THE INCREASE IN SPAWNING BIOMASS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The northern anchovy, *Engraulis mordax*, is a common fish off the west coast of North America. Its biomass has increased markedly since 1951. The various methods of deriving anchovy spawner biomass from the sardine spawner biomass and analogous census estimates of sardine and anchovy larvae are reviewed. A new compilation of anchovy and sardine larval data is presented for 1940, 1941, 1949, 1950, and 1951-69. The effect of several errors of estimate are examined and it is concluded that none is important enough to affect measurably the trend of increase between 1951 and 1966. Lastly, a current interpretation of the larval survey data is used to estimate the spawning biomass of both sardine and anchovy.

The northern anchovy (*Engraulis mordax* Girard) is a common pelagic schooling fish off the west coast of North America between British Columbia and Baja California (lat 53°N to 22°N). The fishery for northern anchovy has usually been small relative to the Pacific sardine (*Sardinops caerulea* (Girard)) off California but the anchovy catch has been increasing since the late 1930's (Figure 1). Following the collapse of the sardine fishery in the early 1950's, the catch of anchovy exceeded that of sardine. The further decline of sardine catch and the eventual moratorium on sardine, combined with a limited reduction fishery on anchovy, have again allowed the anchovy fishery to exceed that of sardine since the mid-1960's (Messersmith and Associates, 1969).

Routine planktonic larva sampling since 1951 shows an increase in the number of anchovy larvae (Murphy, 1966; Ahlstrom, 1966, 1968) and the present consensus estimate of the spawning population of northern anchovy is about 5 million tons for 1966, the last year for which complete data are available. The same sample data for the Pacific sardine now indicate an extremely small number of larvae and the spawning biomass of the northern subpopulation of the sardine may now be less than 5,000 tons. All anchovy biomass estimates must now be referred to analogous sardine biomass estimates based on the sardine fishery and on sardine and anchovy egg and larva surveys because no fishery-based estimate of anchovy biomass has yet been made: this becomes increasingly difficult and imprecise as the sardine "reference" population diminishes.

The purposes of this paper are to:

1) review the estimates of spawner biomass of the anchovy;
2) present a summary of the incidence of larval anchovy by region and season since 1951;
3) examine the effects of three spawning behavior models on the estimates of spawning biomass;
4) establish a standard reference period for the determination of anchovy biomass without further consideration of the current size of the sardine population.

PREVIOUS ESTIMATES OF ANCHOVY BIOMASS

Messersmith and Associates (1969, p. 9) tabulated all the estimates of anchovy spawning biomass for the years 1940-66. Ahlstrom (MRC,

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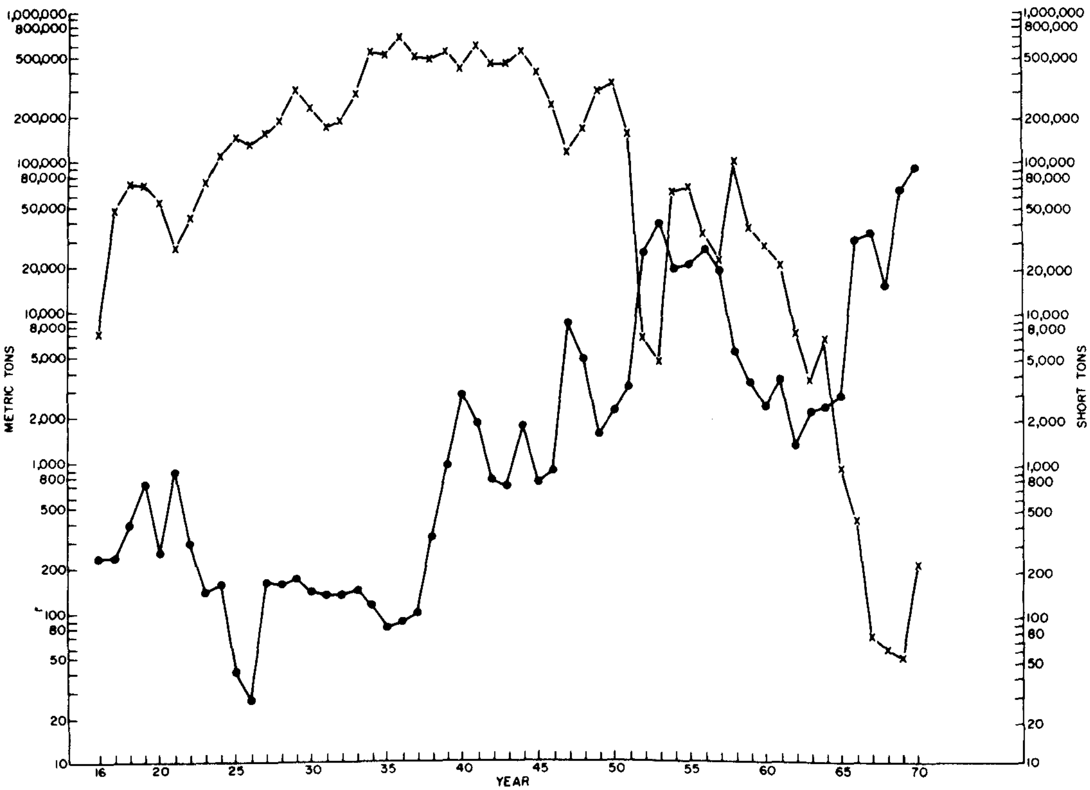

FIGURE 1.—The annual catch of sardine (crosses) and anchovy (solid circles) in the California Current system since 1916. Whole fish reduction was essentially banned in 1919 and a limited whole fish reduction fishery was opened in 1965.

1964)[3] in an informal statement, emphasized the changing ratio of anchovy larvae to sardine larvae from 3.1 to 1 in 1951 to 46.8 to 1 in 1959. In a similarly informal statement, MacGregor (MRC, 1964) described a method for estimating the spawning biomass of pelagic spawning species. That portion of his statement which is related to sardine and anchovy follows:

> Egg and larval surveys conducted over the years have given us a basis for estimating the total numbers of eggs and larvae produced each year in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) survey area for a number of fish species. We also have information on the fecundity of a number of these species and from the combined data can estimate the biomass of spawning adult fish on each species. The number of eggs a fish will produce at one spawning appears to be directly related to the weight of the fish. Thus, we can compute the numbers of eggs produced in one spawning by a ton of female fish as follows:

Species	Millions of eggs
Anchovy	525
. . . .	. .
Sardine	241
. . . .	. .

> The above figures represent female fish only. If we assume, as evidence indicates, that for each ton of adult females there is also present a ton of adult males, we would have to divide the number of eggs produced

[3] A review of estimates and procedures was conducted for the California Marine Research Committee (MRC) in 1964 and the texts of the presentations are to be found there. Statements and calculations were neither edited nor formally derived. Quotations from the Appendix to these minutes will be regarded as informal and cited (MRC, date).

by 2 to obtain the number of eggs produced [in one spawning][a] by one ton of adult fish. If we further assume that . . . . about half the [adult] sardine population spawns twice [a year] (average 1½ times) and the anchovy [adult] population spawns 2 or 3 times a year (average 2½ times), we would also multiply millions of eggs by 1½ for the sardine and 2½ for the anchovy. On the above basis the total number of eggs produced by one ton of adult fish of both sexes in one year would be as follows for each species:

Species	Millions of eggs
Anchovy	656
. . . .	. .
Sardine	181
. . . .	. .

It may be seen from the above that, although numbers of eggs or larvae in the plankton may be used as an index of adult abundance, a sardine egg in the plankton represents 3½ times . . . as much adult biomass as an anchovy egg. Estimates of the average biomass of each . . . species for the 3-year period 1955-57 and the average commercial landings for the same period are as follows:

Species	Biomass (tons)	Catch (tons)
Anchovy*	750,000	29,686
. . . . . .	. . . . .	. . . .
Sardine	254,000	51,508

* Anchovy larvae caught were used as an estimate of eggs. This may have resulted in underestimation by a factor of 2. Application of this factor brings this biomass of anchovies into line with the material in Murphy's (MRC, 1964) estimate of the anchovy harvest . . . .

[a] In brackets added for clarification.

In another informal statement Radovich (MRC, 1965) cited the change in anchovy to sardine larval ratios (Ahlstrom, MRC, 1964) and stated ". . . in this 8-year period the anchovy maintained its population level fifteen times better than the sardine . . . ." He further pointed out that the necessary ratio of annual survival rates to attain this was 1.4. Should this difference in survival be in the larval stage, the MacGregor (MRC, 1964) biomass estimate should be divided by 1.4 or roughly 1.5, resulting in an estimate of about 1 million tons.

Murphy (MRC, 1964) used an anchovy spawner biomass estimate which was essentially double MacGregor's (MRC, 1964) because he believed that the escapement of anchovy larvae through the mesh of the standard CalCOFI silk net exceeded the escapement of the sardine larvae enough to cancel the effect of anchovy fecundity exceeding sardine fecundity. Thus Murphy's calculation (1966, p. 60) of anchovy spawner biomass for the period 1955-57 was 3.3 million short tons as compared to MacGregor's 1.5 million short tons and Radovich's 1.0 million short tons for the same 3-year period. An estimate by Murphy's method for 1958 would be 5.1 million short tons.

Ahlstrom (1968) estimated that the 1958 anchovy biomass was between 1.80 and 2.25 million short tons and observed further that the biomass had reached a plateau of 4.5 to 5.625 million short tons in the mid-1960's.

TABLE 1.—Comparison of data used for estimating the spawning biomass of northern anchovy.

	Standard haul summation[1]		Summation of average quarterly estimates[2]		Larval census estimates[3]		Standard haul summations[4]	
	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine
1951	29,551	11,068	9,826	3,689	15,101	5,774	29,552	11,066
1952	59,626	19,179	20,581	6,437	17,071	5,466	63,057	24,559
1953	99,160	14,400	34,314	4,924	23,680	4,020	103,928	15,055
1954	161,241	26,914	56,665	9,364	38,415	7,297	161,254	26,914
1955	140,183	14,121	51,096	5,554	37,658	4,341	140,183	14,121
1956	134,931	15,523	51,438	5,179	38,508	3,895	134,931	15,523
1957	146,631	9,833	53,921	3,415	40,441	2,432	146,631	9,833
1958	205,733	11,427	75,120	3,845	56,928	2,831	205,457	11,423
1959	206,753	5,374	72,732	2,072	54,168	1,159	206,000	5,308
1960	289,860	8,012	97,602	3,099				
1961	97,103*	1,708*	97,103	1,708				
1962	212,675*	2,258*	212,675	2,258				
1963	205,838*	1,349*	205,838	1,349				
1964	166,517*	2,757*	166,517	2,757				
1965	258,781*	3,573*	258,781	3,603				
1966	380,420	5,640	161,333	2,211				

[1] Ahlstrom 1966, tables 2 and 4 (1965, 1966, numbers from current unpublished data).
[2] Ahlstrom, 1966, 1968.
[3] Ahlstrom, 1968.
[4] Murphy, 1966.
* Quarterly cruises rather than monthly.

TABLE 2.—Stations and pooled areas within each region as used in this study.

Regional name	Pooled areas	Stations
Central California Inshore	6.5	60.52
18 stations	5,270 miles^2	60.55
4 pooled areas		63.52
19,970 miles^2		63.55
		67.50
		67.55
	6.6	60.60
	4,800 miles^2	63.60
		67.60
	7.5	70.52 (51)
	5,100 miles^2	70.55 (53)
		73.51 (50)
		73.55 (53)
		77.50 (51)
		77.55
	7.6	70.60
	4,800 miles^2	73.60
		77.60
Central California offshore	6.7	60.70
6 stations	6.8	60.80
6 pooled areas	6.9	60.90
28,800 miles^2	7.7	70.70
	7.8	70.80
	7.9	70.90
Southern California inshore	8.4	82.47
19 stations	4,589 miles^2	83.40
3 pooled areas		83.43
15,348 miles^2		87.35
		87.40
		87.45
	9.3	90.28
	5,989 miles^2	90.30 (32)
		90.37
		93.27 (28)
		93.30
		97.30
		97.32
		97.35
	9.4	90.45
	4,770 miles^2	93.40
		93.45
		97.40
		97.45
Southern California offshore	8.5	80.51 (52)
18 stations	4,747 miles^2	80.55
4 pooled areas		83.51
19,147 miles^2		83.55
		87.50
		87.55
	8.6	80.60
	4,800 miles^2	83.60
		87.60
	9.5	90.50
	4,800 miles^2	90.55 (53)
		93.50
		93.55
		97.50
		97.55
	9.6	90.60
	4,800 miles^2	93.60
		97.60
Southern California seaward	8.7	80.70
18 stations		83.70
6 pooled areas		87.70
28,800 miles^2	8.8	80.80
		83.80
		87.80
	8.9	80.90
		83.90
		87.90
	9.7	90.70
		93.70
		97.70
	9.8	90.80
		93.80
		97.80
	9.9	90.90
		93.90
		97.90
Baja California inshore	10.3	100.29
29 stations	5,535 miles^2	100.30
4 pooled areas		100.35
21,089 miles^2		103.30
		103.35
		107.32
		107.35
	10.4	100.40
	4,800 miles^2	103.40
		103.45
		107.40
	11.3	110.33 (32)
	5,956 miles^2	110.35
		113.30
		113.35
		117.26
		117.30
		117.35
		118.39
		119.33
		120.25
		120.30
		120.35
	11.4	110.40
	4,798 miles^2	110.45
		113.40
		113.45
		117.40
		117.45
Baja California offshore	10.5	100.50
15 stations	4,800 miles^2	103.50
4 pooled areas		107.50
19,200 miles^2	10.6	100.60
	4,800 miles^2	103.60
		107.60
	11.5	110.50
	4,800 miles^2	110.55
		113.50
		113.55
		117.50
		117.55
	11.6	110.60
	4,800 miles^2	113.60
		117.60
Baja California seaward	10.7	100.70
19 stations	4,800 miles^2	103.70
6 pooled areas		107.70
28,800 miles^2	10.8	100.80
	4,800 miles^2	103.80
		107.80
	10.9	100.90
	4,800 miles^2	103.90
		107.90
	11.7	110.70

TABLE 2.—Continued.

Regional name	Pooled areas	Stations
	4,800 miles^2	113.70
		117.70
		117.75
	11.8	110.80
	4,800 miles^2	113.80
		117.80
	11.9	110.90
	4,800 miles^2	113.90
		117.90
South Baja inshore	12.3	123.37
22 stations	4,459 miles^2	127.34
5 pooled areas	12.4	120.40
22,790 miles^2	4,800 miles^2	120.45
		123.42
		123.45
		127.40
		127.45
	13.2	133.25
	3,931 miles^2	137.23
	13.3	130.30
	4,800 miles^2	130.35
		133.30
		133.35
		137.30
		137.35
	13.4	130.40
	4,800 miles^2	130.45
		133.40
		133.45
		137.40
		137.45
South Baja offshore	12.5	120.50
16 stations	4,800 miles^2	120.55
4 pooled areas		123.50
19,200 miles^2		123.55
		127.50
		127.55
	12.6	120.60
	4,800 miles^2	123.60
		127.60
	13.5	130.50
	4,800 miles^2	130.55
		133.50
		137.50
	13.6	130.60
	4,800 miles^2	133.60
		137.60
South Baja seaward	12.7	120.70
3 stations	12.8	120.80
3 pooled areas	12.9	120.90
14,400 miles^2		

Murphy (1966) estimated the biomass of the spawning stocks of sardine from 1932 to 1959. He also compared the anchovy: sardine larval ratio from 1951 to 1959 and graphically compared this with the larval ratio over a portion (about 20%) of their joint range in 1940 and 1941 (p. 65). The striking decline of the sardine, and the increase of the anchovy biomass, has stimulated speculation on the biological interactions of these species and the MRC (Marine Research Committee of California) has a standing recommendation that 200,000 tons of anchovies and 10,000 tons of sardines be harvested in an experimental attempt to foster the recovery of sardines. It is the primary goal of this recommendation to restore and maintain the balance of sardines and anchovies in the California Current system by manipulation of fishing effort.

The estimates of spawning biomass of the northern anchovy have been based on the spawning biomass of the Pacific sardine as derived from the fishery (Murphy, 1966; Ahlstrom, 1968) and on the assumed relationship between sardine and anchovy fecundity, survival, and escapement of larvae through the meshes of the CalCOFI standard silk survey net (Lenarz, 1972). For convenience, the larva data for all estimates to date are listed in Table 1. A series of stations off southern California was occupied in 1940 and 1941, and the anchovy: sardine ratios were 1.18 (13,962 anchovy to 11,862 sardines) and 1.66 (12,560 anchovy to 7,564 sardines) respectively. The 1940, 1941, 1949, and 1950 data will be referred to later in a section on interaction of sardine and anchovy.

METHOD OF DATA ASSEMBLY

The method of assembling the estimates of larval abundance for this paper differs from that of Sette and Ahlstrom (1948) and Ahlstrom (1954, 1966, 1967, 1968). Two methods of assembly were used previously: the "census estimate" and the "standard haul summation." In the "census estimate" each larva sample count was weighted by the area of a polygon formed by construction of "perpendicular bisectors of lines drawn from the station to each of all surrounding stations" (Sette and Ahlstrom, 1948, p. 521; Ahlstrom, 1968).

$$C_k = 10 \sum_{j=1}^{n} \left[\sum_{i=1}^{m} A_s \left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i \right) \right]_j \qquad (1)$$

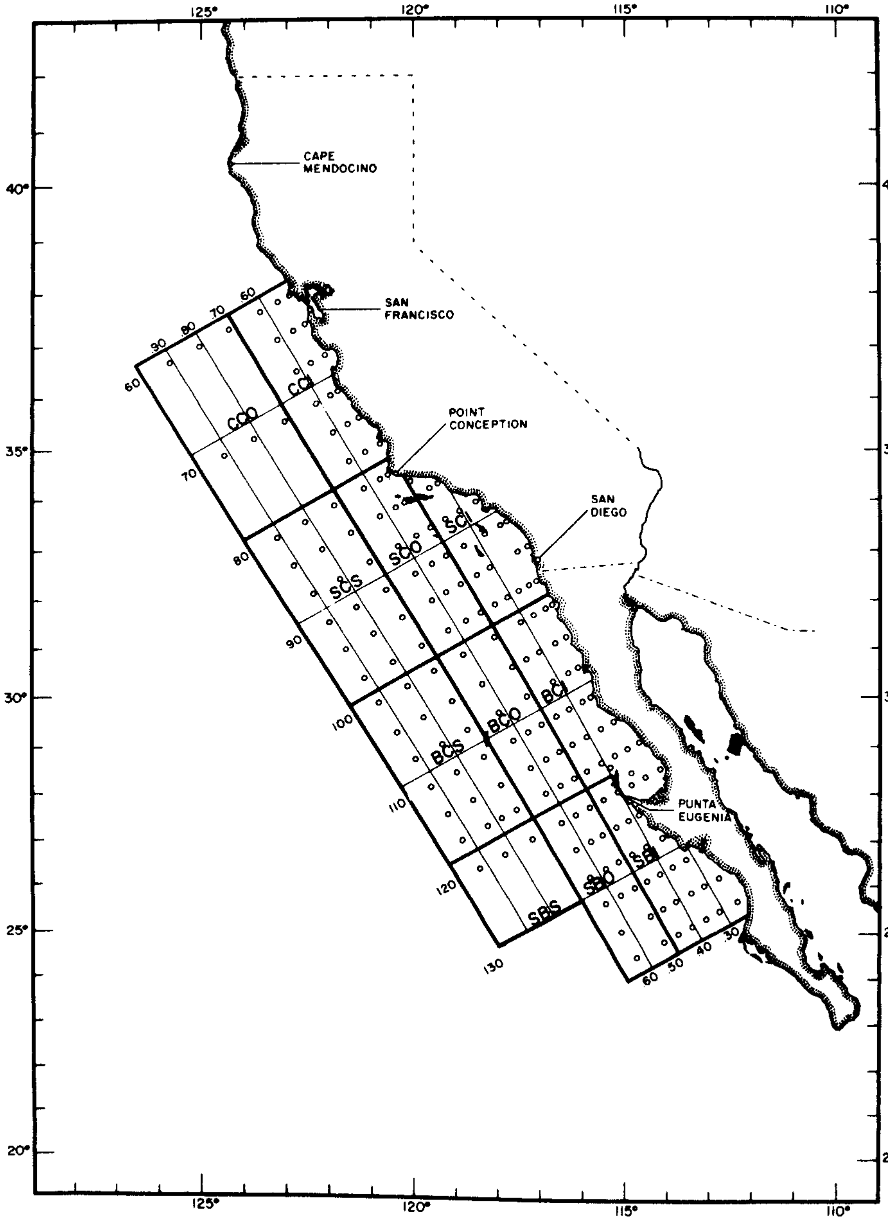

FIGURE 2.—The selected stations of the CalCOFI grid (see Tables 2 and 3) and the regional boundaries defined for this paper. Columns of stations are indicated .30, .40 . . . .90, and rows of lines are indicated 60, 70, . . . 130. The first two letters of each three-letter group stand for coastal bands, i.e., central California (CC), Southern California (SC), Baja California (BC), South Baja (SB) while the last letter of the three stands for offshore zones roughly parallel to the coast, inshore (0-80 miles from the coast, "I", offshore (80-160 miles from the coast, "O"), and seaward (160-280 miles from the coast, "S"), so that the three letters SCI stand for the southern California inshore region.

TABLE 3.—Description of CalCOFI regions used in this analysis.

Regional name	Stations	Pooled areas	Square miles	Area factor
Central California inshore	18	4	19,970	6.85×10^9
Central California offshore	6	6	28,800	9.88
Southern California inshore	19	3	15,348	5.26
Southern California offshore	18	4	19,147	6.57
Southern California seaward	18	6	28,800	9.88
Baja California inshore	29	4	21,089	7.23
Baja California offshore	15	4	19,200	6.58
Baja California seaward	19	6	28,800	9.88
South Baja inshore	22	5	22,790	7.82
South Baja offshore	16	4	19,200	6.58
South Baja seaward	3	3	14,400	4.94
Totals	183	49	237,544	81.48

TABLE 4.—Equivalent station list off southern California for 1940, 1941, and 1950-72.

Southern California inshore			Southern California offshore		
Station no. used in 1940	Station no. used in 1941	Nearest present station no.	Station no. used in 1940	Station no. used in 1941	Nearest present station no.
02	12	82.47	04	15	80.51
01	11	83.40	05	16	80.55
08	23	83.43	03	13	83.51
10	21	87.35	13	14	83.55
17	22	87.40	24	24	87.50
11	34	87.45	12	25	87.55
21	30	90.28	06	28	80.60
19	31	90.30	09	27	83.60
20	32	90.37	18	26	87.60
22	41	93.27	23	35	90.50
28	51	90.30	31	36	90.55
--	60	97.30	39	45	93.50
35	61	97.32	40	46	93.55
36	62	97.35	41	64	97.50
30	33	90.45	14	55	97.55
29	52	93.40	32	37	90.60
34	54	93.45	25	47	93.60
37	63	97.40	33	--	97.60
38	53	97.45			

where A_s = area of a polygon constructed of perpendicular bisectors of lines between station "i" and all adjacent stations expressed as number of 10 m² areas

C_{kf} = estimate of abundance of larvae in year "k" and "f" takes the value of the number of the equation

C_i = number of larvae in "ith" sample

a_i = area of mouth of the net used at the "ith" station

b_i = length of tow in meters estimated from a calibrated flow meter at station "i"

d_i = tow depth in meters estimated from the wire angle at maximum wire out at station "i"

m = number of stations

n = number of monthly cruises.

In the "standard haul summation" approach the sums of all tows on regularly occupied stations for each monthly cruise were totaled for the year without weighting for represented area.

$$C_k = 10\sum_{j=1}^{n}\left[\sum_{i=1}^{m}\left(a_i^{-2}\ b_i^{-1}\ c_i\ d_i\right)\right]_j . \quad (2)$$

To accommodate the quarterly cruises Ahlstrom (1966, 1968) established a modification of this in which the quarterly averages of 1 to 3 monthly cruise summations were added to make an annual total (Ahlstrom, 1966, Table 8; 1968, Table 3).

$$C_k = 10 \sum_{q=1}^{4} \left\{ \sum_{j=1}^{n} \left[\sum_{i=1}^{m} \times \left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i \right) \right]_j n^{-1} \right\}_q . \quad (3)$$

Murphy (1966) used the monthly version of Ahlstrom's standard haul summation (Table 1).

The method used here is called the "regional census estimate"

$$C_{k4} = 10\, A_r m^{-1} \left[\sum_{i=1}^{m} \left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i \right) \right] \quad (4)$$

where C_{k4} = estimate of abundance of larvae in region "r" in each quarter

A_r = Area of region "r" in numbers of 10 m^2 areas.

This method of assembly combines the simplicity of the "standard haul summation" and the areal weighting of the previously used census estimates. The regional census estimate consists of the mean number of larvae per standard area (10 m^2 sea surface) of all stations taken within a region for a quarter of the year times the number of standard areas within the region. The same 183 stations or nearby alternates were used within the routinely occupied area as defined by Smith, Ahlstrom, and Casey (1970, Figure 1). The selected stations and acceptable alternates are listed in Table 2 and the regions are illustrated in Figure 2 and defined by area and area factor in Table 3.

The 1940 and 1941 stations have been assigned to the two southern California regions (Table 4) in which these cruises were conducted. The number of stations per unit area has been held nearly constant by the elimination of excess stations in the early cruises. The 1949 station equivalents are listed in Table 5. From 1950 to 1972 stations have been standard in placement.

TABLE 5.—Equivalent station list for the CalCOFI survey pattern for 1949 and 1950-72.

Area	Station no. used in 1949	Nearest present station no.
Central California inshore	601	63.58
	701	72.56
Central California offshore	602	62.68
	603	61.78
	604	61.87
	702	71.66
	703	71.76
	704	71.85
Southern California inshore	901	92.39
Southern California offshore	801	82.57
	902	92.48
	903	92.58
Southern California seaward	802	82.67
	803	82.77
	804	82.87
	904	92.68
	905	92.78
Baja California inshore	1001	101.34
	1002	101.44
	1101	111.38
	1102	111.48
Baja California offshore	1003	102.54
	1004	102.64
	1103	111.58
Baja California seaward	1005	102.74
	1006	102.84
	1007	102.94
	1104	111.68
	1105	112.78
	1106	112.88
	1107	112.98
Southern Baja inshore	1201	122.44
Southern Baja Offshore	1202	122.53
Southern Baja seaward	1203	123.63
	1204	123.73
	1205	124.83

Extra cruises, additional lines, and stations on lines have been added periodically, resulting in some increase in station density in some areas. To stabilize sampling effort and remove possible effects of added effort nearshore, all but 183 stations and their nearby equivalents have been eliminated from further consideration for the 16-year compilation of regional census estimates. The number of stations eliminated each year are summarized in Table 6.

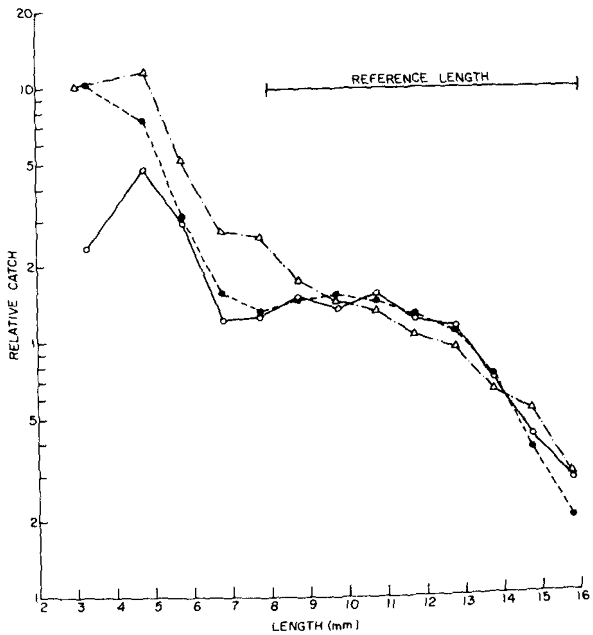

FIGURE 3.—The size frequency of sardine larvae caught in the CalCOFI standard silk net (0.55 mm). The triangle dot-dash curve represents the 1951-60 catch from the selected stations in all eleven regions; the black dot-dash curve represents the 1940 catch from selected stations in the southern California inshore and offshore region and the clear dot solid line represents the 1941 catch from the same two regions. Relative catch refers to the catch at a standard size group (3.00, 3.25 (1940-41), 4.75, 5.75 ... 15.75 mm), divided by the average catch from size groups 8.75 to 15.75.

ESCAPEMENT AND AVOIDANCE BY ANCHOVY AND SARDINE LARVAE

The chief errors causing underestimates of *C* for both anchovy and sardine larvae are those attributable to larvae "escaping" through the meshes of the standard plankton net (see Lenarz, 1972, p. 839) and larvae "avoiding" the mouth of the net (Silliman, 1943; Ahlstrom, 1954, 1959; Clutter and Anraku, 1968). While "escapement" and "avoidance" are important biases to consider in the study of larva growth and mortality, I consider them beyond the scope of this paper. The estimate of anchovy biomass is based on a relative estimate of the number of anchovy larvae and sardine larvae. I must treat escapement and avoidance briefly, since they act differently on the anchovy and sardine and vary from season to season and with changes in sampling gear.

Lenarz (1972) found no appreciable difference in size-specific escapement of sardine and anchovy through net apertures. However, newly hatched anchovy larvae are considerably smaller than sardine larvae. This leads to a variation in the degree of bias (Murphy, 1966) to such escapement. In Figure 3 the catch of all standard sizes of sardine is related to the average catch between 8.75 and 15.75 mm, a size range I assume to be completely retained on 0.55-mm mesh width silk. The primary line is the average size composition for the period 1951-60 for the sardine. The size composition of the 1940

TABLE 6.—Stations eliminated from data assembly for regional census estimates.

Year	No. of stations occupied	183 stations reported each cruise	Stations not reported	Percent reported
1951	1,436	1,026	410	71.4
1952	1,376	1,167	209	84.8
1953	1,346	1,137	209	84.5
1954	1,473	1,217	256	82.6
1955	1,425	1,121	304	78.7
1956	1,399	1,129	270	80.7
1957	1,493	1,165	328	78.0
1958	1,851	1,276	575	68.9
1959	2,182	1,574	608	72.1
1960	1,810	1,305	505	72.1
1961	953	699	254	73.3
1962	920	659	261	71.6
1963	881	659	222	74.8
1964	877	680	197	77.5
1965	1,099	658	441	59.9
1966	1,979	1,487	492	75.1

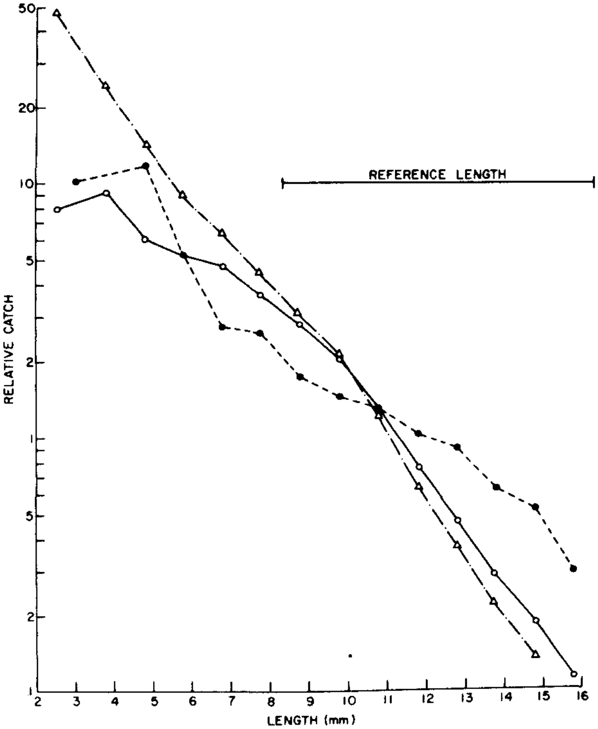

FIGURE 4.—The size frequency of sardine and anchovy larvae. The black dot-dash line is sardine larvae caught in the standard CalCOFI silk net between 1951 and 1960 in all regions from January to June inclusive. The clear dot solid line is anchovy larvae caught in the standard CalCOFI silk net between 1951 and 1960, in all regions from January to June inclusive. The triangle dot-dash line is anchovy larvae caught in the new CalCOFI nylon net (0.505-mm nylon rather than 0.55-mm silk) from January to June 1969 in all regions.

and 1941 sardine catches are included for later reference. In Figure 4, the 1951-60 size composition of sardine is compared to the anchovy for the same period. Anchovy retention in a new net with smaller, more regular meshes (0.505-mm nylon) and more mesh area is included for comparison. All samples reported in the size frequency graphs are from the first half of the year to facilitate comparison with earlier samples and eliminate the effects of poor sampling coverage in the latter half of the year.

Ahlstrom (1954) acknowledged that larger larvae may avoid capture at night as in the daytime. Avoidance is more pronounced in the daylight. In the sardine the night-to-day ratio of catches increases 0.6971 per mm of growth after 4.75 mm (Ahlstrom, 1954, p. 129). Similarly, the anchovy night-to-day catch ratio increases 0.64 for each millimeter growth after 3.5 mm (Ahlstrom, 1959, p. 136). Lenarz (in press) described the annual and diurnal variation in size specific catch rate for sardine, anchovy, hake, and jack mackerel. An important source of variability in avoidance bias is a shift of spawning season. For example, length of day varies from 9.6 hr in winter to 14.8 hr in summer at the latitude of San Francisco near the northern boundary of the survey grid and from 10.6 to 13.7 hr off south Baja California at the southern boundary of the sample grid (54% and 29% respectively). For the 10-year period, 1951-60, the ratio of night-caught to day-caught larvae was 1.72 for sardines and 2.45:1 for anchovy. When the average catch per positive tow by month is corrected for day length at San Francisco the anchovy:sardine ratio changes from 2.96:1 to 3.75:1 for the same decade. A proportionate shift of anchovy spawning toward June would for example, accentuate this difference.

The importance of avoidance and escapement

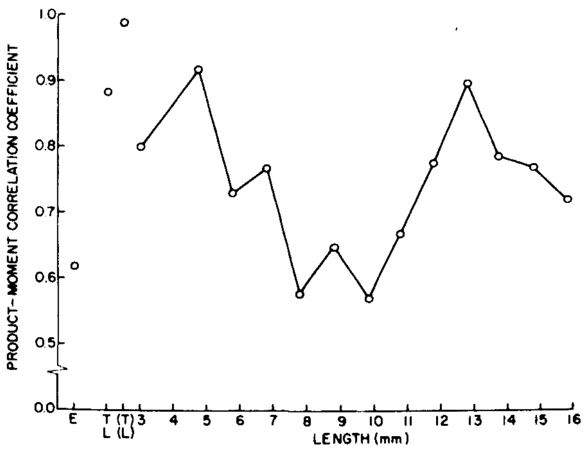

FIGURE 5.—The correlation coefficient between the annual total regional census estimates of sardine eggs and larvae by size class with the Murphy (1966) sardine biomass estimates. The first point is for total eggs, 1951-59; the second point is for total larvae, 1951-59; the third point is for total larvae with 1953 and 1959 censored. The succeeding points are for standard-size classes for all years 1951-59.

TABLE 7.—A comparison of the regional census estimate (A), separately weighted nearshore (B), and 1 month per quarter sampling (C), in the southern California inshore region, 1951-60.

		Winter	Spring	Summer	Fall	Total	Annual rank
1951	A	135	609	111	540	1,395	9
	B	175	879	92	441	1,587	9
	C	289	251	76	276	892	10
1952	A	87	261	314	134	796	10
	B	70	229	336	119	754	10
	C	52	315	531	122	1,020	9
1953	A	578	184	763	1,904	3,429	6
	B	519	139	734	1,409	2,801	6
	C	163	339	1,089	728	2,319	8
1954	A	3,123	516	519	237	4,395	3
	B	1,006	445	412	180	2,043	7
	C	2,577	332	934	149	3,992	5
1955	A	2,012	1,074	849	150	4,085	4
	B	1,682	1,006	737	117	3,542	4
	C	1,941	930	1,111	55	4,037	4
1956	A	236	1,166	708	156	2,266	8
	B	186	1,009	635	117	1,947	8
	C	302	1,632	708	129	2,771	7
1957	A	3,314	3,601	791	267	7,973	1
	B	3,650	3,264	933	238	8,085	1
	C	4,951*	4,060	791	154	9,956	1
1958	A	2,316	2,912	403	63	5,694	2
	B	2,186	3,226	417	36	5,865	2
	C	1,753	4,246	554	51	6,604	2
1959	A	972	2,303	108	101	3,484	5
	B	907	2,550	111	72	3,640	3
	C	413	5,354	218	19	6,004	3
1960	A	1,579	1,448	198	34	3,259	7
	B	1,692	1,564	189	36	3,481	5
	C	263	2,394	296	34	2,987	6

* February
B r_s = 0.85
C r_s = 0.90

to biomass estimation is solely a function of the variability these biases cause with respect to year-to-year differences between the capture and retention of sardine and anchovy larvae. For example, in Figure 5 the product moment regression coefficients, r for sardine egg or larval census estimate versus sardine biomass are plotted by total eggs, total larvae (1951-59), total larvae with outlyer censored (1953-59), and each larval size interval through 15.75 mm. All the coefficients are high and positive with pronounced minima at the egg stage and at the 9.75 mm stage. One might ascribe the minimum associated with eggs to the effect of "patchy" distribution on precision of estimate. I have no ready explanation of the 9.75 mm minimum or the 12.75 mm maximum which follows it.

Sette and Ahlstrom (1948, p. 521) discussed the concept of "area of station" relative to sardine eggs. Trial calculations of the same kind suggest that with respect to sardine larvae, assigning equal areas to stations is also close to the more exact method of erecting perpendicular bisectors to each nearest station and using the area of the polygon so formed. For anchovy larvae, however, there may be an important problem. To study this problem, the southern California inshore region was divided into "nearshore", i.e., the standard station closest to shore on each line, and "nearshore-excluded" segments. In the 40 quarters of the years 1951-60, the mean concentration of eggs per positive station in the "nearshore" region exceeded that of the "nearshore-excluded" section by 35%. Similarly the proportion of positive stations was 87% "nearshore" and 68% in the "nearshore-excluded" region with respect to anchovy larvae.

In Table 7 I have compared the annual estimates of anchovy larvae using the quarterly regional census estimate of the entire region with the same estimate using the sum of the nearshore and nearshore-excluded segments of the region. The latter estimate is 8% lower than the regional census estimate, but it is not likely to be a bias since of the 10 annual estimates, the single estimate exceeds the partitioned estimate 5 times while the reverse is true an equal number of times. The Spearman rank coefficient of correlation is 0.85. Also, a comparison of the annual estimates from 1951 to 1959 regional census estimates and those from a census estimate by Ahlstrom (1967, Table 2) shows a Spearman rank correlation coefficient of 1.00. Thus, we may conclude that errors of the kind involving nearshore gradients in the incidence and intensity of anchovy spawning and larval survival, while important for some applications, do not measurably affect the regional census estimates.

One may reasonably ask whether estimates generated from monthly cruises are comparable to larval abundance estimates from a single cruise in each quarter. In Table 7 I have compared the annual estimates of anchovy larvae using all regular occupied stations within the quarter and a similar estimate using only January, April, July, and October, with February used in 1957 because the January cruise was incomplete. The Spearman rank coefficient for the comparison is 0.90: the mean value of the estimates from monthly cruises is 10% below the estimates from one cruise per quarter but in 5 years the monthly derived estimates exceed the quarterly and in 5 years the reverse is true. Thus, I conclude that differences which may arise from comparing estimates from quarterly and monthly cruises are not large enough to affect this study.

Technical errors should be relatively small and affect the catches of sardine and anchovy similarly. For example, the factor a_i, the area of mouth of the net is usually known to within 5%, the factor b_i is modified by the flow through the mouth of the net so that the length of tow is

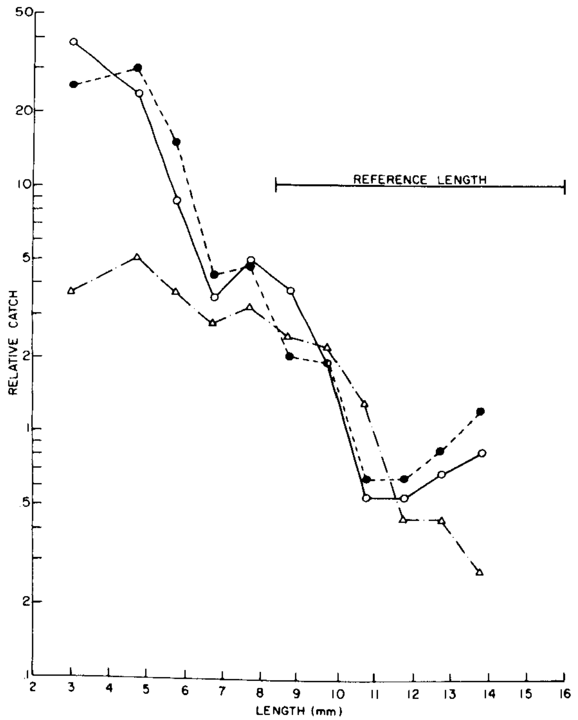

FIGURE 6.—The size frequency of sardine larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

underestimated by 13-15%: an error as great as 5-10% results from the flowmeter being centered in the backwash of the bridle apex hardware (Smith and Clutter, 1965; Tranter and Smith, 1968; Mahnken and Jossi, 1967).

Two biases, which have yet to be evaluated, are likely to be important. In cold water, the larvae may tend to grow more slowly. Thus the regional census estimate for a cold quarter or cold year could prolong the period for which the larvae are vulnerable to sampling. Similarly, larvae may persist without food for extended periods yielding the same kind of error mentioned for temperature. No estimate has been made for either bias for anchovy or sardine larvae.

All the sardine and anchovy larvae collected by the CalCOFI net have been subjected to transport with the wind-driven layer of the ocean (Sette, 1943). While the entire problem of transport is beyond the scope of this paper, a comparison of size frequencies of larvae in the southern California inshore, offshore, and seaward regions shows a disproportionately lower number of younger larvae in samples from farther offshore (Figures 6 and 7). The most likely explanation of these data is that older larvae transported to the offshore regions are present in excess of the numbers that have been spawned and hatched there. Further, this implies that the larva size frequency slope in the spawning area is biased for the same reason. If the usual sampling grid encloses the spawning area and the areas to which larvae are transported no overall bias should ensue.

The MacGregor estimate of anchovy and sardine biomass cited above, mentioned specific numbers of spawnings per year and sex ratios. Neither of these has been suitably evaluated as yet. At present, there is no way of calculating the number of batches spawned per year. In this paper, I assume that the anchovy is twice as fecund as sardine. An attempt will be made to evaluate the sensitivity to multiple spawning by proposing three spawning models, below. The sex ratio is presently derived from the fishery which is conducted over a very small proportion of the anchovy range. Since males are somewhat smaller, they may be expected to be recruited to the fishery somewhat later than females. In this report, the simple assumption of equality of biomass will be maintained. This will tend to overestimate the adult biomass by the degree in which the male biomass is overestimated.

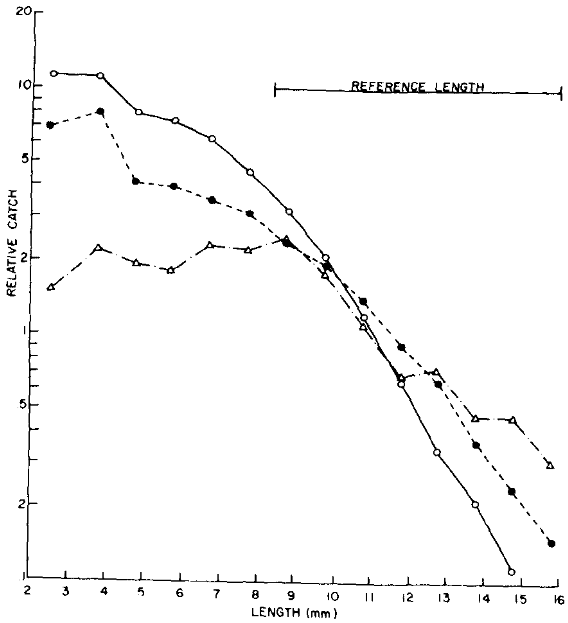

FIGURE 7.—The size frequency of anchovy larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

TABLE 8.—Sample size frequency distribution for sardine and anchovy. Total larvae per 10 m² sea surface.

Mid-range x	Sardine f	fx	$fx/\Sigma fx$	Cumulative percent	Anchovy f	fx	$fx/\Sigma fx$	Cumulative percent
0.7	4	2.8	0.000	0.0	4	2.8	0.000	0.0
1.4	51	71.4	0.000	0.1	79	110.6	0.000	0.0
2.8	453	1,268.4	0.009	0.9	886	2,480.8	0.002	0.2
5.6	320	1,792.0	0.012	2.2	707	3,959.2	0.003	0.4
11.2	312	3,494.4	0.024	4.6	814	9,116.8	0.006	1.0
22.4	289	6,473.6	0.045	9.1	789	17,673.6	0.012	2.2
44.7	257	11,487.9	0.079	17.0	752	33,614.4	0.022	4.4
89.1	179	15,948.9	0.110	28.0	725	64,597.5	0.043	8.7
177.8	127	22,580.6	0.156	43.7	618	109,880.4	0.072	15.9
354.8	78	27,674.4	0.191	62.8	579	205,429.2	0.135	29.4
707.9	44	31,147.6	0.216	84.4	369	261,215.1	0.172	46.6
1,412.5	14	19,775.0	0.137	98.0	247	348,887.5	0.230	69.6
2,818.4	1	2,818.4	0.019	100.0	94	264,929.6	0.174	87.1
5,623.4					23	129,338.2	0.085	95.6
11,220.2					4	44,880.8	0.030	98.5
22,387.2					1	22,387.2	0.015	100.0
N	2,129				6,691			
$\bar{X}$	67.88				226.95			
Σfx		144,535.4				1,518,503.7		

TABLE 9.—Regional census estimates of total anchovy larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	OCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0–	0–	771	196	0–	0–	0–	0–	0–	0–	0–	967
	2	0–	0–	258	214	0–	0–	0–	0–	0–	0–	0–	472
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1941	1	0–	0–	184	351	0–	0–	0–	0–	0–	0–	0–	535
	2	0–	0–	422	579	0–	0–	0–	0–	0–	0–	0–	1,001
	3	0–	0–	27	8	0–	0–	0–	0–	0–	0–	0–	35
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1950	1	0	0	10	9	4	43	17	1	13	5	0	102
	2	0	0	232	319	27	115	23	0	152	13	0	881
	3	994	265	338	5	2	9	1	0	2	3	0	1,619
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1951	1	5	0	135	8	0	289	17	150	2,537	147	1	3,289
	2	4	6	609	24	5	203	66	78	289	179	80	1,543
	3	25	53	111	21	0	454	0	0	49	57	0	770
	4	18	0	540	21	0	266	2	0	55	0	0	902
1952	1	0–	0–	87	33	0	1,372	111	0	1,762	40	0	3,405
	2	0	0	261	7	1	732	32	0	1,665	145	0	2,843
	3	7	69	314	16	3	462	1	2	240	12	2	1,128
	4	0	0	134	23	0	558	31	0	8	2	0	756
1953	1	0–	0–	578	67	6	1,649	247	2	4,160	78	227	7,014
	2	0	0	184	17	0	535	85	2	424	238	14	1,499
	3	2	0	763	38	7	373	2	0	150	33	0	1,368
	4	0–	0–	1,904	882	0	831	48	0	84	2	0	3,751
1954	1	654	0–	3,123	723	6	1,090	97	6	4,116	474	615	10,904
	2	1	0	516	98	2	878	28	3	1,872	498	350	4,246
	3	451	0	519	307	426	182	0	0	231	191	0	2,307
	4	58	0–	237	73	11	234	153	0	301	9	0	1,076
1955	1	0–	0–	2,012	283	6	7,152	499	11	750	312	2	11,027
	2	2	0	1,074	246	6	540	266	296	787	380	24	3,621
	3	7	0	849	184	35	257	3	0	602	9	27	1,973
	4	5	10	150	19	0	210	15	0	59	7	4	479
1956	1	0–	0–	236	203	46	1,140	832	409	1,786	1,107	2	5,761
	2	0	0	1,166	63	14	2,239	37	1	1,737	154	2	5,413
	3	247	0	708	562	21	1,413	0	0	807	8	0	3,766
	4	0–	0–	156	115	4	0–	0–	0–	0–	0–	0–	275
1957	1	0–	0–	3,314	1,085	969	2,720	102	3	2,683	69	0	10,945
	2	20	21	3,601	814	69	853	104	8	426	44	13	5,973
	3	5	20	791	592	64	380	1	0	358	234	17	2,462
	4	64	0	267	229	4	86	0	0	10	0	0	660
1958	1	1,620	1,227	2,316	2,407	268	4,680	618	16	4,606	788	5	18,551
	2	252	15	2,912	1,168	497	1,099	384	2	165	57	44	6,590
	3	413	387	403	1,508	84	143	5	0	15	0	0	2,958
	4	11	5	68	34	0	54	2	0	4	0	0	173
1959	1	1,722	0	972	4,452	654	701	51	1	1,595	51	0	10,199
	2	1,101	318	2,303	3,074	498	3,227	651	1	464	453	0	12,090
	3	232	128	108	242	33	82	1	1	197	9	0	1,033
	4	5	0	101	2	0	9	4	0	20	0	0	141
1960	1	185	0	1,579	1,393	279	4,647	1,697	592	6,821	2,327	686	20,206
	2	127	64	1,448	2,694	1,065	2,679	626	259	582	472	11	10,027
	3	155	105	198	70	22	106	69	6	294	7	0	1,032
	4	1	0	34	9	0	67	0	0	21	2	15	149
1961	1	7	0	144	45	0	2,145	143	0	13,436	234	0	16,154
	2	10	0	1,513	955	2,258	2,186	516	215	3,068	1,683	115	12,519
	3	677	310	359	1,127	1,070	114	1	0	27	9	0	3,694
	4	35	15	18	25	4	32	3	2	30	7	0	171
1962	1	56	0	2,285	825	3	2,413	1,021	24	12,570	2,248	0	21,445
	2	877	0	6,555	5,953	5,900	15,483	1,516	228	1,208	1,631	186	39,537
	3	0–	0–	1,214	120	40	505	4	5	162	92	0	2,142
	4	41	5	134	65	8	124	1	0	256	0	0	634

TABLE 9.—Continued.

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1963	1	7	0	7,543	1,481	73	8,088	5,446	688	8,730	381	184	32,621
	2	1,395	175	3,291	6,132	12,821	1,810	389	42	507	182	86	26,830
	3	0—	0—	180	649	133	187	8	8	305	21	7	1,498
	4	0—	0—	279	161	2	92	3	2	45	0	0	584
1964	1	1,420	0	4,137	3,552	7,213	2,895	133	66	6,678	148	5	26,247
	2	3,056	82	4,524	6,223	3,656	1,063	1	0	384	73	77	19,139
	3	538	125	353	1,814	1,516	1,058	26	15	204	6	0	5,655
	4	0—	0—	945	110	3	71	0	2	81	0	0	1,212
1965	1	16	0	10,145	3,803	669	6,158	1,136	1,013	7,171	396	5	30,512
	2	1,160	0	6,870	7,561	6,219	2,257	424	1,112	6,205	91	17	31,916
	3	75	5	6,304	3,130	3,042	1,056	286	4	866	5	0	14,773
	4	0—	0—	1,037	733	121	185	0	0	15	0	0—	2,091
1966	1	2,973	0	7,078	4,285	409	4,426	275	9	3,289	189	15	22,948
	2	181	0	7,823	9,902	1,164	1,065	63	5	1,023	2	0	21,228
	3	738	56	2,427	960	214	881	36	2	454	90	0	5,858
	4	51	2	1,022	62	14	181	4	0	830	0	0	2,166
1967	1	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
	2	0—	0—	5,646	2,565	367	1,901	59	0	618	23	0	11,179
	3	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0
	4	0—	0—	0—	0—	0—	966	155	8	224	605	0	1,958
1968	1	458	0	3,318	3,259	406	2,342	1,851	0	0—	0—	0—	11,634
	2	4	0	4,020	1,194	697	960	397	0	303	361	0	7,936
	3	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
	4	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
1969	1	919	0	16,404	11,163	1,028	5,712	1,671	5	4,198	588	38	41,726
	2	3	0	5,982	2,364	294	3,459	350	196	612	237	3	13,500
	3	28	91	3,101	678	92	282	13	19	178	13	0	4,495

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

The anchovy spawns over a small portion of its range apparently while still schooled; it also spawns over a small portion of the day (25%); it now appears that most spawning takes place just after the full moon, ca. 20% of the lunar month (Smith).[4] In addition, the spawning behavior is highly seasonal with most spawning occurring in the first half-year. Biases result from sampling during a period in which spawning is occurring (Sette and Ahlstrom, 1948, p. 520), and similar errors may result from missing or oversampling spawning peak periods or dense small patches. Although patches would tend to disperse toward randomness, this process appears to be very slow relative to the duration of the larval stage. Patchiness persists and may be augmented by predation. For this reason, the samples have been pooled to reduce variance wherever possible. Nevertheless, sample sizes range from zero to tens of thousands of larvae, and a pooled summary may still be based on a chance large sample. In all cases, the above error analysis was done with a sample frequency plot in view and all "outlyers" were examined for effect on the sampling question. All samples taken between 1951 and 1960 are listed by frequency distribution in Table 8 for sardine and anchovy total larvae.

Anchovy larvae abundance (Table 9) and sardine larvae abundance (Table 10) for 11 regions and the years 1940, 1941, 1949-69, are listed for each region and quarter in which sampling took place at standard stations. Figure 8 shows the comparison of the regional census estimates and standard haul summations from 1951 to 1966 (Ahlstrom, 1968). The close agree-

[4] Smith, P. E. Lunar periodicity in the spawning of the northern anchovy (*Engraulis mordax*). Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

TABLE 10.—Regional census estimates of total sardine larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0-	0-	81	343	0-	0-	0-	0-	0-	0-	0-	424
	2	0-	0-	141	210	0-	0-	0-	0-	0-	0-	0-	351
	3	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-
	4	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-
1941	1	0-	0-	154	211	0-	0-	0-	0-	0-	0-	0-	365
	2	0-	0-	277	313	0-	0-	0-	0-	0-	0-	0-	590
	3	0-	0-	1	5	0-	0-	0-	0-	0-	0-	0-	6
	4	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-
1949	1	0	0	0	0	0	9	2	0	0-	20	3	34
	2	0	0	2	11	14	259	1	1	300	2	3	593
	3	304	7	5	12	5	0	0	0	0	0	1	334
	4	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-
1950	1	0	0	0	0	0	92	1	0	117	128	2	340
	2	0	2	116	206	128	60	91	3	1,951	402	0	2,959
	3	9	4	3	2	2	1	2	0	10	11	0	44
	4	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-
1951	1	0	0	3	0	0	19	4	0	235	63	0	324
	2	0	0	3	89	18	101	103	8	1,313	107	17	1,759
	3	0	0	4	1	0	270	0	0	94	7	0	376
	4	0	0	0	0	0	146	0	0	79	1	0	226
1952	1	0-	0-	1	5	0	117	90	0	464	87	2	766
	2	0	0	27	51	1	95	194	0	427	731	0	1,526
	3	0	0	8	39	0	49	12	0	168	5	0	281
	4	0	0	0	0	0	37	0	0	19	4	0	60
1953	1	0-	0-	0	0	0	48	199	0	342	94	40	723
	2	0	0	1	0	0	73	509	0	123	370	4	1,080
	3	0	0	1	0	0	86	0	0	100	22	0	209
	4	0-	0-	0	0	0	62	0	0	113	2	0	177
1954	1	0	0-	0	1	0	20	185	93	681	51	110	1,141
	2	1	0	80	320	204	355	63	37	290	140	9	1,499
	3	0	0	4	0	0	59	2	0	166	75	0	306
	4	0	0-	0	0	0	5	0	0	239	3	0	247
1955	1	0-	0-	1	2	8	179	278	285	142	110	0	1,005
	2	0	0	35	146	85	72	99	70	14	8	0	529
	3	0	0	1	31	34	228	4	0	34	9	0	341
	4	0	0	0	0	0	18	0	0	64	2	0	84
1956	1	0-	0-	0	0	0	71	58	33	330	54	0	546
	2	0	0	2	173	48	52	11	14	70	93	0	463
	3	0	0	2	43	9	307	0	0	335	0	0	696
	4	0-	0-	1	0	0	0-	0-	0-	0-	0-	0-	1
1957	1	0-	0-	0	0	0	177	1	2	144	12	0	336
	2	0	0	3	188	4	19	3	1	1	0	0	219
	3	0	20	15	0	0	303	0	0	108	0	0	446
	4	0	0	0	38	0	80	0	0	15	3	0	136
1958	1	0	0	83	52	0	259	0	0	224	21	0	639
	2	3	0	52	27	4	9	2	0	12	1	67	177
	3	0	0	26	94	2	287	1	0	217	0	0	627
	4	0	0	0	0	0	9	0	0	1	0	0	10
1959	1	0	0	74	15	3	24	0	0	35	5	0	156
	2	0	0	33	31	1	15	0	0	19	1	0	100
	3	2	0	2	44	0	82	0	0	78	0	0	208
	4	0	0	19	0	0	67	0	0	20	0	0	106
1960	1	0	0	33	13	0	6	0	0	207	0	0	259
	2	0	0	40	7	0	2	0	0	6	0	0	55
	3	0	0	13	0	0	228	81	0	121	2	0	445
	4	0	0	1	0	0	138	0	5	72	0	0	216
1961	1	0	0	0	29	0	1	0	0	54	0	0	84
	2	0	0	7	4	6	0	8	0	73	0	0	98
	3	0	0	14	2	0	90	0	0	17	0	0	123
	4	0	0	15	0	0	8	0	0	295	19	0	337

TABLE 10.—Continued.

Year	Quarter	Regions[1] CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1962	1	0	0	10	0	0	1	0	0	204	0	0	215
	2	0	0	7	7	0	18	0	0	9	2	0	43
	3	0–	0–	26	1	0	240	0	0	56	23	0	346
	4	0	0	1	1	0	14	0	0	109	2	0	127
1963	1	0	0	50	0	0	62	0	0	3	0	0	115
	2	3	0	1	0	0	0	3	0	10	0	0	17
	3	0–	0–	1	0	3	54	0	0	49	0	0	107
	4	0–	0–	7	5	0	96	1	0	31	0	0	140
1964	1	0	0	1	0	0	0	0	0	229	0	0	230
	2	0	0	0	0	0	0	0	0	9	1	0	10
	3	0	0	4	0	0	22	0	0	159	0	0	185
	4	0–	0–	19	0	0	3	0	0	58	0	0	80
1965	1	0	0	2	0	0	5	0	0	7	0	0	14
	2	1	15	0	0	0	3	0	0	0	0	0	19
	3	0	0	7	0	0	4	0	0	429	1	0	441
	4	0–	0–	1	0	0	406	0	0	216	1	0–	624
1966	1	3	0	1	0	0	19	0	0	49	0	0	72
	2	0	0	10	0	0	1	0	0	2	0	0	13
	3	0	0	1	0	0	50	4	0	262	1	0	318
	4	0	0	1	0	0	238	4	0	87	2	0	332
1967	1	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	2	0–	0–	5	0	0	105	0	0	1,111	0	0	1,221
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	11	0	0	59	0	0	70
1968	1	0	0	0	0	0	0	0	0	0–	0–	0–	0
	2	0	0	2	0	0	5	1	0	0	0	0	8
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1969	1	1	0	1	1	0	5	1	0	0	0	0	9
	2	0	0	3	0	0	10	3	0	30	0	0	46
	3	0	0	1	0	0	48	0	0	25	3	0	77

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

ment between these values lends support to the idea that the method of data assembly causes little bias relative to size of the major fluctuations in anchovy larva abundance. Both the Spearman rank difference and the product-moment correlation coefficients are 0.99.

MacGregor (1968) suggested that the problem of determining the number of batches of eggs spawned per year per female is the major source of imprecision and bias in the adult biomass estimates from egg census and fecundity data. He further suggested that the best strategy for egg census would be to conduct an intensive cruise over a brief period in which no female is likely to spawn more than once. For the purpose of this paper, a preliminary judgment as to the importance of multiple spawnings in the larva ratio estimate of anchovy biomass may be made by comparing three models of spawning behavior. The first model is that the adult biomass is proportional to the regional census estimate. This model assumes that the product of the number of eggs spawned per ton of female, the number of spawnings per year, and the mortality rate of the larvae is stable. The second model is that each anchovy spawns once in the winter quarter. The third model is that each anchovy spawns in the single maximum quarter. Restated, the adult biomass is proportional to the 1) annual average regional census estimate of larval abundance, 2) winter quarter regional census estimate, or 3) annual maximum quarterly regional census estimate. The 1951-66 data for the Ahlstrom standard haul summation, the

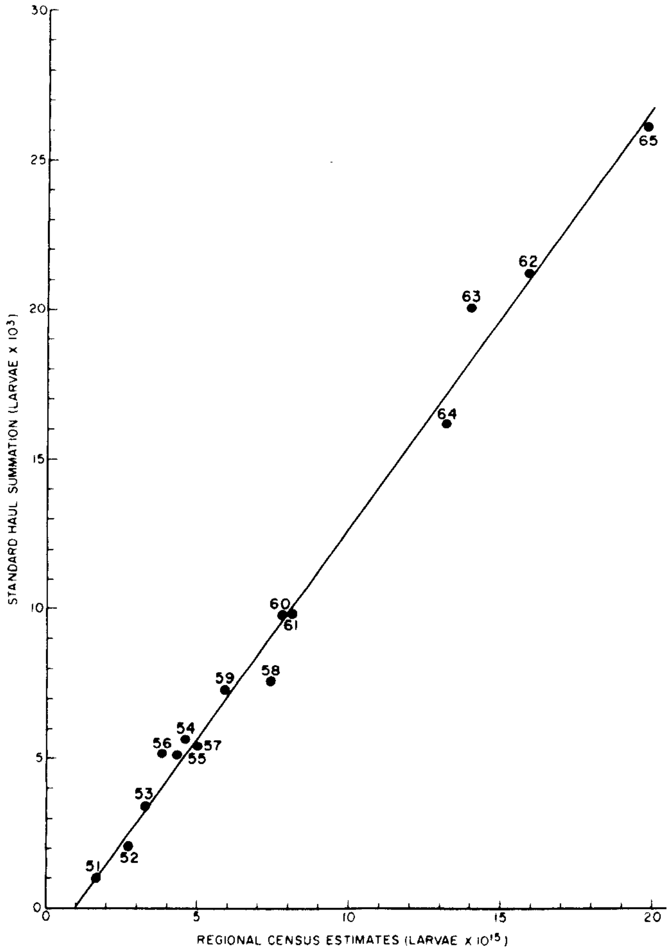

FIGURE 8.—A 16-year comparison of the regional census estimate derived for this paper and the standard haul summation quarterly average (Ahlstrom, 1968).

average regional census estimate, the winter spawning, and seasonal maximum are found in Figure 9. It is clear that the same trend and magnitude of increase are seen from each model. Since there is no obvious difference, the annual average regional census estimate of larva abundance will be used for the current biomass estimates.

It may be seen from Table 9 that the anchovy larvae have increased in number, particularly in the southern California section. Figure 10 illustrates the subdivision of the regional census estimate annual totals by section of the coast from 1951 to 1966. Within the southern California section, the inshore region was the dominant producer of anchovy larvae for the first 7 years. In the next 3 years, the southern California offshore became equally important in numbers of anchovy larvae. Between 1962 and 1965, the seaward region (160-280 miles off the coast) was a very important locality for anchovy larvae and this influence dropped radically to pre-1961 values in 1966 (Figure 11). This change and a smaller one inshore resulted in an appreciable lowering of the overall total in 1966 (Figure 10). The subpopulations of the northern anchovy have been assigned to coastal sections (Vrooman[5]; Vrooman and Smith, 1972),

[5] Vrooman, A. M. Anchovy subpopulations. Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

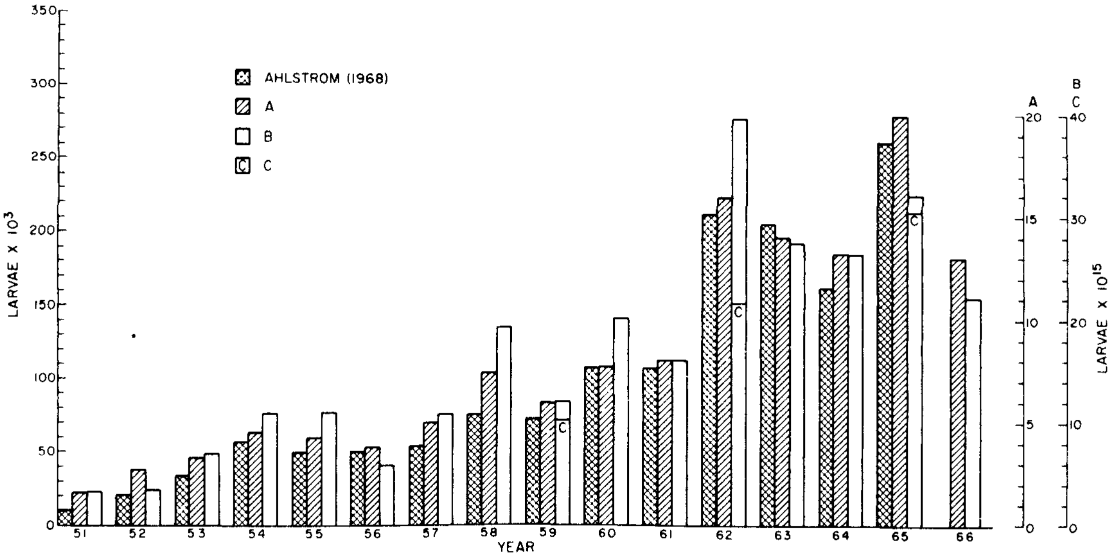

FIGURE 9.—A time-series comparison of the annual quarterly average standard haul summation (Ahlstrom, 1968, double cross-hatch) and the annual quarterly average regional census estimate ("C", clear bar including line C if any).

and the major portion of increase of northern anchovy is ascribed to the "central" subpopulation which spawns off southern California.

The seasonal contribution of anchovy larva abundance from 1951 to 1966 is illustrated in Figure 12. From 1951 through 1959, winter-caught larvae dominated the total. Beginning in 1960, spring larva abundance became increasingly important and, in 1962, substantially exceeded winter larva abundance. As mentioned above, the changing day-length in the spring quarter makes an appreciable difference for which the data have not yet been corrected. The spring-caught larvae are underestimated as a result. No correction has been applied for temperature- or food-specific growth rate changes, by season.

The increase of numbers of anchovy larvae shown in the foregoing regional census estimates could result from the traditional spawning areas being more completely covered with larvae, from new spawning areas being covered, or there being more larvae per unit area. There are instances of all three in the 1951-66 period. In particular, in the southern California section of the coast, where most of the increase took place, the primary effect has been the additional covering of traditional spawning areas. For example, in the southern California offshore region, April through June, 7 of 50 tows contained anchovy larvae in 1953, 25 of 48 tows contained larvae in 1955, and 51 of 53 tows had anchovy larvae in 1959 (14.0%, 52.1%, and 96.2% respectively). If one fits a regression line to the increasing proportions of positive stations with respect to anchovy larvae off southern California the slopes in percent per year from 1952 to 1966 follow:

	Winter	*Spring*	*Summer*	*Fall*
Inshore (0-80 miles)	1	2	1	1
Offshore (80-160 miles)	4	6	4	1
Seaward (160-280 miles)	2	7	2	1

Also, there are more anchovy larvae per positive station than before. In the years 1962-66 there are 5-8 times as many larvae per positive station as in 1951 (Table 11). The number of larvae per positive station is not independent of the proportion of positive stations. One interpretation of samples of larvae is that they are drawn from relatively small (100's of meters, Smith, in press) patches of larvae which are dispersing in such a way that they tend to overlap. For example, for randomly distributed

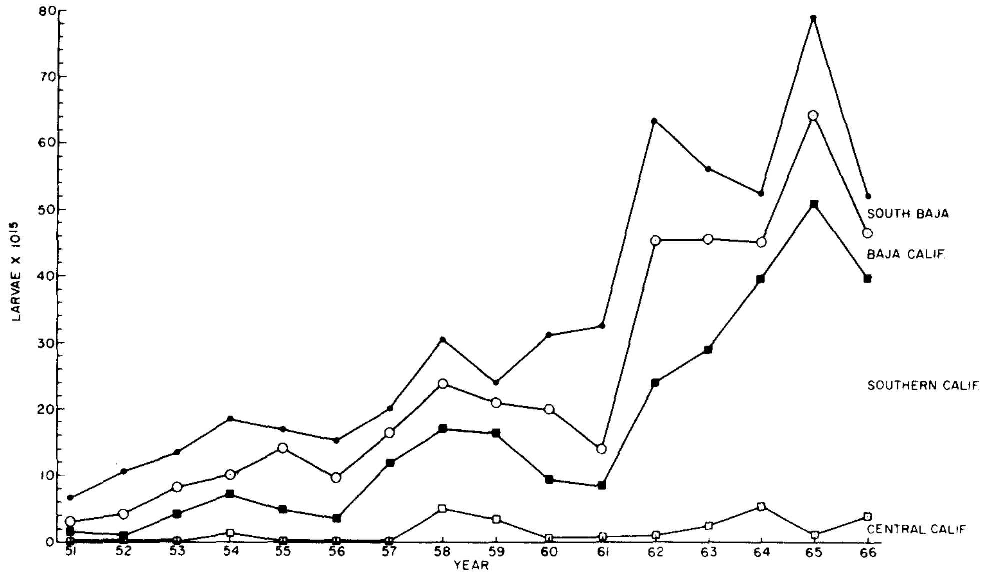

FIGURE 10.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by coastal section. The highest line (solid circle) is comparable to the quarterly average of "A" in Figure 9. The space between the top line and the line with open dots represents the contribution to the total by stations in the south Baja section. The space between the open dot line and the line connecting the solid squares represents the contribution of the Baja California section to the total. The space between the line connecting solid squares and the line connecting open squares represents the contribution of the southern California section. The space between the lines connecting open squares and the abscissa represents the contribution of the central California section to the total. For relative areas of the sections refer to Table 3 and Figure 2.

patches covering 0.1 of the area, the chance of encountering two patches is 0.01; with patches covering 0.9 of the area, the chance of encountering two patches simultaneously is roughly 0.8. In the southern California inshore and offshore regions, the proportion of positive stations is related to the number of larvae per positive station in the following way:

$$\log_{10} N_1 = 3.20\, P_1 - 0.218 \quad t = 11.17 \quad 37\text{ df}$$
$$\log_{10} N_2 = 2.13\, P_2 + 0.748 \quad t = 9.95 \quad 37\text{ df}$$
$$\log_{10} N_3 = 2.32\, P_3 + 0.573 \quad t = 14.40 \quad 76\text{ df}$$

where N_i = number of larvae per 10 m² per positive station in the ith region, when $i = 1$ = southern California inshore region, when $i = 2$ = southern California offshore region, when $i = 3$ the inshore and offshore regions are combined;

P_i = proportion of positive stations in winter and spring in offshore ($i = 2$) or inshore areas ($i = 1$), or both ($i = 3$).

If the patchy model applies, this set of equations is good only for the CalCOFI standard tow, in these two regions. For example on theoretical grounds, if the standard tow were to sample under 20 m² rather than the average 3 m² as at present, one would expect the proportion of positive tows to rise and the number per positive tow to decrease for any given average of anchovy larvae per total unit area.

In addition to an increasing proportion of positive tows in traditional spawning areas and increasing numbers of larvae per positive tow, the southern California seaward region is an example of a new spawning area being invaded in

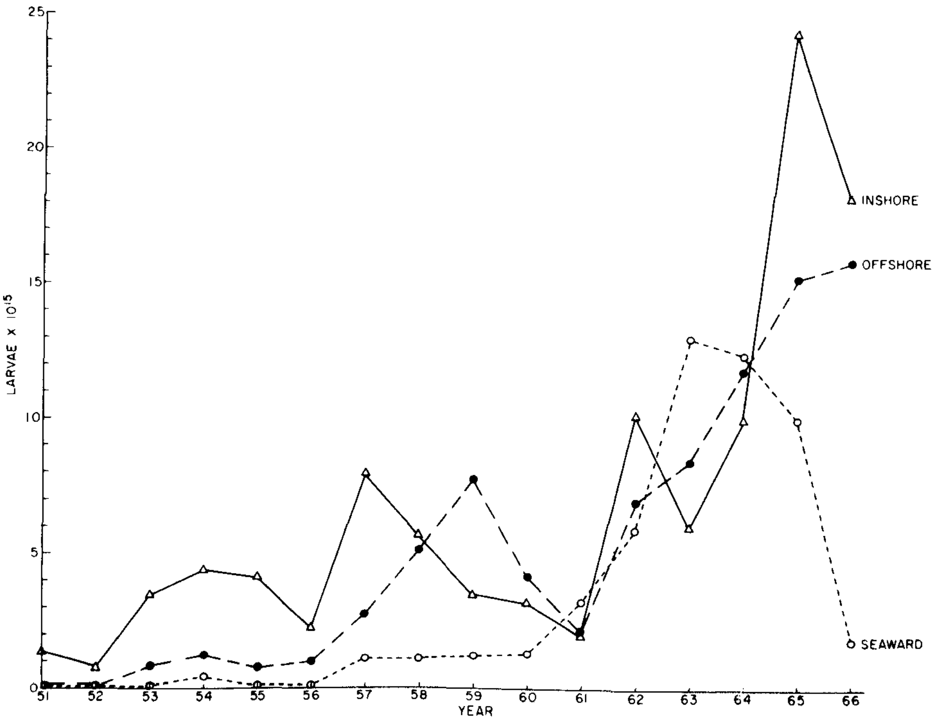

FIGURE 11.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by distance from shore within the southern California section. Lines connecting open triangles represent the southern California inshore, closed circles, the southern California offshore, and open circles, the southern California seaward. For relative areas of the regions refer to Table 3 and Figure 2.

the early sixties and becoming largely unused by the mid-1960's. The incidence of larvae has continued at less than 10% of the 1962 peak year in the southern California seaward region (Table 9).

THE CURRENT ESTIMATE OF ANCHOVY SPAWNING BIOMASS

The practice adopted in this paper for estimating anchovy spawning biomass consists of 1) regression estimates of the relationship between sardine larval abundance and Murphy's estimate (1966) of sardine biomass; 2) the ratio of anchovy: sardine larva abundance until 1958; 3) the regression estimate of the relationship between anchovy larva abundance between 1951 and 1958 and the sardine-derived anchovy biomass; and 4) the use of regression estimates to calculate anchovy and sardine biomass estimates outside the regression period. This differs from Murphy's (1966) method of using an anchovy: sardine ratio for each anchovy estimate. It also differs from Ahlstrom's (1968) method of tying each estimate to the biomass of sardine adults in 1958. Since regressions between two variables with time trends are influenced by the degree of temporal coherence of each variable, caution is warranted in their use. Confidence intervals may be calculated but their meaning is not clear due to the violation of the assumption of independence among the values used to calculate the regression. The regression estimates are used here as a simple shorthand method of reporting an apparent relationship.

The spawner biomass estimates of anchovy and sardine which result from this and previous

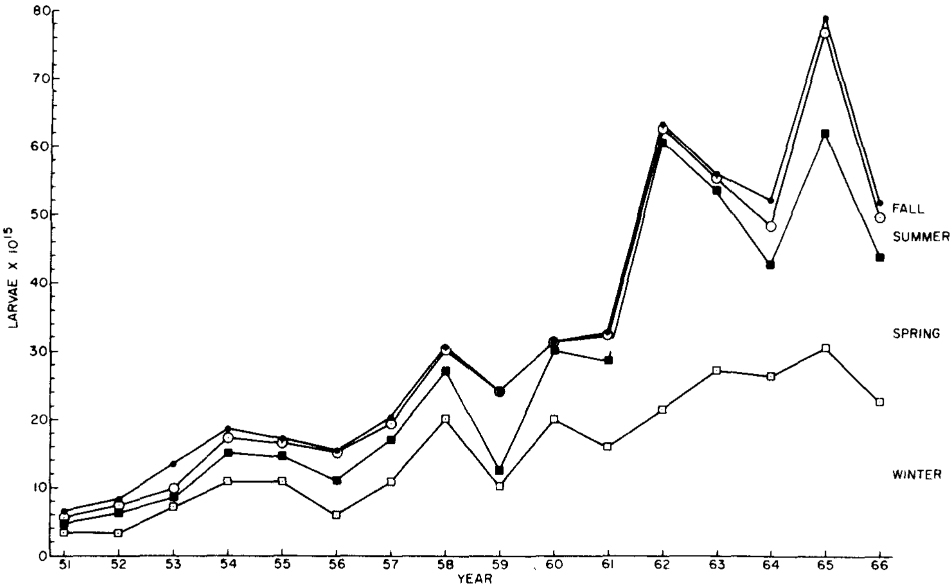

FIGURE 12.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by season of spawning. The highest line (solid circle) is comparable to that found in Figure 10 and to the height of "A" in Figure 9.

studies are found in Table 12. The primary objective of this study concerns the period of increase from 1951 to 1966. Despite various technical deficiencies in the basic data, the years 1940, 1941, 1950, and 1969 are also estimated in the section to follow.

The first column of Table 12, Murphy's (1966) sardine spawner biomass estimates, is reproduced without change. If those estimates are changed by later studies, all other values in the table must be adjusted. The important features of Table 12 are 1) a regression estimate to derive sardine spawner biomass estimates from the regional census estimates of total sardine larvae; 2) a ratio estimate of anchovy spawner biomass which is half the product of the anchovy: sardine ratio and the sardine biomass; and 3) a regression estimate of anchovy spawner biomass derived from the regional census estimate of total anchovy larvae.

The equation for a least squares estimate of sardine spawner biomass and sardine total larvae derived for this study is:

$$B_s = 0.230L_s - 0.057$$

where B_s is the annual estimate of sardine spawner biomass in thousands of short tons and L_s is the regional census estimate annual total of sardine larvae in numbers times 10^{12} in the years 1951-58, excluding 1953. The years 1953 and 1959 were eliminated as outlyers on a scatter diagram when it was found that the assumption of constant size distribution of larvae had been violated. The equation was later simplified by assuming a zero intercept to:

$$B_s = 0.206L_s$$

The anchovy spawner biomass estimates were derived from the ratio of anchovy: sardine larvae and the Murphy sardine biomass estimate in the following way:

$$B_a = c\left(\frac{L_a}{L_s} B_s\right)$$

where B_a is the ratio estimate of anchovy spawner biomass, L_a is the regional census estimate

TABLE 11.—Anchovy larvae per positive station.

Year	No. of positive stations	No. of anchovy larvae	No. of larvae per positive station
1951	344	26,951	78
1952	399	53,457	134
1953	539	85,178	158
1954	626	126,191	202
1955	558	134,017	240
1956	482	104,192	216
1957	518	135,966	262
1958	667	197,082	295
1959	729	182,176	250
1960	628	254,263	405
1961	420	88,925	258
1962	374	190,735	510
1963	370	172,611	466
1964	372	141,498	380
1965	392	234,850	599
1966	738	364,689	494

of anchovy total larvae, and c is a constant representing the relative fecundity of sardine relative to anchovy, here assumed to be approximately 0.5. Lenarz (1972) suggests a constant of escapement of 1.1 to counteract the tendency for anchovy larvae to pass through the mesh openings of the standard silk net to a greater extent than sardine larvae. This experimentally derived estimate from paired tows which captured both species in standard and fine mesh nets is considered too small to be appreciable on the scale of variability encountered in plankton tows. Murphy's (1966) estimate of the escapement factor, i.e., 2, is rejected.

The equation for a least squares estimate of the anchovy spawner biomass and anchovy total larvae is:

$$B_a = 0.094\, L_a + 0.072$$

defined in the same way as the sardine case above. Similarly, the zero intercept was forced, giving:

$$B_a = 0.098 L_a$$

which is the equation used for the regression estimate of anchovy spawner biomass.

The aberrant years 1953 and 1959 were recalculated assuming the slope and the Murphy sardine spawner biomass estimate are correct and that the sardine larva estimates are biased or imprecise. The recalculated estimates (parentheses, Table 12) appear to conform better to the trends of anchovy biomass and anchovy-sardine ratio.

The data from 1940, 1941, 1950, and 1969 have been manipulated to extend the biomass estimates. The 1940 and 1941 cruises were

TABLE 12.—Sardine and anchovy spawner biomass estimates by ratio and regression methods.

	Murphy sardine spawner biomass (×10³T)	Regression sardine spawner biomass (×10³T)	Sardine larval estimate (×10¹²)	Anchovy larval estimate (×10¹²)	Anchovy sardine ratio	Ratio anchovy spawner biomass (×10³T)	Regression anchovy spawner biomass (×10³T)
1940	1,296		1,634*	5,943*	3.64	2,359	
1941	2,001		2,476*	7,104*	2.87	2,871	
. . .							
1950	716		3,343	2,602	0.78	279	
1951	570	553	2,685	6,504	2.42	690	637
1952	554	542	2,633	8,132	3.09	856	797
1953	709	450	2,189 (3,442)**	13,632	6.23 (3.96)**	2,209 (1,404)**	1,335
1954	668	658	3,193	18,533	5.80	1,937	1,816
1955	425	404	1,959	17,100	8.73	1,855	1,676
1956	293	351	1,706	15,215	8.92	1,307	1,491
1957	212	234	1,137	20,040	17.63	1,869	1,964
1958	281	299	1,453	28,272	19.46	2,875	2,771
1959	190	117	570 (922)**	23,463	41.16 (25.45)**	3,910 (2,418)**	2,299
1960		201	975	31,414	32.22		3,079
1961		132	642	32,538	50.68		3,189
1962		151	731	63,758	87.22		6,248
1963		78	379	61,533	162.36		6,030
1964		104	505	52,253	103.47		5,121
1965		226	1,098	79,292	72.21		7,771
1966		151	735				
. . .				52,200	71.02		5,116
1969		27†	132†	33,623†	254.72†		3,293†

* 1940, 1941—larval estimates seasonally adjusted.
** Parenthetic numbers for 1953 and 1959 assume larval numbers biased.
† 1969—larval counts 75% complete; adjusted for extra retention of small larvae.

conducted during the sardine spawning season, but excluded an important portion of the anchovy spawning season. Similarly, the cruises only sampled 20% of the area we now consider routinely surveyed. The ratio of sardine and anchovy larvae was used for 1950 and will not be discussed further. The 1969 samples systematically violated the assumption of stable size composition of larvae.

The cruises of 1940 and 1941 were conducted over the southern California inshore and offshore regions in the spring and summer. The total for both species in both regions and in both years was derived by simulation of analogous cruises within the 1951-60 survey period and the product-moment correlation coefficient is listed for each species, for each region, and year.

Year	*Species*	*Region*	*Original*	*Seasonally adjusted*	*Correlation coefficient*
1940	Anchovy	SCI	1,545	3,229	0.794
		SCO	820	2,714	0.945
		Total	2,365	5,943	
1940	Sardine	SCI	502	726	0.794
		SCO	891	908	0.955
		Total	1,393	1,634	
1941	Anchovy	SCI	1,494	3,257	0.845
		SCO	2,104	3,847	0.962
		Total	3,598	7,104	
1941	Sardine	SCI	987	1,305	0.807
		SCO	1,161	1,171	0.981
		Total	2,148	2,476	

The ratio of this group of samples, within the same boundaries as the other regional census estimates used here, change from 1.70 to 3.64 in 1940 and change from 1.68 to 2.87 in 1941. Accordingly, these ratios are used in Table 12.

The 1969 data point for anchovy is modified in a crude attempt to adjust for the extra retention of anchovy larvae in a new sampling net (see Figure 4) which retains approximately 50% more larvae. The 1969 surveys were conducted with a 1-m net with 50% more open area, more regular mesh apertures, and an average mesh width of 0.505 mm rather than the 0.55 mm aperture silk net (used and wet). The effect of additional mesh on reducing the extrusion effect of filtration pressure is discussed in Tranter and Smith (1968).

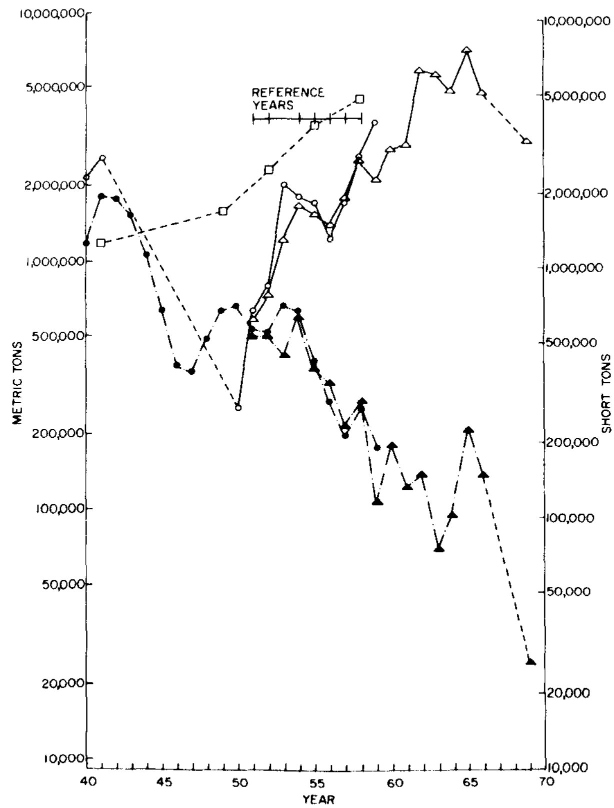

FIGURE 13.—A time-series comparison of sardine and anchovy biomass estimates from 1940 through 1969. The solid circle represents sardine biomass as calculated from the fishery by Murphy (1966) and extends from 1940 to 1959. The solid triangle represents sardine biomass derived from a regression estimate of the relationship between the Murphy biomass estimate and the annual total regional census estimate of sardine larvae during the reference years and is extended from 1951 through 1969. The open circle represents the estimates of biomass derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate from 1940 to 1959. The open triangle represents anchovy biomass derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy:sardine larvae ratio, and the annual total regional census estimate of anchovy larvae and extends from 1951 through 1969. The open squares represent the Murphy estimate of anchovy spawning biomass by 3-year averages (Murphy, 1966, Figure 17, p. 65). Dashed lines represent interpolations between nonadjacent years.

Figure 13 contains all the estimates resulting from this study. Murphy's sardine biomass estimates are plotted from 1940 to 1959. The anchovy biomass estimates derived from the anchovy sardine ratio and the anchovy larva regional census in 1940, 1941, and 1950 through 1959. The regression estimates are reproduced from 1951 to 1959 for comparison with the Murphy sardine biomass and ratio-derived anchovy biomass. The regression estimates of both sardine and anchovy spawner biomass are extended through 1966 and a tentative estimate for 1969 is placed for comparison.

DISCUSSION

Important changes in the size of the anchovy population have occurred in the California Current area over the past two decades. The increase of anchovy has coincided with the continuing decrease of sardine in the same area. All available evidence indicates that the anchovy and sardine populations declined between 1941 and 1951, and thereafter the anchovy underwent a sustained increase reaching a plateau of 5-8 million metric tons between 1962 and 1966. This population size may be between 2 and 3 times the anchovy spawning population of 1940-41 and between 5 and 10 times the anchovy population in 1950-51. Changes of this magnitude in the absence of a fishery underscore the importance of natural fluctuations in the population size of a fish species. Fishery management of such a species must be responsive to changes of this magnitude and rapidity.

Murphy (1966, 1967) speculated on the effect of the anchovy population on the recovery of the sardine population. Neither the feeding of anchovy and sardine nor the population dynamics of the food organisms is well enough understood in the California Current. Since the size frequency curves of larvae are relatively invariable (Ahlstrom, 1965; Lenarz, in press) one would expect competition, if any, to occur in the juveniles and pre-recruits of either species.

One interesting fact may be the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. In the estimates of spawner biomass of sardine and anchovy, no attention has been given the possibility that fecundity in numbers of eggs per batch and number of batches per unit time is plastic.

The numbers of anchovy and sardine larvae have been used here exclusively to describe changes in the adult biomass which spawned them. Since this process seems so effective, one might wonder what is required to refine techniques so that spawning, and larval and juvenile survival, may be used to predict the recruitment of year classes to the fishery. I believe the two major barriers are that 1) the size composition of the larvae of both species is so dependent on the sampling gear that mortality rates will remain too crude to project survival and 2) the effect of transport of larvae, particularly offshore to "unfavorable" areas, is neither well enough measured nor understood to effect predictive sampling systems.

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