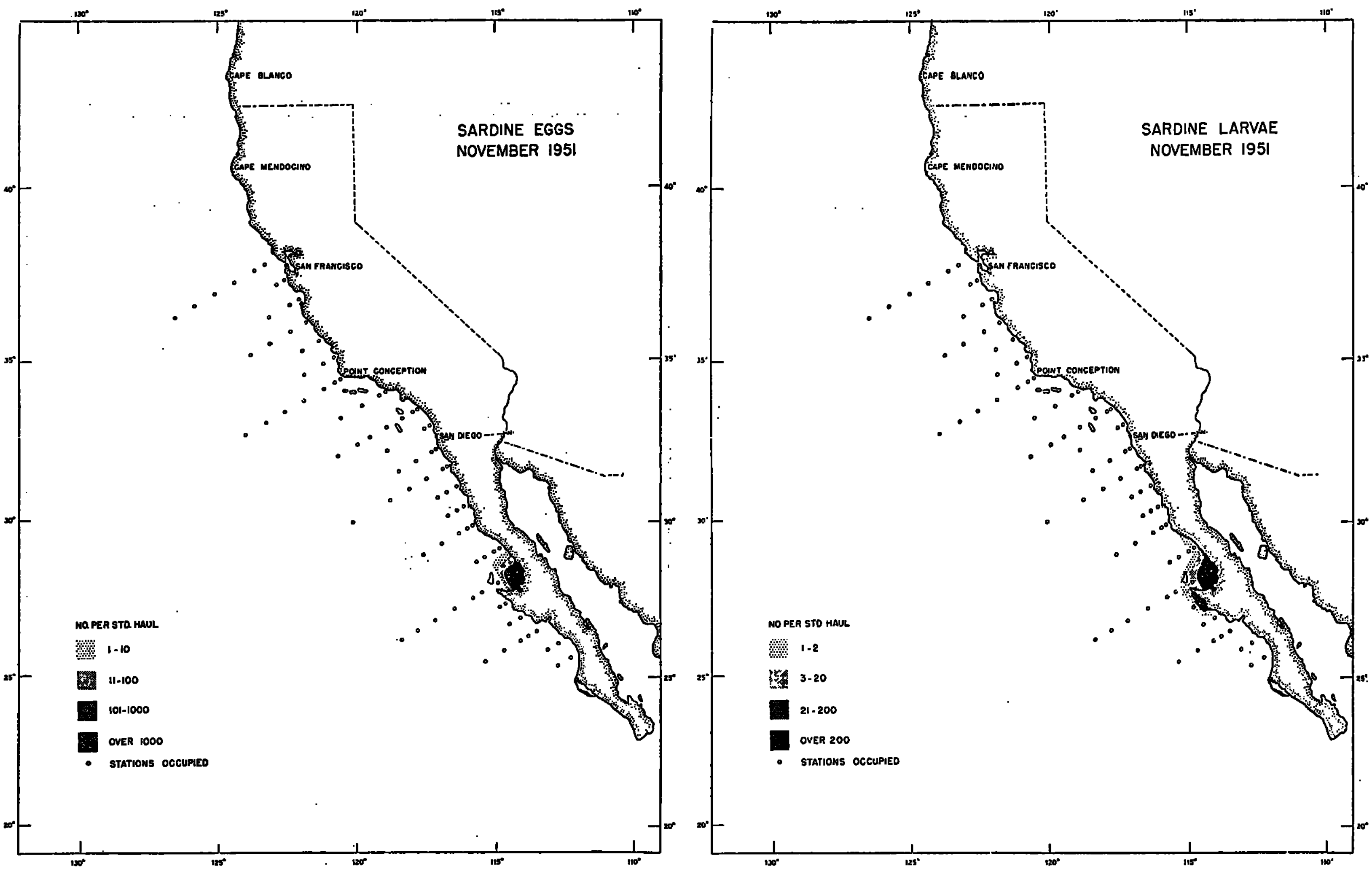

FIGURE 27.—Distribution and abundance of sardine eggs and larvae, November 1951.

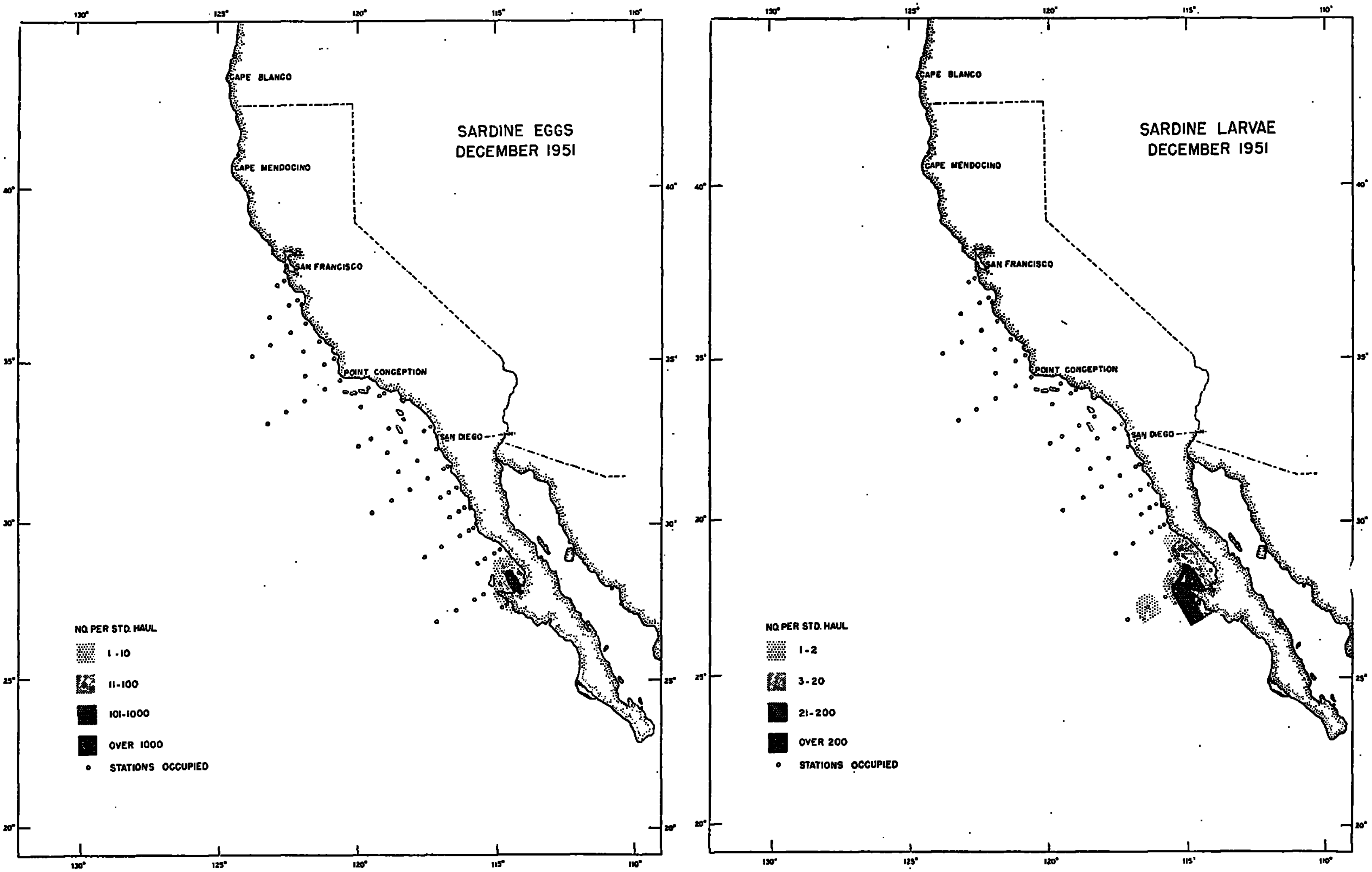

FIGURE 28.—Distribution and abundance of sardine eggs and larvae, December 1951.

plankton, as arrow worms, medusae, carnivorous copepods and ctenophores, to mention a few. Furthermore, it is at the mercy of its physical environment, since it is passively carried by currents.

As the larva develops, it becomes better able to cope with its environment. It can utilize a larger segment of the plankton as food and can move about in search of food. It develops the ability to escape predators. Furthermore, as it increases in size, the number of potential predators in the plankton community becomes fewer.

The validity of the theory that the survival of larvae during the planktonic period is critical in determining the success or failure of year classes can be tested, but it may require a number of years of investigation. If this theory is valid, there will be a correlation between good survival of larvae and successful year classes; between poor survival and poor year classes. But to test the theory, it is necessary that we measure the survival of larvae with sufficient accuracy, that we have a measure of the strength of each year class as adults, and that we obtain a range of survival rates of larvae from good to poor, or a range of year-class sizes from good to poor. If the theory is substantiated, it should be possible to predict year-class strength from survival data on larvae. Furthermore, if the relation between survival rate and environmental conditions can be established, a prediction may be possible from "skeletal" observations of critical factors in the environment. If, on the other hand, no correlation is found between larval survival and year-class strength, it must be concluded either that the aforementioned conditions cannot be satisfactorily fulfilled, or that the survival during the larval period is not critical as regards subsequent success or failure of year classes.[3]

SIZE OF LARVAE TAKEN IN PLANKTON HAULS

The sardine larva at time of hatching is about 3 mm. in length. It has a slender, threadlike form. The yolk is absorbed in 3 to 5 days, during which time the larva increases in length to about 4.5 mm. Most of the larvae taken in plankton hauls are between 3 and 24 mm. standard length, but occasionally larvae up to 30 mm. are taken.

PROBLEMS IN SAMPLING LARVAE

Quantitative sampling of sardine larvae presents a number of difficulties not involved in sampling sardine eggs. The eggs are large enough to be fully retained by the plankton nets, and are passive, so they cannot elude capture. A portion of the smaller-sized larvae, however, have been lost through the mesh openings of the several kinds of plankton nets employed, introducing a problem in net selectivity. The larger larvae have been markedly undersampled during daylight hours, posing a problem in daytime escapement.

Net selectivity.—The problem of net selectivity was first brought to our attention following the 1940 survey season, when it was discovered in analyzing the data that the smaller larvae were not being fully sampled by the plankton nets. The nets then routinely employed were constructed either of No. 24xxx silk grit gauze, or of a cotton scrim netting of similar mesh size. These materials had mesh openings about 0.9 to 1.0 mm. wide in new netting, shrinking to about 0.7 to 0.8 mm. wide after use. To obtain data on net selectivity, two nets having different mesh sizes were hauled side by side at most stations occupied during 1941. The finer-meshed net was constructed on No. 40xxx grit gauze, with openings 0.45 mm. wide in new netting, shrinking to about 0.3 mm. wide after use. It was found that the coarser-meshed nets retained most larvae about 9 mm. in length, but that their retention of smaller sizes might be as low as 7 percent. There is evidence that even the fine-meshed control nets did not retain all of the very small sardine larvae.

All nets employed since 1949 have been constructed of No. 30xxx silk grit gauze. The openings between threads in this grade of grit gauze measure about 0.70 mm. wide in new material, shrinking to about 0.55 mm. after use. The mesh openings are intermediate in size between those of the nets tested during 1941. The extent of the loss of larvae through the openings of this netting material has not been determined. Until the present analysis was made, the nets were considered sufficiently fine-meshed to retain most sizes of sardine larvae. However, from the slope of

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[3] The extent of the area over which sardine spawning takes place may have an important bearing on the success or failure of year classes of sardines. Good year classes may result from unusually widespread spawning, poor year classes from contracted spawning. If so, important data would be derived from the surveys, even though we might not be able to measure survival satisfactorily.

the survival curves for sardine larvae, obtained for both 1950 and 1951, it has been concluded that net selectivity must still be an important consideration. We plan to obtain more definite information on the extent of loss of smaller larvae through the mesh openings of No. 30xxx grit gauze. It should not be difficult to check on net selectivity. We plan to enclose a standard plankton net constructed of No. 30xxx grit gauze in a larger net constructed of mesh fine enough to retain all sizes of larvae. By this means it will be possible to determine the proportion of the larvae of each size category usually retained by standard gear.

Undersampling of sardine larvae in daylight hours.—Larger sardine larvae are markedly undersampled during daylight hours. This is obvious from a comparison of the numbers taken in day and in night hauls. To determine extent of the undersampling, a comparison was made, by size, of larvae taken in day and night hauls during 4 years of surveys, 1940, 1941, 1950, and 1951, excluding from the comparison only those taken at sunrise or sunset. (The time of sunrise or sunset for any given date and locality was determined from Tide Table, West Coast for the appropriate years.) A total of 626 hauls was used: 316 collected during the night, 310 during daylight hours. The results are shown in figure 29.

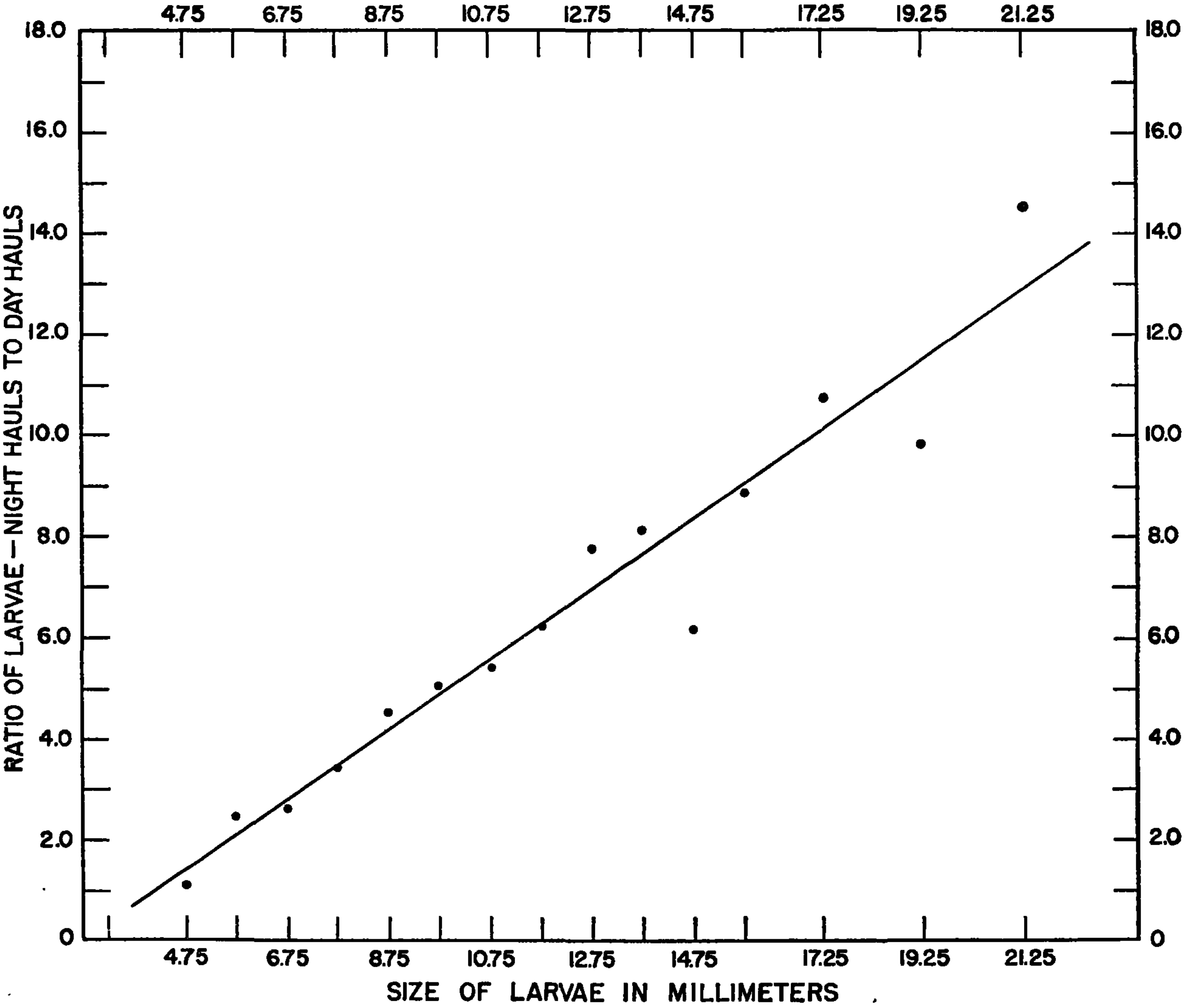

FIGURE 29.—Undersampling of sardine larvae in daylight hauls as compared with those in night hauls as a function of size. The linear-regression line was fitted by the method of least squares. Values for the line in the formula $y=a+bx$: $\bar{x}=12.05$, $\bar{y}=6.48$, $a=-1.9154$, $b=0.6971$, $s=0.957$.

The extent of undersampling of sardine larvae in the day hauls can be conveniently expressed as a ratio of the relative abundance of each size group in night hauls as compared to day hauls. This ratio for the two smallest size groups, 3.25 mm. (larvae 2.26 to 4.25 mm.) and 4.75 (larvae 4.26 to 5.25 mm.), was about equal: 1.35 for the smallest category, 1.15 for the 4.75 mm. group. The fact that the ratios are slightly greater than 1 probably is due to chance, as the smaller larvae have too feeble powers of locomotion to avoid the net. Larvae 5.75 mm. (5.26 to 6.25 mm.) were 2.5 times as abundant in night hauls as in day hauls. Thereafter the disparity became progressively greater with increase in larval size. Larvae 9.75 mm. in length (9.26 to 10.25 mm.) were five times as numerous in night hauls as in day hauls; larvae 15.75 mm. in length (15.26 to 16.25 mm.) were nearly nine times as numerous. Were no correction made for day escapement, the larger larvae would be underestimated by nearly one-half.

A part of the larger larvae may escape capture in hauls made during the night. If this happens, the estimates of abundance of larger larvae will always be minimal, and mortality would be overestimated; however, the percentage error should be reasonably constant from year to year.

Undersampling sardine larvae during daylight hours is probably due either to migration below the level routinely sampled by the net or to avoidance of the net. The weight of evidence favors the latter explanation. Very few sardine larvae have been taken deeper than 60 meters. For example, on the 1940 survey cruises, a 1-meter closing net was used below the upper net at a majority of the stations occupied. The approximate depth zone sampled by the closing net was between 125 and 55 meters. The average depth sampled by the upper net was between 73 meters and the surface. The upper net took sardine larvae at 109 of the stations where both nets were used, the closing net at only 5. In numbers taken (standardized for comparability), 5,900 larvae were taken in the upper-net hauls as compared with 38 in the closing-net hauls. The lower net took only two-thirds of 1 percent as many larvae as the upper net. This finding was reinforced by similar evidence obtained from other studies and was discussed in some detail by Silliman (1943) and Ahlstrom (1948).

The problem of day escapement is not unique for sardine larvae. To a greater or lesser degree it seems to apply to all clupeid larvae and many other pelagic-fish larvae. Russell (1926, 1928) called attention to a similar discrepancy in the number of pilchard, sprat, and herring larvae taken in day hauls as compared with those in night hauls. Marshall, Nicholls, and Orr (1937) found daylight sampling of herring larvae to be so inadequate that sampling was restricted to night collections. Furthermore, if the data given by Sette (1943) for Atlantic mackerel are analyzed for day versus night abundance, the difference in numbers taken in night hauls as compared with those in day hauls is even more marked for the larger sizes of mackerel than it is for the sardine.

LARVAL GROWTH RATE

Sette (1943) has summarized the available information on growth of fishes during the larval and postlarval periods. He concluded, after analyzing the data available for four species, Atlantic mackerel, haddock, Atlantic herring, and northern pike, that growth was logarithmic in character, having a uniform percental rate during the larval period except when there was a change in mode of living (such as yolk-sac absorption). He used length as an index of size because this information was available, although he believed that mass, or volume, would provide a more exact index. For the species that undergo little change in form during early life history, such as mackerel or haddock, he found that a simple logarithmic curve fitted their growth as indicated by length. On reexamining the data on growth of herring larvae in Marshall, Nicholls, and Orr (1937), Sette concluded that logarithmic curves with a change in slope at 30 days of age, or length of 19 mm., provided a better fit for the observation than the straight-line arithmetical relationship proposed by the original investigators. The herring larva, like the sardine, is slender, almost threadlike when young, growing stouter as development proceeds. As a result, length measurements overestimate growth in bulk during the early larval period and underestimate it later. The change in slope at 19 mm. suggests that after this length the herring increases more rapidly in mass than in length.

Because of the similarity in the form of sardine and herring larvae, growth of the sardine probably follows a pattern similar to the Atlantic herring's. It is likely that the growth of the sardine larva will be found to be logarithmic. Whether growth (based on length as an index of size) over the length range in which we are particularly interested, i.e., larvae between 2.5 and 24 mm. in length, can be expressed by a simple logarithmic curve without a change in slope or will require a more complex expression, can be determined only when sufficient data are at hand. For the present, I am assuming that the growth of sardine larvae can be represented by a simple logarithmic curve.

The growth rate of sardine larvae cannot be determined adequately from present survey data. Duration of the embryonic period, which can be determined with a fair degree of accuracy, has been found to average about 3 days, but it can be as short as 1 day or as long as 5 days, depending on the temperature at which development has taken place. For example, sardine eggs developing at 12.6° C. require approximately 4 days from fertilization to hatching, while eggs developing at 18° C. require only 2 days. Our information on the length of time needed to complete the yolk-sac stage is not as precise as for the embryonic period. Living larvae have been observed to absorb the yolk sac completely in 3 to 5 days. Although the relation to temperature has not been determined, 3½ days is probably a fair estimate of the average duration of the yolk-sac stage. Hence, a sardine larva developing under average conditions would be about 6.5 days old at the time it completed the yolk-sac stage, and would measure about 4.5 to 5 mm. in length (the range of this size class is 4.26 to 5.25 mm.).

From an inspection of seasonal curves of abundance of sardine larvae, grouped by size categories, it appears that between 1 and 2 months are required for a sardine to develop to 24 mm. length ("zero" age at fertilization). Two series of seasonal curves of larval abundance are illustrated in figure 30. One of the series is based on collections made off southern California during 1941 (data from Ahlstrom 1948), the other from collections obtained from the central Baja California spawning center during 1951. In both, the season of maximum abundance of larvae of 19.25-mm. size class is not more than a month later than the season of maximum abundance of larvae of the 5.25-mm. group. It is interesting to note that the peaks of abundance during 1941 off southern California occurred slightly earlier in the year than corresponding peaks off central Baja California during 1951.

The seasonal curve of egg abundance in the 1951 series appears to be out of phase with the curves of larval abundance for that year. The peak month for egg abundance in 1951 was March, a month earlier than in 1950. The seasonal curves of larval abundance are similar for the 2 years in the central Baja California area, however, with the peak month for most stages occurring in May.

Only a rough estimate of the growth rate of sardine larvae can be obtained from the foregoing and similar series.[4] It is difficult to refine further the rough estimate of between 1 and 2 months as the time required to complete the planktonic phase of the life history. Until more exact data are available I feel justified in using the midpoint of this estimate, 45 days, as an approximation of the average age of a sardine larva 24 mm. in length. Inasmuch as the embryonic and yolk-sac stages would take approximately 6.5 days, 38.5 days would be left for a larva to grow from 4.5 to 24 mm. in length. Assuming that the growth is logarithmic, the logarithm of the increase per day would be a constant 0.01916.

The duration of each size category can be computed from the following formula, modified from that given by Sette (1943: 179):

$$\text{Duration of size category (in days)} = \frac{\log 1'' - \log 1'}{0.01916}$$

in which 1′ is the lower boundary of the size-class interval in millimeters and 1″ is the upper boundary.

Determination of the average age of the larvae in each size category can be computed from the formula:

$$\text{Age (in days)} = 6.50 + \frac{\log 1'' - \log 1'}{0.01916}$$

where 1″ is the midvalue of the size-class interval and 1′ is 4.26 mm., the lower boundary of the first larval size category following yolk-sac absorption. Values for the duration of all size classes routinely used in tabulations of sardine larvae are given in table 11. The estimate of duration of the

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[4] One of the chief limitations on the use of survey data for determining growth rate of sardine larvae arises from infrequency of sampling. Cruises are spaced at monthly intervals. With such wide spacing in time, it is nearly impossible to follow homologous modes from cruise to cruise.

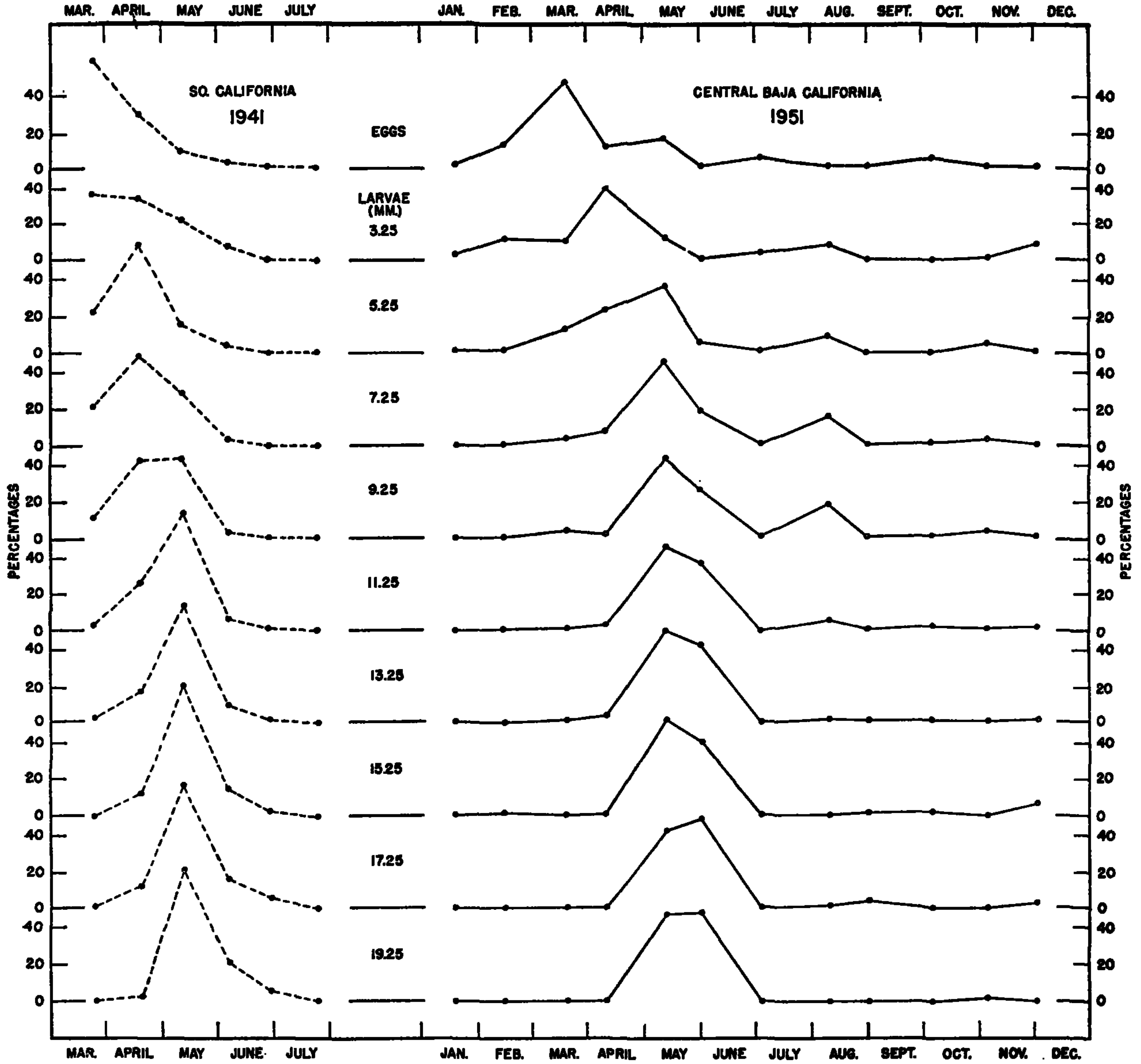

Figure 30.—Two series of diagrams illustrating season of maximum occurrence of sardine eggs and of nine stages of sardine larvae (grouped by 2-mm. intervals). The series on the left is based on collections made off southern California during 1941, that on the right on material collected off central Baja California during 1951. In the 10 separate diagrams comprising each series, the vertical scale represents the percentage of the season's total for the category that was taken on each cruise; the horizontal axis indicates the distributions of the observations in time.

smallest size class of larvae, 4.26 to 5.25 mm. in length, is 4.75 days, while it is estimated that less than 1 day would be required for a larva to grow from 23.26 to 24.25 mm. in length.[5] Also included in this table are estimates of the age in days to the midpoint of each size class. As indicated previously, these determinations are rough approximations. Since age estimates are essential in determinations of the abundance of size categories of larvae, I believe that the best present estimates should be used, even though they might introduce errors of as much as 25 percent.

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[5] Obviously, this accelerated growth cannot continue indefinitely. There probably is a change in rate before the larva reaches 24 mm. in length. However, more exact data are needed before this can be determined.

TABLE 11.—*Survival of young stages of sardine, 1950 and 1951*

Category	Size range	Duration	Average age	1950		1951	
				Estimated abundance	Survival per 100,000 eggs	Estimated abundance	Survival per 100,000 eggs
	Mm.	*Days*	*Days*	*Billions*		*Billions*	
Egg	----------	3.0	1.5	285,676	----------	610,847	----------
Yolk-sac larvae	2.26–4.25	3.5	4.8	11,850	4,148	12,083	1,978
Larvae 4.75 mm	4.26–5.25	4.8	8.9	10,778	3,772	9,327	1,527
Larvae 5.75 mm	5.26–6.25	3.9	13.2	5,590	1,957	7,153	1,171
Larvae 6.75 mm	6.26–7.25	3.3	16.8	6,197	2,169	6,852	1,122
Larvae 7.75 mm	7.26–8.25	2.9	20.0	5,931	2,076	7,979	1,306
Larvae 8.75 mm	8.26–9.25	2.6	22.7	4,834	1,692	6,233	1,020
Larvae 9.75 mm	9.26–10.25	2.3	25.1	3,738	1,308	7,015	1,148
Larvae 10.75 mm	10.26–11.25	2.1	27.3	2,880	1,008	5,938	972
Larvae 11.75 mm	11.26–12.25	1.9	29.3	1,942	680	6,152	1,007
Larvae 12.75 mm	12.26–13.25	1.8	31.2	2,214	775	4,600	753
Larvae 13.75 mm	13.26–14.25	1.6	32.8	1,701	595	4,281	701
Larvae 14.75 mm	14.26–15.25	1.5	34.4	1,198	419	4,676	765
Larvae 15.75 mm	15.26–16.25	1.4	35.9	1,046	366	1,509	247
Larvae 17.25 mm	16.26–18.25	2.6	37.9	750	262	1,128	185
Larvae 19.25 mm	18.26–20.25	2.4	40.4	337	118	550	90
Larvae 21.25 mm	20.26–22.25	2.1	42.6	253	88	688	113
Larvae 23.25 mm	22.26–24.25	1.9	44.7	18	6	354	58

DETERMINING ABUNDANCE OF LARVAE

The simplest kind of estimate of abundance is based on total numbers of larvae. This type of estimate can be made even when the size composition of the samples of larvae has not been determined. Except for certain limited uses, as in comparisons of the relative abundance of larvae of different species in the survey area, such an estimate has little value. It cannot be used in determinations of larval survival, for these require a knowledge of the size composition of the larval population. Furthermore, unless size measurements were recorded it would be impossible to make necessary adjustments for day escapement, for net selectivity, or for differences in growth rate.

Another complicating factor is that homologous groups of larvae may be sampled on two or more cruises, depending on frequency of sampling and rate of growth. If larvae require approximately a month and a half to grow from 2.5 to 24 mm. in length and cruises are spaced at monthly intervals, approximately one-half of the larvae would be sampled on two successive cruises, one-half would be sampled on one cruise only. If cruises are spaced at weekly intervals, however, homologous groups of larvae would be sampled on a minimum of five successive cruises. Sampling the same population of larvae at several stages during the larval period, although desirable from the standpoint of mortality determinations, must be taken into account in determinations of abundance. This is difficult to do in determinations of abundance based on total numbers of larvae, but the problem would cease to exist if determinations of abundance were based on sufficiently fine size groupings of larvae. The requirement that would have to be met is that the growth period from the lower to the upper limit of size categories should not exceed the time interval between successive cruises.

Sardine larvae have been grouped into a number of size categories, usually by 1-mm. intervals. Estimates can be obtained of the magnitude of the sardine population at each of these different stages of the larval period. Adjustments can be made for the time duration of each category (length of time required to grow from the lower limit to the upper limit of the category), for day escapement, and for net selectivity, all of which are different for each size category. The numbers of larvae can then be integrated over space and time to obtain an estimate of abundance of the larval population at any given size. By comparing the abundance of the different size categories, an estimate can be obtained of the survival rate.

To determine the abundance of larvae of a given size category during a cruise, the following procedure was followed:

1. The standardized number of larvae of the size category taken at each station was divided by d_c, the estimated duration of the size category in days.

2. The samples were then divided into two groups, those collected by day and those obtained at night. The day hauls were adjusted for daytime escapement.

3. The adjusted number of larvae of the size category taken at each station was integrated over area and time in the manner already described for eggs.
4. The cruise total was obtained by summing the values for the individual stations.

Estimates of the several cruises were added together to obtain an estimate of the abundance of the size category for the year. The estimated abundance of larvae in all size categories from 3.25 to 23.25 mm. during 1950 and 1951 is given in tables 11, 12, and 13.

TABLE 12.—*Abundance of sardine larvae, by month and area, 1950*

[In billions]

Month and area	Size in millimeters																		Disintegrated[1]	Total
	3.25	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	17.25	19.25	21.25	23.25	27.25		
Area north of Point Conception:																				
June	29	52	24	0	0	0	0	200	0	0	0	0	0	0	0	0	0	0	0	305
July	12	0	0	10	0	13	14	0	0	149	0	19	407	248	0	0	0	0	0	872
August	0	8	10	6	34	0	0	10	0	0	0	0	0	0	0	0	0	18	0	86
Total	41	60	34	16	34	13	14	210	0	149	0	19	407	248	0	0	0	18	0	1,263
Southern California area:																				
March	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
April	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	1,039	452	52	8	15	0	0	0	0	0	0	0	0	0	0	0	0	0	29	1,595
June	567	395	715	684	883	717	797	418	549	946	551	388	0	94	68	0	0	0	30	7,802
July	0	0	0	0	0	0	0	0	0	0	15	0	17	25	55	148	0	0	0	260
Total	1,606	849	767	692	898	717	797	418	549	946	566	388	17	119	123	148	0	0	59	9,659
Northern Baja California area:																				
April	186	281	53	13	0	9	0	0	0	0	27	0	0	0	0	0	0	0	0	569
May	612	1,133	762	567	442	657	520	506	227	483	128	159	364	163	31	53	0	0	32	6,839
June	58	237	441	895	763	1,151	136	264	109	55	40	22	0	16	4	15	0	0	0	4,206
July	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
Total	856	1,679	1,256	1,475	1,205	1,817	656	770	336	538	195	181	364	179	35	68	0	0	32	11,642
Central Baja California area:																				
February	246	673	112	312	332	170	292	112	41	0	17	15	0	0	0	0	0	0	22	2,344
March	368	707	259	170	165	131	202	163	58	67	37	11	0	0	0	0	0	0	144	2,482
April	2,466	4,246	1,585	1,182	1,162	543	838	517	550	171	474	488	0	0	14	0	0	0	204	14,440
May	6,183	2,522	1,541	2,337	2,115	1,431	939	678	389	312	379	96	258	189	82	37	0	0	163	19,651
June	6	17	6	13	0	0	0	0	13	0	15	0	0	6	73	0	0	0	0	149
July	14	25	30	0	20	12	0	0	0	17	18	0	0	9	10	0	0	0	0	155
August	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
September	64	0	0	0	0	0	0	12	6	14	0	0	0	0	0	0	0	0	0	96
Total	9,347	8,190	3,533	4,014	3,794	2,287	2,271	1,482	1,057	581	940	610	258	204	179	37	0	0	533	39,317
Aggregate, all areas:																				
February	246	673	112	312	332	170	292	112	41	0	17	15	0	0	0	0	0	0	22	2,344
March	368	709	259	170	165	131	202	163	58	67	37	11	0	0	0	0	0	0	144	2,484
April	2,652	4,527	1,638	1,195	1,162	552	838	517	550	171	501	488	0	0	14	0	0	0	204	15.009
May	7,834	4,107	2,355	2,912	2,572	2,088	1,459	1,184	616	795	507	255	622	352	113	90	0	0	224	28,085
June	660	701	1,186	1,592	1,646	1,868	933	882	671	1,001	606	410	0	116	145	15	0	0	30	12,462
July	26	53	30	10	20	25	14	0	0	166	33	19	424	282	65	148	0	0	0	1,315
August	0	8	10	6	34	0	0	10	0	0	0	0	0	0	0	0	0	18	0	86
September	64	0	0	0	0	0	0	12	6	14	0	0	0	0	0	0	0	0	0	96
Grand total	11,850	10,778	5,590	6,197	5,931	4,834	3,738	2,880	1,942	2,214	1,701	1,198	1,046	750	337	253	0	18	624	61,881

[1] In too poor condition to be measured.

How adequate are these abundance determinations? It should be noted that no adjustment has been made for net selectivity. As a result, the abundance of the smaller-sized groups is underestimated by an undetermined amount.

The 1950 estimates of larger-sized sardine larvae are probably too low, because of incomplete coverage of the distributional range of the larvae off central Baja California. The lowermost line occupied routinely during 1950 was off Point Abreojos. Although very few sardine eggs have been taken south of this point, during the 1951 and 1952 surveys a considerable proportion of the larvae had drifted to the south of this area. During 1951, for example, only 0.66 percent of the eggs and 0.65 percent of the larvae 2.5 to 5 mm. in length taken off central Baja California occurred to the south of Point Abreojos (lines 133 and 137). But 6 percent of the larvae 5.5 to 10 mm. in length, over 39 percent of the larvae 10.5 to 15 mm. in

TABLE 13.—*Abundance of sardine larvae, by month and area, 1951*

[In billions]

Month and area	Size in millimeters																		Disintegrated [1]	Total
	3.25	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	17.25	19.25	21.25	23.25	27.25		
Area north of Point Conception: June	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	0	48
Southern California area:																				
February	16	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29
March	0	6	0	0	6	0	0	0	0	0	0	0	0	6	0	0	0	0	0	18
April	8	100	146	16	158	126	66	43	0	0	0	147	0	0	13	0	0	0	0	823
May	62	98	42	41	0	80	0	0	0	0	19	0	0	0	0	0	0	0	0	342
June	96	39	0	6	25	0	0	0	0	0	419	0	0	51	12	13	0	0	0	661
July	14	15	12	14	16	37	0	0	0	0	23	0	0	0	0	0	0	0	0	131
Total	196	271	200	77	205	243	66	43	0	0	461	147	0	57	25	13	0	0	0	2,004
Northern Baja California area:																				
February	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
March	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
April	140	162	47	8	0	11	0	89	16	17	0	21	230	0	0	0	0	0	0	741
May	944	684	188	331	115	54	92	53	150	10	22	24	38	21	8	0	0	0	0	2,734
June	103	165	230	76	74	0	63	0	10	0	0	164	0	0	158	181	15	0	0	1,239
Total	1,187	1,024	465	424	189	65	155	142	176	27	22	209	268	21	166	181	15	0	0	4,736
Central Baja California area:																				
January	270	89	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	400
February	1,281	98	44	0	23	29	0	16	35	0	0	24	0	0	0	9	0	0	0	1,559
March	1,131	959	716	157	249	273	256	189	106	347	0	0	0	0	0	0	0	0	0	4,383
April	4,152	2,350	1,239	635	511	225	264	138	697	371	173	21	0	0	0	0	0	0	0	10,776
May	1,300	3,051	2,476	3,734	4,481	3,168	4,136	3,673	2,839	2,373	2,553	2,865	835	559	298	15	0	0	0	38,356
June	6	144	447	507	1,017	1,033	824	920	1,272	1,055	896	731	320	334	61	452	119	34	296	10,468
July	419	276	76	50	139	78	63	0	0	0	0	0	0	0	0	0	0	0	0	1,101
August	870	458	832	771	759	788	528	294	162	54	20	0	0	15	0	0	0	0	0	5,551
September	50	12	41	38	26	23	9	26	0	25	0	0	15	21	0	0	0	0	0	286
October	7	19	43	55	44	7	375	379	708	279	12	197	0	0	0	18	48	0	0	2,191
November	249	396	357	233	245	287	233	62	17	3	8	0	0	81	0	0	0	0	0	2,171
December	930	140	92	38	73	14	32	7	113	8	27	128	35	19	0	0	0	0	0	1,656
Total	10,665	7,992	6,404	6,218	7,567	5,925	6,720	5,704	5,949	4,515	3,689	3,966	1,205	1,029	359	494	167	34	296	78,898
Southern Baja California area:																				
April	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	15
June	25	29	64	133	18	0	74	49	27	58	94	354	36	21	0	0	172	0	0	1,154
September	10	11	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
Total	35	40	84	133	18	0	74	49	27	58	109	354	36	21	0	0	172	0	0	1,210
Grand total	12,083	9,327	7,153	6,852	7,979	6,233	7,015	5,938	6,152	4,600	4,281	4,676	1,509	1,128	550	688	354	82	296	86,896

[1] In too poor condition to be measured.

length, and about 53 percent of the larvae 15.5 mm. and over were taken to the south of Point Abreojos.

There is good reason to assume that an even larger proportion of the larvae would have occurred to the south of Point Abreojos in 1950 than in 1951. More spawning occurred in the southern part of the area that year, as is shown by the following tabulation, summarizing the percent of spawning in the central Baja California center taken on different station lines.

	1950	1951
	Percent	*Percent*
Lines 110–117	3.6	8.0
Line 120	28.2	36.4
Line 123	33.7	46.9
Line 127	.4	6.8
Line 130	34.1	1.2
Line 133	--------	.7
Line 137	--------	0
Total	100.0	100.0

A third of the spawning occurred off Point Abreojos in 1950, and we can assume that nearly all of the larvae from this spawning would have drifted to the south of the area being sampled. Hence, at the very least, the abundance of larvae off central Baja California would have been underestimated by one-third; also, many of the larvae resulting from spawning off Point San Eugenio would have drifted south of the area. In 1951, when spawning was centered off Point San Eugenio, more than 50 percent of the larvae over 15.5 mm. in length were collected to the south of Point Abreojos. For these sizes of larvae the underestimation of their abundance may be as much as two-thirds.

The rate of drift in this area can be shown from a special study made during late April 1952. It was determined by following a buoy fitted with a drag at a depth of 10 meters, that this water mass moved southward in the area between Point San Eugenio and Point Abreojos at the rate of about 15 miles a day. This study was made during a period of heavy sardine spawning. Even though the water mass would be moving more slowly at the levels where most of the sardine larvae occur, still the larvae would be transported southward at a fairly rapid rate.

Other lines of evidence tend to support the foregoing conclusions relative to this southward drift. The two major spawning centers contributed the following percentages of eggs and larvae in 1950 and 1951:

	1950		1951	
	Southern California and adjacent Baja California	Central Baja California	Southern California and adjacent Baja California	Central Baja California
	Percent	*Percent*	*Percent*	*Percent*
Eggs	17.3	82.7	5.6	94.4
Larvae to 5.0 mm	22.4	77.6	13.3	86.7
Larvae 5.5 to 10.0 mm	37.1	62.9	6.8	93.2
Larvae 10.5 to 15.0 mm	49.9	51.1	3.7	96.3
Larvae 15.5 mm. and larger	66.8	33.2	10.4	89.6

About one-half of the larvae 10.5 to 15 mm. in length, and two-thirds of the larvae 15.5 mm. and larger were taken in the northern spawning center, despite the fact that less than one-fifth of the spawning occurred in this area during 1950. The following explanations could account for this: (1) Markedly better survival in the northern spawning center in 1950 as compared with the southern center, (2) undersampling of the larvae in the southern center, or (3) a combination of both. In view of the evidence previously presented, there is little doubt that much of the discrepancy in regard to abundance of older larvae in the northern and southern spawnings centers in 1950 must have resulted from the southward drift of larvae out of the survey area off central Baja California.

DETERMINING LARVAL SURVIVAL

The initial strength of a year class is dependent on the amount of spawning; its subsequent strength, on survival after spawning. In actual numbers of individuals, a year class at its inception is many times as large as the total adult population. If an average-sized adult female sardine spawned 100,000 eggs per year,[6] and if the sexes were equally divided, a year class at the embryonic, or egg, stage would be 5×10^4 times as abundant as the total adult population. Consequently, the history of each year class is one of rapid decrease in numbers.

Much of the decline in abundance occurs during the first month or two of life. This can be shown graphically by plotting the estimated abundance of a year class at various stages during its planktonic existence (fig. 31). The decline is quite precipitous, so instead of plotting actual numbers, logarithms of the estimated abundance at each stage are used. The stages are based on size (standard length) groupings, for each of which an approximation of the average age (in days) has been derived (*cf.* table 11).

The plots of population abundance during the early history of the 1950 and 1951 year classes (fig. 31) are, in effect, survival curves. The actual survival rate is better shown in a somewhat different diagram, as illustrated in figure 32. I am calling the latter diagram a survival curve, the former (shown in fig. 31) a graph of population abundance. The survival curves are based on the estimated survival per 100,000 eggs spawned, and the data used in constructing them for 1950 and 1951 are summarized in table 11. Survival to 21.25 mm. was about 1 in 1,000 in both 1950 and 1951.

The survival curves for 1950 and 1951 are fairly similar—in both there is an abrupt decline between egg and yolk-sac stages. This may be a real decline due to very high mortality during the critical period immediately following yolk-sac absorption, or it may be an artifact resulting from net selectivity (loss of larvae through the apertures of the nets used). I favor the latter explanation. The survival curve for 1951 levels off in the section based on larvae between 5.75 to 11.75 mm. in length.[7] This means, interpreted literally, that mortality during this period of life was negligible, after having been precipitous im-

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[6] This estimate is based on the data presented by Clark (1934). She estimated that the Pacific sardine would spawn from 30,000 to 65,000 eggs in a batch, depending on the size of the fish, and as many as three batches a season.

[7] The survival curve for 1941 (southern California area) is nearly flat for the section based on larvae between 6.75 to 12.75 mm. in length.

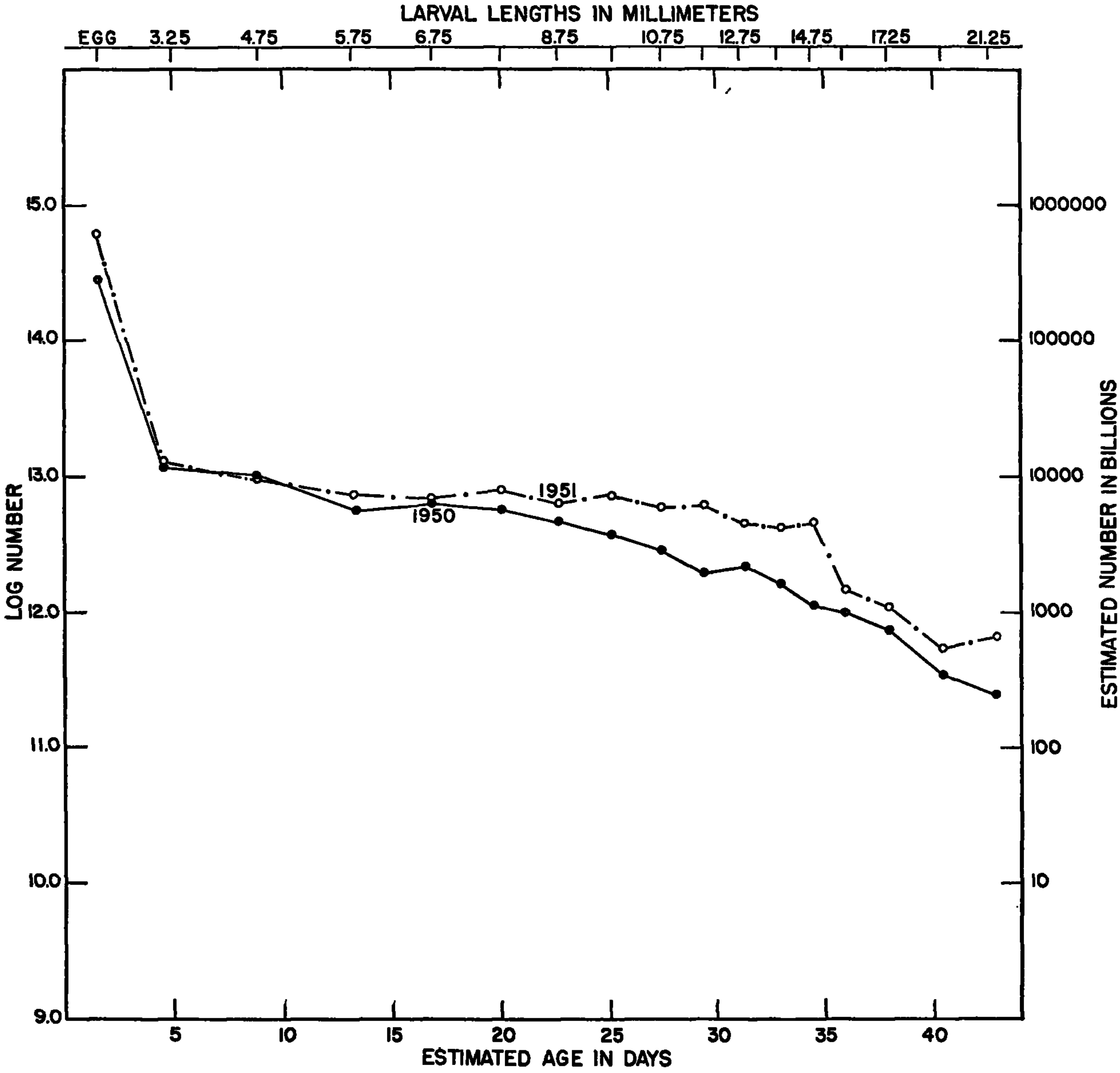

FIGURE 31.—Curves of population abundance during the planktonic phase of 1950 and 1951 year classes.

mediately following hatching. This does not seem reasonable. Net selectivity, severest on newly hatched larvae and becoming progressively less severe with increase in larval size, could produce the flat section of the curve. If the latter interpretation is correct, selectivity of standard nets is considerable. The extent of such loss will be determined and taken into account in future work.

The terminal slopes in the survival curves are probably the result of larvae dodging the nets, rather than of an increase in mortality in larvae of 15.75 mm. and larger. The decline would be even more precipitous if the curves had been extended to include the few larvae larger than 21.25 mm. taken each season.

A survival curve is no more reliable than the data on which it is based, and I have already indicated some of the limitations of the 1950 data. The larger sizes are probably underestimated by as much as 50 percent, due to the inadequacy of our "southern" coverage in 1950. The collections of 1951 appear to have covered the distributional

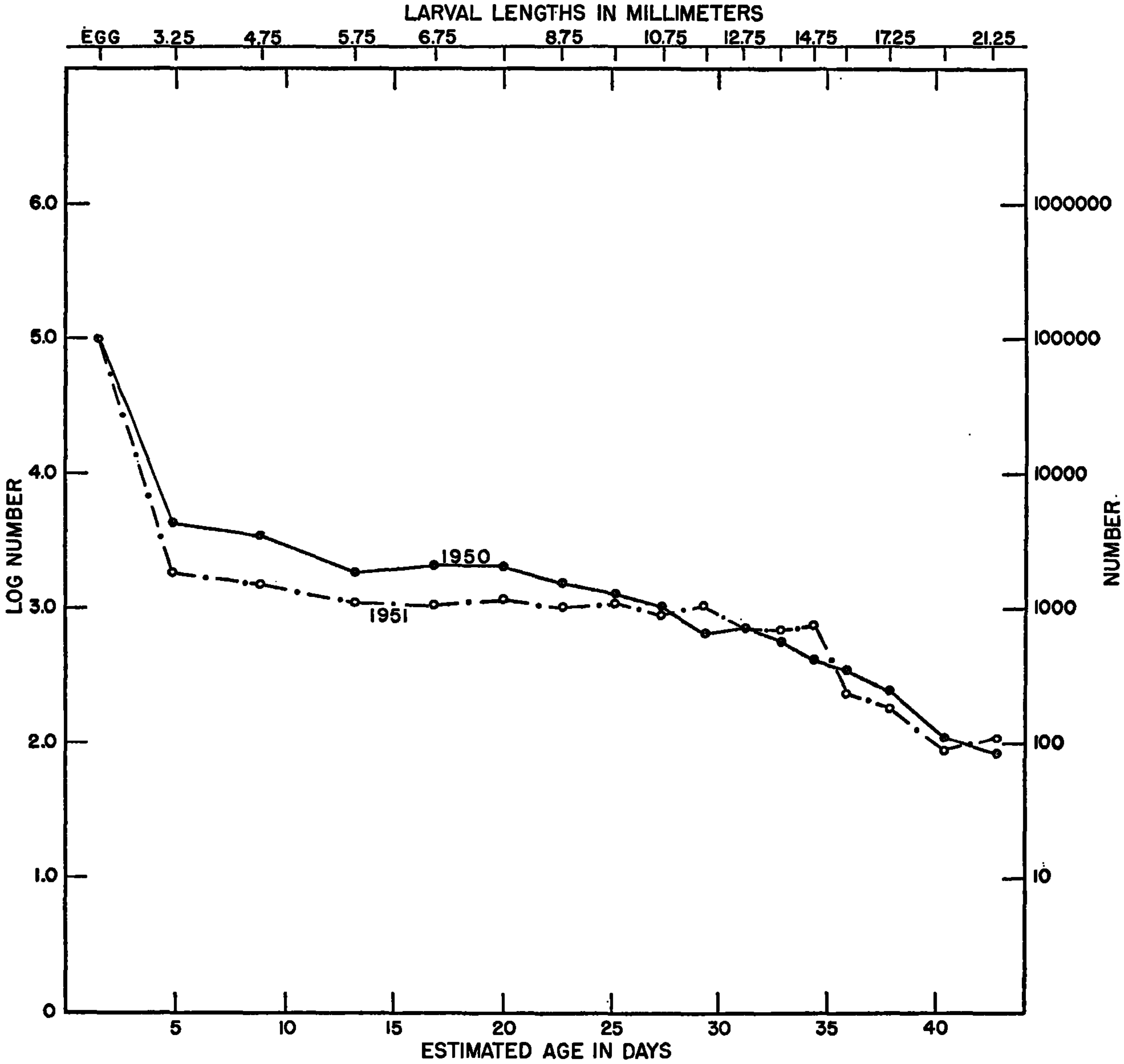

FIGURE 32.—Survival of young stages of sardines per 100,000 eggs spawned during 1950 and 1951.

range of the larvae adequately, and the 1951 estimates are probably as reliable as can be obtained with present methods of sampling.

SUMMARY

1. Distribution and abundance of egg and larval populations of the Pacific sardine, or pilchard, are being determined by means of quantitative plankton hauls taken at regular intervals over an extensive grid of stations off California and Baja California. The results of 3 years of surveys, 1949 through 1951, are presented.

2. Distribution of sardine eggs affords, at present, the only reliable information on the distribution of the sardine spawning stock during the spawning season. An estimate of the total number of eggs spawned during a year is one of the values needed in determining the survival rate of larvae. When used in conjunction with data on fecundity, an estimate of egg abundance can be

translated into an estimate of the size of the spawning stock.

3. The method followed in estimating the total abundance of sardine eggs is similar to that described by Sette and Ahlstrom (1948). The number of eggs taken in any given haul has been made comparable with other samples by referring all collections to a common basis, the number of eggs under a standard area of 10 square meters, and by determining for each sample the average number of sardine eggs spawned per day. The data from each cruise have been treated as a problem of integration over space, the combining of the monthly cruises as a problem of integration on time.

4. Estimates of the number of sardine eggs spawned during 1950 and 1951 were 286×10^{12} and 611×10^{12}, respectively.

5. There are, at present, two major areas of sardine spawning, a compact area of intense spawning off central Baja California, and a larger area of diffuse spawning off southern California and adjacent Baja California. In 1950, approximately 82 percent of sardine spawning occurred off central Baja California, 17 percent in the area off southern California and adjacent Baja California, and 1 percent off central California. In 1951, 94 percent of all eggs taken were obtained off central Baja California, the remaining 6 percent were from southern California and adjacent Baja California.

6. Most sardine spawning has been found to occur within a 4-degree temperature range, 12.5° to 16.5° C. Only negligible amounts of spawning have been found at temperatures lower than this. The upper temperature limit does not appear to be so sharply defined, since some off-season spawning has been obtained at temperatures exceeding 20° C.

7. Sardine eggs have been collected during every month of the year off central Baja California, although the period of major abundance has been limited to the months of February through May. Off-season spawning, especially that occurring from August through December, has been largely confined to Sebastian Viscaino Bay. In the waters off southern California and adjacent Baja California, most spawning (over 98 percent) has occurred during a 3-month period, April through June.

8. A basic reason for conducting sardine larval studies is to test the assumption that the early postembryonic period is probably the most critical in regard to mortality, hence the period during which the success or failure of a year class probably is determined.

9. In the quantitative sampling of sardine larvae, several difficulties have been encountered, important among which are (1) net selectivity, i. e., the loss of smaller larvae through the mesh openings of plankton nets, and (2) a marked undersampling of the larger larvae during daylight hours.

10. Exact data on the rate of growth of sardine larvae are not available. Sardine larvae taken in plankton hauls are between 3 mm. (the size at hatching) and 24 mm. in length. From an inspection of seasonal curves of abundance of sardine larvae, grouped by size categories, it appears that between 1 and 2 months are required for a newly fertilized egg to develop into a larva 24 mm. in length. Growth during the larval period is assumed to be logarithmic. Based on a total time period of 45 days between fertilization of the egg and attainment of a larval length of 24 mm., values for the time duration of all size classes routinely used in tabulation of sardine larvae have been determined.

11. Estimates have been obtained of the magnitude of the sardine population at a number of different larval stages. The survival rate of sardine larvae has been determined per 100,000 eggs spawned. During both 1950 and 1951, the minimal estimate of survival to 21 mm. was about 1 in 1,000.

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