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Racial and Seasonal Variation in the Pacific Herring, California Sardine and California Anchovy[*]

BY

CARL L. HUBBS

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1. I. INTRODUCTION

This study of the variation in certain commercially important clupeoid fishes of western North America is one of a series by which it is designed to determine the relation which the varying characters of fishes bear toward the physical features of their environment. Although other characters and other environmental factors are receiving attention in these investigations, chief stress is now being laid on the correlation

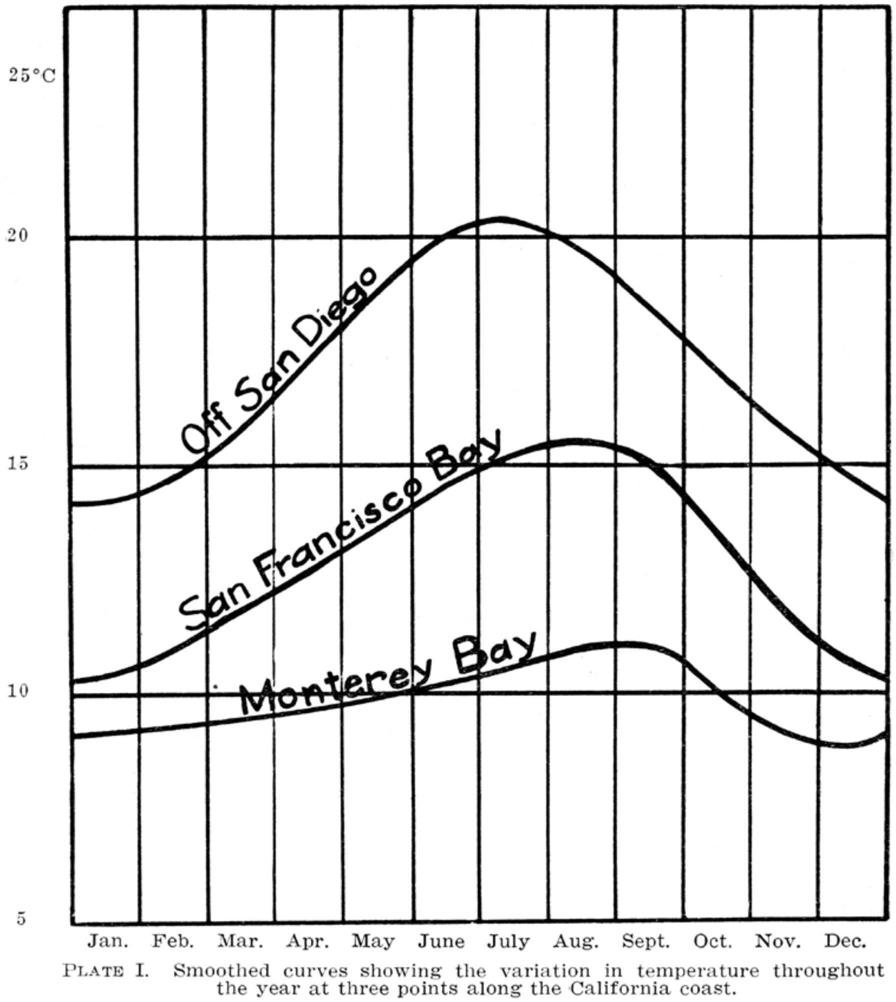

PLATE I. Smoothed curves showing the variation in temperature throughout the year at three points along the California coast

between the average number of vertebrae and the temperature of the water.

The average surface temperature of the coast waters of San Francisco Bay (Golden Gate), Monterey Bay (Pacific Grove) and San Diego (off Coronado Beach) is indicated for the whole year by the three curves on Plate I. The marked difference in temperature between the ocean water of southern California and central California is illustrated by the curves for the San Diego region and for Monterey Bay, which is really a very open gulf. The usual maximum temperature for Monterey is lower than the ordinary minimum off San Diego. These is not an even gradation of temperature between these two localities, Point Conception marking the boundary between the cold waters of the central coast and the warmer waters of southern California. In each region, moreover, there is much local variation in temperature conditions, due not only to differences in protection and depth, but also, probably, to the differential upwelling of deep, cold water (McEwen, 1912, 1916). The curve for San Diego is taken from McEwen's 1916 paper; that for Monterey is smoothed from unpublished data supplied by Director Walter K. Fisher of the Hopkins Marine Station at Pacific Grove. The temperature curve at the entrance to San Francisco Bay, constructed by slightly smoothing Davidson's (1886) monthly averages, is intermediate between the San Diego and the Monterey Bay curves. The higher temperatures at San Francisco as compared with the Monterey records are due to the greater warming of the waters in the shallows of San Francisco harbor.

As the fishes here treated are of great importance from the standpoint of the commercial fisheries, this paper is published in the present form largely as a contribution to the fishery-biology of these species. An attempt to determine definitely the racial status of the various populations of each form would, however, be beyond the scope of the present paper. Our data, however, are brought to bear on such problems. This is done to suggest conclusions, and to make our data available to the fishery investigators.

We have applied to our data on the herring and the anchovy a method of analysis which we have found useful in studying the seasonal variation in the number of segments in freshwater fishes (Hubbs, 1922, 1924). By this method the correlation between individual variations and environmental factors is determined. Measure is obtained, also, of the degree to which the average number of segments fluctuates on a purely individual, as contrasted with a racial basis. The results so secured are of value in interpreting the significance of observed differences in the average number of segments for samples from different localities.

2. II. THE PACIFIC HERRING
(Clupea pallasii)

This study of variation in the Pacific herring is a continuation and extension of the investigations made by Thompson (1917). Our results are in essential agreement with his.

2.1. Material

Our material of the Pacific herring used in these variation studies comprises 208 young collected by Mr. Will F. Thompson in the Straits of Georgia, British Columbia; several series from San Francisco Bay, as described below; 89 adult specimens taken with sardines in Monterey Bay, and obtained for us by Mr. W. L. Scofield, and four mature specimens from the ocean side of Point Loma, near San Diego.

Our San Francisco Bay series were obtained in the fall of 1922 and the spring of 1923. During October, November and the early part of December, young herring 63 to 90 mm. long (to caudal fin) were obtained in several parts of the bay by means of shrimp nets, shrimp trawls and beach seines, and a few adults, representing the vanguard of the breeding run, were seined at Sausalito. A good series of adults, 149 to 199 mm. long, were obtained on December 21, at about the beginning of the breeding season. A large number of immature, half-grown fish, 79 to 115 mm. long, were collected with a shore seine at Sausalito on April 14–17 at almost the close of the breeding season. With these were taken a very few young of the year, a series of small adults 116 to 151 mm. long, and a single mature female of larger size (176 mm. long). Many young, 36 to 71 mm. long, were taken at the same place on June 5, in a large fine-meshed beach seine, dragged in from a depth of about twenty feet.

2.2. Age determinations

Since the San Francisco material was utilized in studying seasonal as well as geographical variation in the number of vertebrae, it was analyzed into age groups. The age determinations were made by means of the size frequency method, supplemented by the examination of a few scales. The size frequency data are given as Plate II.

The five very young, 22 to 33 mm. long, taken in April, were obviously the young of the year, hatched out earlier in the same spawning season; the specimen 55 mm. long taken with these was presumably of the same year group, for no annulus (winter line) could be found on its scales. The young, 36 to 71 mm. long, taken June 5, assuredly represent *in toto* the same year group.

The skewness of the curve representing the lengths of these specimens is probably caused by the seaward migration, and hence elimination, of the majority, but not all, of the larger young. The small herring, 53 to 90 mm. long, taken in October, November and December, doubtless represent the few young of the year which remain in the bay to, or during, their first winter.

The half-grown herring, 79 to 115 mm. long, taken about the middle of April, are of course yearling fish. They are all immature, and their

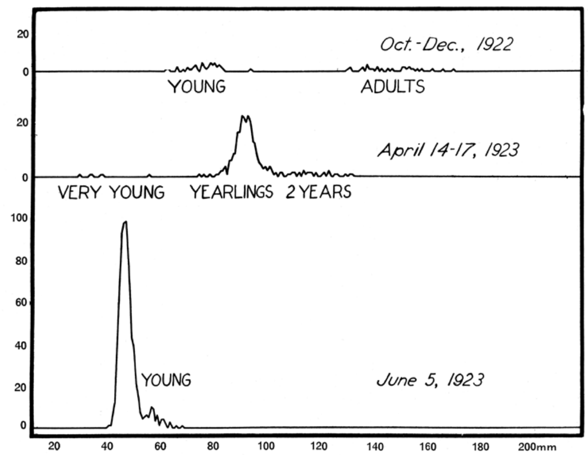

PLATE II. Year groups of herring in San Francisco Bay.

PLATE II. Year groups of herring in San Francisco Bay presence in the bay in large numbers points to a pre-spawning inshore migration. The larger herring taken at the same time are mostly mature or maturing. They are mostly smaller than the mature herring taken about the beginning of the breeding season, the latter being represented by the December 21 sample. Most of these small, late-spawning herring are probably two years old (a maturing female 118 mm. long, shows two clear-cut annuli on the scales). The single large herring taken in April, a mature female 176 mm. long, shows several annuli on its scales.

2.3. Variation in number of fin rays

Thompson compared counts of dorsal fin rays of herring from Point Grey and Nanaimo in British Columbia, and from San Francisco in California. From his study he concluded, "In so far as the number of dorsal rays is concerned, the results seemed to show no decided differences between herring from Nanaimo and San Francisco." The average number of rays was somewhat higher for the San Francisco than for the Nanaimo lot, but the difference between the averages for these localities was less than the differences between the averages for the two British Columbia series. Our own counts are confined to the San Francisco Bay form, and give an average considerably lower than Thompson's for this race, although also higher than his averages for the British Columbia series. The differences are on the border line of statistical significance. It is probable, however, that the average number of dorsal rays is slightly higher in the San Francisco than in the British Columbia race, but further counts are required to determine the degree to which the variation may fluctuate within each race. The available data are all tabulated (Table 1) .

FREQUENCY TABLE 1.[1]

Variation in number of dorsal rays in different samples of herring.

Locality	Branched rays					N.	Av.	P. E.
	12	13	14	15	16			
Point Grey, B. C.	2	15	**87**	57	—	161	14.24	0.04
Nanaimo, B. C.	—	12	**106**	86	5	209	14.40	0.03
San Francisco Bay (Thompson)	—	5	33	**40**	7	85	14.58	0.05
San Francisco Bay (Hubbs)	2	13	**103**	92	17	227	14.48	0.03

Locality	Total rays					N.	Av.	P. E.
	16	17	18	19	20			
Point Grey, B. C.	2	27	**96**	36	—	161	18.03	0.03
Nanaimo, B. C.	—	16	**114**	74	4	208	18.32	0.03
San Francisco Bay (Thompson)	—	8	**38**	34	5	85	18.42	0.05
San Francisco Bay (Hubbs)	2	16	**111**	85	15	229	18.41	0.03

[1]In this and following tables the number of specimens having each given number of rays (or other character) is given for each lot of specimens. In the three last columns, N.=the total number of specimens of each lot; Av.=the arithmetic average; P.E.=the probable error (plus or minus) of the average, computed by means of the following well-known formula:

$$\pm 0.6745 \frac{\text{Standard deviation}}{\sqrt{N}}$$

FREQUENCY TABLE 1.
Variation in number of dorsal rays in different samples of herring

In the case of the average number af anal rays, Thompson found a much sharper difference to separate the San Francisco sample from those of British Columbia. In this case the southern race had the lower average number of rays. This difference our San Francisco counts fully confirm, as our averages are even lower than Thompson's. The counts and computations involved are presented in Table 2.

FREQUENCY TABLE 2.

Variation in number of anal rays in different samples of herring.

Locality	Branched rays							No.	Av.	P. E.
	10	11	12	13	14	15	16			
Point Grey, B. C.	—	—	9	63	**69**	21	2	164	13.66	0.04
Nanaimo, B. C.	—	—	8	81	**90**	19	2	200	13.63	0.04
San Francisco Bay (Thompson)	—	1	12	**36**	30	5	1	85	13.34	0.06
San Francisco Bay (Hubbs)	1	5	47	**115**	51	6	—	225	13.01	0.04

Locality	Total rays							N.	Av.	P. E.
	13	14	15	16	17	18	19			
Point Grey, B. C.	—	—	16	59	**68**	21	—	164	16.57	0.04
Nanaimo, B. C.	—	—	19	77	**84**	18	2	200	16.53	0.04
San Francisco Bay (Thompson)	—	1	13	**38**	27	5	1	85	16.29	0.06
San Francisco Bay (Hubbs)	1	9	56	**109**	45	6	—	226	15.91	0.04

FREQUENCY TABLE 2.

Variation in number of anal rays in different samples of herring

2.4. Geographical variation in number of vertebrae

There are now available for comparison vertebral counts for 2226 specimens of the Pacific herring. The data may be arranged, by approximation of averages, in three distinct groups, each in all probability representing a distinct race or complex of races.

The White Sea race, from the Arctic coast of Europe, shows the highest average number (53.56) of vertebrae, and the highest modal number (54). This race, studied by Heincke (1898) in his classical work on the natural history of the herring, has usually been regarded as representing the Atlantic species Clupea harengus. Considering it as such, Schmidt (1917, pp. 333–335) has laid emphasis on the fact that the characters of this race are a marked exception to the rule that the number of vertebrae increases toward colder water. This point can hardly be regarded as valid, however, for not only the low number of vertebrae, but also the greatly reduced carination of the belly, the deep body, and the small size attained, all indicate that the White Sea herring should be aligned with the Pacific species, Clupea pallasii. As such, it shows, as would be expected, an increased number of segments.

The various British Columbia samples, representing one or more races, all exhibit an intermediate number of vertebrae, the average fluctuating from 52.69 to 52.83, the mode being in all cases 53. Five of the seven samples were counted by Thompson (1917).[2] Our counts are based on additional material collected by Thompson in the Straits

[2] Since Thompson's results were given with the hypural excluded, all his counts are here increased by one to bring them into agreement with our own.

of Georgia, British Columbia. of our two series, one yields an average almost identical with the grand average of Thompson's series; the other gives an average a little lower than any of Thompson's five.

The California race, possibly a compound of several local races, exhibits the lowest average and modal number of segments. The average fluctuates between 51.53 and 52.03, while the mode remains constantly at 52. Thompson's one series from San Francisco, comprising only 85 specimens, gives the lowest average number of vertebrae (51.53).[3]

FREQUENCY TABLE 3.

Variation in the number of vertebrae in the Pacific herring.

Locality	Authority	Vertebrae										N.	Av.	P.E.
		46	47	48	49	50	51	52	53	54	55			
White Sea, Arctic Europe	Heincke (1898, p. 89)	—	—	—	—	—	—	2	21	**24**	3	50	53.56	0.06
Pender, B. C. (Oct. 18)	Thompson (1917)	—	—	—	—	—	2	23	**60**	11	—	96	52.83	0.04
Pender, B. C. (Oct. 16)	Thompson (1917)	—	—	—	—	1	7	89	**150**	32	2	281	52.75	0.03
Kildonan, B. C.	Thompson (1917)	—	—	—	—	—	8	73	**189**	35	—	305	52.82	0.02
Nanaimo, B. C.	Thompson (1917)	—	—	—	—	—	4	51	**136**	19	—	210	52.81	0.03
Point Grey, B. C.	Thompson (1917)	—	—	—	—	—	5	50	**88**	19	1	163	52.76	0.04
Straits of Georgia, B. C.	Original counts	—	—	—	1	—	1	35	**53**	10	—	100	52.69	0.05
Straits of Georgia, B. C.	Original counts	—	—	—	—	—	1	33	**62**	12	—	108	52.79	0.04
British Columbia totals		—	—	—	1	1	28	354	**738**	138	3	1263	52.78	0.01
S. F. Bay	Thompson (1917)	1	—	—	3	3	29	**39**	10	—	—	85	51.53	0.08
S. F. Bay (Dec. 21)	Original counts	—	—	—	—	5	74	**122**	30	—	—	231	51.77	0.03
S. F. Bay (June 5)	Original counts	—	—	1	1	10	153	**249**	85	5	—	504	51.83	0.02
Monterey Bay, Calif.	Original counts	—	—	—	—	2	20	**41**	25	1	—	89	52.03	0.06
Off San Diego, Calif.	Original counts	—	—	—	—	—	2	1	1	—	—	4	51.75	0.28
California totals		1	—	1	4	20	278	**452**	151	6	—	913	51.81	0.02

FREQUENCY TABLE 3.
Variation in the number of vertebrae in the Pacific herring

2.5. Seasonal and annual variation in number of vertebrae

In order to determine whether observed differences in the number of vertebrae (or other character) between different localities are racial or only individual expressions, it is of high value to determine to what degree the average varies at one locality, in respect to the year and to the season of hatching. We find that this viewpoint and method of analysis, although to that time generally overlooked, was realized and utilized by Thompson in his 1917 paper on the Pacific herring.

Thompson analyzed his counts of the vertebrae into year groups III, IV and V, and into the larger and smaller specimens in each of these three groups. The various averages thus obtained fluctuate about as widely as the averages for the different localities in British Columbia. Unfortunately, however, the number of specimens is so few that the results, although of probable, are not of certain, statistical significance. In comparing the average number of vertebrae of the smaller and the larger specimens of given year groups, Thompson assumed that he was determining "the effect of rate of growth on the number of vertebrae, or, to put it more correctly, the correlation between rate of growth and vertebrae." He computed the average number of segments: For 63

[3] Thompson gives the average twice as 50.68 (equivalent to 51.68), but his data yield the average here adopted. In several other cases our computations from his figures differ slightly from his own averages.

"slow-growing" fish as 51.71; for 77 "fast-growing" fish as 51.81. He thought that the difference "might be of significance when corroborated by a greater number of counts." If the difference should prove valid, however, we would be more inclined to interpret it as due to seasonal variation, since the number of vertebrae is fixed at a very early stage in development. In this view, the earlier spawned fish, developing on the average at colder temperatures, form the higher average number of segments. Due to their earlier start they would grow on the average more during their first year. This would account, then, for the higher average number of segments exhibited by the larger fish of given year groups. This latter view is corroborated by our own work on the Pacific herring (see below) as well as that on the anchovy (p. 14) and on certain freshwater fishes (Hubbs, 1922, 1924).

Our San Francisco material is more suitable than Thompson's for a study of seasonal variation in segment number in the herring. It involves a sample of mature fish taken December 21, 1922, which may be regarded as roughly representing the parent stock of the 1923 brood, and a large representative sample of that brood, seined after the close of the spawning period, on June 5, 1923.

The average number of vertebrae for the 1923 brood was determined as 51.83, a value hardly significantly higher than the average (51.77) for the parent stock. The smaller of the young specimens (36 to 46 mm. long, to caudal fin), however, exhibited an average even lower (51.73) than for the adult fish. The larger specimens, which on the average were developed earlier in the season, and hence at a lower temperature, showed a notably higher average number of segments (51.99). This last average is almost as high as the average for the Monterey set (52.03) a fact casting a very serious doubt on the racial distinction of the San Francisco and Monterey herring. Even without including Thompson's value (51.53) for the San Francisco Bay herring, which is much lower than any of ours, the observed fluctuation of the average number of segments within this one race is greater than the fluctuation recorded for all the British Columbia samples. As this fluctuation of the average number of segments in the San Francisco herring is presumably individual, the differences in vertebral number between the averages for different localities in British Columbia can not be regarded as of demonstrated racial meaning. On the other hand, our results do not prove that the differences are not racial.

FREQUENCY TABLE 4.

Annual and seasonal variation in the number of vertebrae in herring from San Francisco Bay.

Date	Remarks	Vertebrae									N.	Av.	P.E.
		46	47	48	49	50	51	52	53	54			
	Thompson (1917)	1	—	—	3	3	29	**39**	10	—	85	51.53	0.08
Dec. 21, 1922	"Parent stock"	—	—	—	—	5	74	**122**	30	—	231	51.77	0.03
June 5, 1923	36 to 46 mm. long	—	—	1	1	8	111	**143**	43	4	311	51.73	0.03
June 5, 1923	47-71 mm. long	—	—	—	—	2	42	**106**	42	1	193	51.99	0.03
June 5, 1923	All material	—	—	1	1	10	153	**249**	85	5	504	51.83	0.02

FREQUENCY TABLE 4.

Annual and seasonal variation in the number of vertebrae in herring from San Francisco Bay

3. III. THE CALIFORNIA SARDINE.
(Sardinia caerulea)

In the case of the sardine of the California coast we have made a study of the variation in only one character, namely the total number of vertebrae. Other characters in addition to this one have been investigated by the staff of the State Fisheries Laboratory. Until the results of these more extensive investigations are published, it would be premature to offer any generalizations regarding the existence or non-existence of genetically distinct races within the species Sardinia caerulea.

3.1. Material

We ourselves have counted the vertebrae in series of sardines from four localities—San Francisco Bay and Monterey Bay in central California, and the vicinity of San Pedro and of San Diego in southern California.

The material from San Francisco Bay was seined with a fine-meshed beach seine in a cove near Sausalito, on April 17, 1923. The fishes were apparently nearly all of the yearling group, since a similar sample taken the day previous were regarded as such by members of the State Fisheries Laboratory staff.

The Monterey lot comprised a market sample taken by Mr. W. L. Scofield, and kindly submitted to us by Mr. Will F. Thompson. Many of these specimens were very large, most were rather large, but some were rather small.

The 120 specimens from Redondo Beach, Los Angeles County, were picked out of a large quantity of bait anchovies on a Japanese mackerel boat at the San Pedro market in October, 1922. These small sardines were examined by Mr. Elmer Higgins of the Fisheries Laboratory, and interpreted by him as being all young of the year. The 92 specimens composing our San Pedro series were all of large size. They were obtained from fishermen through Mr. Thompson.

The San Diego sardines, mostly of medium to rather small size, were also secured from the Fisheries Laboratory.

Other market samples from San Pedro and San Diego were used for vertebrae counts by Mr. Gale Hunt, and others from Monterey by Mr. W. L. Scofield, while working at the Fisheries Laboratory under the direction of Mr. Thompson. These counts have very generously been made available for use in the present connection.

3.2. Results

We embody in the following table (5) the counts of the vertebrae in all the material listed above.

FREQUENCY TABLE 5.

Number of vertebrae in different series of California sardines.
(Localities listed from north to south.)

Locality	Vertebrae				N.	Av.	P. E.
	50	51	52	53			
San Francisco Bay	—	49	**123**	17	189	51.83	0.03
Monterey Bay	1	66	**139**	15	221	51.76	0.03
Monterey Bay*	4	114	**244**	28	390	51.76	0.02
Redondo Beach	—	35	**80**	5	120	51.75	0.03
San Pedro	1	28	**53**	10	92	51.78	0.04
San Pedro*	9	113	**181**	14	317	51.63	0.02
San Diego	—	84	**177**	15	276	51.75	0.02
San Diego*	6	107	**177**	15	305	51.66	0.02
Central California	5	229	**506**	60	800	51.78	0.01
Southern California	16	367	**668**	59	1,110	51.69	0.01

*Series so indicated were counted by Mr. Gale Hunt or Mr. W. L. Scofield, under the direction of Mr. Will F. Thompson. The other sets were counted by the present writer.

FREQUENCY TABLE 5.
Number of vertebrae in different series of California sardines. (Localities listed from north to south.)

3.3. Interpretation

The 800 sardines counted from central California show a higher average number of vertebrae than do the 1110 examined from southern California. The difference, though slight (0.09 of a vertebrae), appears to be statistically significant, being five times the probable error of the difference (0.018). But even greater differences appear between the averages obtained from different samples taken at the same port (San Diego, San Pedro). These differences between samples can be most readily explained as the consequence of annual variation, and hence as having a purely individual and not a racial significance. Alternative possibilities are, however, not excluded. Some of the values for southern California samples are about as high as the average number for Monterey.

Hence it can not be assumed that a real racial distinction between central Californian and southern Californian sardines has been demonstrated. On the other hand, we have not indicated that such a distinction does not exist. Further studies will be required to determine this point. The announcement of the results of such investigations will be awaited with much interest.

In the European sardine (Sardinia sardina), according to the determinations of Fage (1920), the average number of vertebrae increases fairly regularly and extensively toward the north.

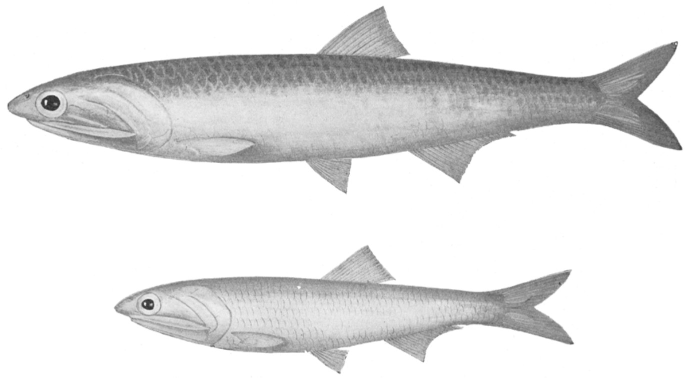

PLATE III. The two subspecies of the California anchovy (life size).

PLATE III. The two subspecies of the California anchovy (life size)

4. IV. THE CALIFORNIA ANCHOVY.
(Engraulis mordax)

The study we have made of the variation of the California anchovy has indicated the existence of two very sharply differentiated races (see Plate III) . of these, one is very local in its distribution, being confined to San Francisco Bay. It may be regarded as a distinct subspecies, to be named Engraulis mordax nanus Girard. Its status is discussed at the end of this section. The ocean subspecies, when distinguished as such, will be known as Engraulis mordax mordax.

4.1. Material of ocean subspecies

of the typical or ocean race of the California anchovy, Engraulis mordax mordax, we have studied material from five localities in central and southern California, namely San Francisco Bay, Monterey Bay, Redondo Beach, Anaheim Bay, Coronado (listed from north to south).

The specimens of the ocean anchovy from San Francisco Bay, chiefly adults, were largely collected at Sausalito on April 16, and 17, 1923. They were seined along shore in company with a typical example of E. m. nanus. A few other examples, half grown, were picked out of a series of nanus caught November 3, 1922, in Chinese shrimp nets in San Francisco Bay proper (off Hunter's Point and off Alameda).

The Monterey Bay specimens, all adults, were caught October 16, 1922, in sardine nets. They were kindly obtained and preserved for us by Mr. W. L. Scofield of the Fish Commission staff.

The anchovies from the nearly open coast at Redondo Beach, Los Angeles County, were taken in a fine-meshed bait net by a Japanese mackerel boat, on October 9, 1922. They were all young, varying in length from about 44 to 83 mm. Probably all were young of the year, since approximately three-fourths (74 per cent) of the lot varied in length from 45 to 60 mm., and thus overlapped the limits of size of the next set, which were obviously young of the year.

Those from Anaheim Bay, a muddy slough system in Orange County, were collected by means of a shore seine on October 7, 1922, with the help of Mr. Will F. Thompson. They were obviously all young of the year, the smallest being in transformation from the postlarval to the juvenile stage. In size they varied from 32 to 60 mm. (see page 17).

The Coronado lot represents a sample from a single large school of nearly ripe adults. It was obtained April 30, 1923.

4.2. Latitudinal variation in the ocean subspecies

The number of vertebrae of the ocean subspecies of the California anchovy was found to vary from 44 to 47, most individuals having either 45 or 46. With locality the averages obtained fluctuate between 45.89 and 45.48, or nearly half a vertebra. As in the case of the sardine the central California samples show somewhat higher averages than the southern California series, the difference (0.10) being five times as great as its probable error (0.02). The southward decrease, however, is highly irregular. The data are presented in the table following:

FREQUENCY TABLE 6.

Number of vertebrae in different series of the ocean subspecies of the California anchovy.

Localities (north to south)	Vertebrae				N.	Av.	P. E.
	44	45	46	47			
San Francisco Bay	3	41	70	13	127	45.73	0.04
Monterey Bay	4	102	182	20	308	45.71	0.02
Redondo Beach	13	287	341	26	667	45.57	0.01
Anaheim Bay	5	103	95	5	208	45.48	0.03
Coronado	6	212	341	43	602	45.70	0.02
Central California	7	143	252	33	435	45.71	0.02
Southern California	24	602	777	74	1,477	45.61	0.01

FREQUENCY TABLE 6.

Number of vertebrae in different series of the ocean subspecies of the California anchovy

In the European anchovy Engraulis enchrassicholus, Fage (1911, 1920) found likewise a very irregular decrease southward in the number of segments. The differences between the various samples of the European species, however, are much more pronounced than in the case of Engraulis mordax.

In addition to the differences in the number of vertebrae, our samples of the ocean anchovies show other slight average differences. The Monterey Bay specimens have, on the average, a somewhat less terete body. They also show a slightly longer head than those from San Francisco, and possibly a longer head than those from southern California (difference in average respectively 4.2 and 1.7 times its probable error). In these respects the Monterey race barely approaches the San Francisco Bay supspecies. The variation in the length of the head, measured to the end of the opercular membrane, and expressed in percentages of the total length to the base of the caudal fin (end of hypural bone) is indicated in Table 7.

FREQUENCY TABLE 7.

Length of the head (in hundredths of the total length) in Engraulis mordax mordax.

Locality	Proportionate length of head											N.	Av.	P. E.
	26.5	27.0	27.5	28.0	28.5	29.0	29.5	30.0	30.5	31.0	31.5			
San Francisco Bay	1	1	6	8	20	14	14	10	4	2	1	81	28.97	0.14
Monterey Bay	—	—	—	—	3	6	12	11	6	5	—	43	29.80	0.14
Southern California	—	—	—	1	6	21	13	12	7	1	2	63	29.51	0.12

FREQUENCY TABLE 7.

Length of the head (in hundredths of the total length) in Engraulis mordax mordax

The differences shown in Table 7 can not be due to the size of the specimens, for all are adult (more than 100 mm. long), and those from Monterey average the largest. Among the adult anchovies, the proportionate length of the head decreases with increased size of the body, as is indicated in Plate IV.

The wide difference between the average number of vertebrae for the Anaheim Bay and Coronado samples of the California anchovy is surprising, as these localities lie within a rather small area of almost complete faunal identity. On *a priori* grounds, it would appear highly

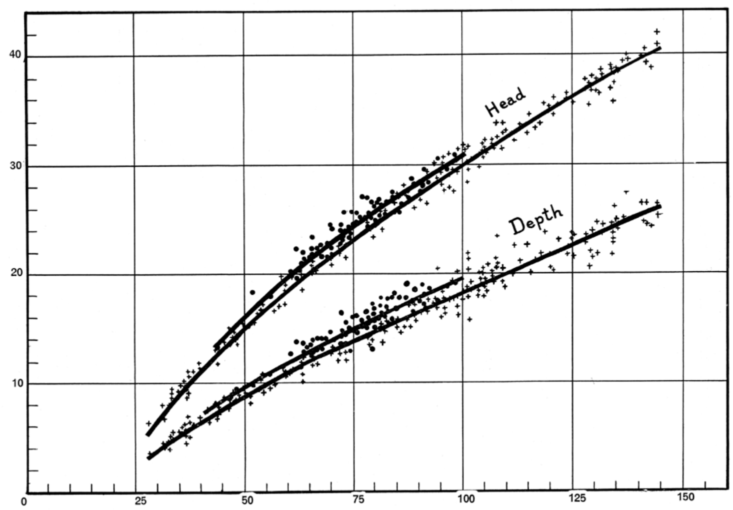

PLATE IV. Relation of length of head and depth of body to the total length in the two subspecies of *Engraulis mordax.*

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PLATE IV. Relation of length of head and depth of body to the total length in the two subspecies of Engraulis mordax improbable that the semi-pelagic anchovies of the two localities belong to distinct races. That the observed difference may be of individual and not racial significance appears not improbable from the following evidence:

4.3. Seasonal variation in the ocean subspecies

As already observed, the anchovies from Anaheim Bay were obviously all young of the year. In length to the end of the hypural they varied as indicated in Table 8.

FREQUENCY TABLE 8.

Variation in size of young anchovies taken in Anaheim Bay on October 7.

Length	Specimens	Length	Specimens	Length	Specimens
32	2	42	30	52	2
33	--	43	20	53	1
34	2	44	13	54	1
35	4	45	13	55	2
36	14	46	8	56	1
37	26	47	13	57	--
38	23	48	9	58	--
39	**45**	49	6	59	1
40	27	50	2	60	1
41	28	51	3		

FREQUENCY TABLE 8.

Variation in size of young anchovies taken in Anaheim Bay on October 7

The mode of the variation in size is at 39 mm., much nearer the lower than the upper end of the variation. This fact suggests the possibility that only stragglers of the older and larger young were remaining in the enclosed bay[4] and that most of these had already departed to more open waters. This suggestion is confirmed by an examination of a large series of young taken two days later at Redondo Beach, not many miles distant. of 667 Redondo specimens examined, 494 (74 per cent) varied in length from 44 to 60 mm., and thus overlapped in range of size the specimens from Anaheim Bay; 173 specimens were larger, ranging from 61 to 83 mm. in standard length.

It is almost certain that the anchovies from both localities represent the young of the year. Those from Redondo Beach, however, averaged larger and were presumably older than those from Anaheim Bay. Similarly the specimens from Anaheim Bay, smaller than any from Redondo, were doubtless on the average, the youngest of all; those from Redondo larger than 60 mm., doubtless the oldest. Now the spawning season of the California anchovy extends roughly from April to June,[5] that is, during the period of rapidly rising temperature (see Plate I). Therefore the largest (and oldest) individuals taken in October were, on the average, hatched out under the lowest temperature; the smallest and youngest anchovies in the warmest water. It was of considerable interest to determine that the average number of vertebrae of these two size groups differs as much as do the averages for the Anaheim Bay and Coronado series. It is of equal interest to note that the average number of segments varies inversely with the developmental temperature. The detailed data are tabulated.

[4] The California anchovy, like other species of Engraulis, spawns chiefly in bays.

[5] The date of commencement of breeding was determined for both southern and central California; the date for the close only for the San Francisco region.

FREQUENCY TABLE 9.

Number of vertebrae in different size groups of young anchovies from Anaheim Bay and Redondo Beach.

Length to caudal fin	Locality	Vertebrae 44	45	46	47	N.	Av.	P. E.
38-43 mm.	Anaheim Bay	3	**73**	58	1	135	45.42	0.03
44-60 mm.	Anaheim Bay	2	30	**37**	4	73	45.59	0.05
44-60 mm.	Redondo Beach	9	235	**236**	14	494	45.52	0.02
61-83 mm.	Redondo Beach	4	52	**105**	12	173	45.72	0.03

FREQUENCY TABLE 9.

Number of vertebrae in different size groups of young anchovies from Anaheim Bay and Redondo Beach

4.4. Sexual variation in the ocean subspecies

In the following table the counts of vertebrae for the Coronado lot are separated by sexes. It will be observed that the average number of vertebrae is slightly higher in the males than in the females. The difference (0.12 of a vertebrae) is of probable but hardly certain significance, being less than four times the probable error (0.034) of the difference.

FREQUENCY TABLE 10.

Number of vertebrae in each sex of anchovies from Coronado.

Sex	Vertebrae 44	45	46	47	N.	Av.	P. E.
Adult females	5	138	197	22	362	45.65	0.02
Adult males	1	74	144	21	240	45.77	0.03

FREQUENCY TABLE 10.

Number of vertebrae in each sex of anchovies from Coronado

4.5. The San Francisco Bay subspecies. (See Plate III)

The outstanding result of our study of the variation in the California anchovy is the demonstration of the existence in the brackish waters of San Francisco Bay of a very distinct race, analogous to the Baltic race of herring (Heincke, 1898). This form is so sharply differentiated from the ocean anchovy that it may be separated from it as a distinct subspecies, for which the name Engraulis mordax nanus Girard is available.[6]

Both in average and in mode the number of vertebrae is two fewer in the bay than in the ocean form. The figures are given in Table 11.

FREQUENCY TABLE 11.

Number of vertebrae in the two subspecies of anchovies in the San Francisco region.

Subspecies	Vertebrae 42	43	44	45	46	47	N.	Av.	P. E.
E. m. nanus	7	47	94	21	3	--	172	43.80	0.04
E. m. mordax	--	--	3	41	70	13	127	45.73	0.04

[6]*Engraulis nanus* was described as a distinct species by Girard in 1858, but currently is quoted as a synonym of *E. mordax*.

FREQUENCY TABLE 11.

Number of vertebrae in the two subspecies of anchovies in the San Francisco region

In several other characters the San Francisco Bay anchovy differs from the typical coast form. It is a much smaller fish, our largest specimen of this race measuring only 99 mm. to caudal fin, while the largest examples of the ocean anchovy collected in the San Francisco region are 144.5 mm. long, and only a few mature specimens are smaller than the largest of nanus. The early development, furthermore, is apparently more accelerated, young between 30 and 40 mm. in standard length, unlike those of true mordax,[7] being fully transformed from the postlarval to the juvenile stage. This is in correlation with the fact that it develops in waters of increased temperature and reduced salinity.

The bay subspecies can further be distinguished by differences in form and proportions. On comparison of measurements we find that the head averages longer; the body deeper and more compressed, less terete. The data are presented in Tables 12 and 13, and in Plate IV. The differences show sharply on contrasting the adults of the two forms, but by no means disappear on comparing the adults of the smaller bay race with specimens of like size, mostly immature, of the ocean race. In these differential features, the anchovies from other California localities agree almost perfectly with the ocean race from San Francisco, those from Monterey Bay alone showing a barely evident approach toward the San Francisco Bay subspecies.

FREQUENCY TABLE 12.

Length of head (in hundredths of total length to caudal) in the two subspecies of anchovies in the San Francisco region.

Proportionate length of head	**E. m. nanus,** 55 to 99 mm.	**E. m. mordax,** 55 to 100 mm.	**E. m. mordax,** 100 to 145 mm.
26.5	--	--	1
27.0	--	1	1
27.5	--	--	6
28.0	--	1	8
28.5	--	2	**20**
29.0	1	1	14
29.5	1	4	14
30.0	3	3	10
30.5	8	5	4
31.0	14	3	2
31.5	16	6	1
32.0	**20**	3	--
32.5	18	--	--
33.0	9	--	--
33.5	3	--	--
34.0	5	--	--
34.5	2	--	--
35.0	1	--	--
35.5	1	--	--
N.	102	29	81
Av.	31.90	30.33	28.98
P.E.	0.155	0.316	0.143

[7]As determined from the Anaheim Bay collection.

FREQUENCY TABLE 12.

Length of head (in hundredths of total length to caudal) in the two subspecies of anchovies in the San Francisco region

[7] As determined from the Anaheim Bay collection.

FREQUENCY TABLE 13.

Depth of body (in hundredths of total length to caudal) in the two subspecies of anchovies in the San Francisco region.

Proportionate depth of body	**E. m. nanus,** 55 to 99 mm.	**E. m. mordax,** 55 to 100 mm.	**E. m. mordax,** 100 to 145 mm..
15.5	--	--	1
16.0	--	--	2
16.5	--	2	4
17.0	3	5	11
17.5	--	2	12
18.0	6	7	15
18.5	7	4	**17**
19.0	16	1	6
19.5	**22**	2	5
20.0	14	1	3
20.5	15	1	--
21.0	12	--	1
21.5	4	1	1
22.0	1	--	--
N.	100	26	78
Av.	19.69	18.19	18.06
P. E.	0.14	0.32	0.17

FREQUENCY TABLE 13.

Depth of body (in hundredths of total length to caudal) in the two subspecies of anchovies in the San Francisco region

The bay subspecies differs also in color, the back being paler and grayer in tone than in the ocean form.

In order to understand the distributional relations of this bay subspecies of such restricted habitat to its wide-ranging ocean relative, and, presumably parent form, it will be profitable to consider the habits of the two forms in the San Francisco Bay region. The ocean type is almost completely lost sight of during the fall and winter, probably living then somewhere offshore. The exact situation then inhabited is unknown to us, except as vaguely indicated by the capture on November 2, of one specimen with a trawl just southeast of Point Reyes, a few miles north of San Francisco, on a sandy bottom at a depth of about fifteen fathoms.

Before the breeding season, however, large schools appear at the surface off the Golden Gate, the entrance to San Francisco harbor. Soon after, they enter the bay, in fewer or larger numbers, depending on unknown causes. So far as could be determined, however, they do not penetrate far into the bay, and according to intelligent fishermen, they retreat into the ocean when the streams tributary to the bay are in flood. Most of the catches are made in and near the entrance to the bay, especially near Sausalito, where ripe specimens were collected from about the middle of April to about the first of June. Spawning doubtless takes place in this vicinity throughout the spring of the year, in water of only slightly reduced salinity. Scattering individuals are said to be caught in the bay during the summer. From October 27 to November 3, a few large young of the ocean race were found mixed with the shrimp net catches of the bay subspecies in San Francisco Bay, at depths of 2 to 9 fathoms, off Berkeley, off Hunter's Point, and off Alameda. None, however, were found among the nanus caught in San Pablo Bay, which is more brackish.

In the late fall of the year the bay subspecies was found to inhabit the harbor to the almost total exclusion of the ocean race. From October 26 to November 5, specimens were seined near the entrance of the bay at Sausalito and in Richardson Bay nearby, and were caught in the Chinese shrimp nets set in nine fathoms off Hunter's Point and in six fathoms off Alameda, both in South San Francisco Bay, and in shrimp trawls on the shallow mud-flats off Berkeley and in San Pablo Bay. During this season the race is doubtless generally distributed in San Francisco Bay. In the spring, however, it is almost certain that the bay race migrates, as anchovies have the habit of doing, into waters of reduced salinity. This movement would carry them toward the head of San Francisco Bay, most probably into San Pablo Bay, which at this season exhibits a very low salinity (Sumner et al., 1914). Only stragglers of the bay race were taken in the spring toward the mouth of the bay, although diligently sought for; one was taken April 16, fifteen others from May 25 to June 5, all at Sausalito.

Although the spawning grounds of the two subspecies of anchovies in the San Francisco Bay region are probably well separated, a certain amount of interbreeding between the two forms probably takes place. The stragglers of nanus just mentioned as having been taken in the spring at Sausalito were fully ripe fish, taken with similarly mature adults of the ocean race. Furthermore, the stragglers of each type found in the territory of the other race were not wholly typical in their characters, in the size of the head particularly, approaching the other subspecies.

5. V. SUMMARY

In the Pacific herring (Clupea pallasii) there is evident a southward decrease in the number of vertebrae. The dorsal rays perhaps average slightly more numerous in California than in British Columbia, but the anal rays average distinctly fewer. Herring hatched early in the season were found to exhibit a significantly higher average number of segments than those developing in warmer water later in the season. An annual variation is also demonstrated. The San Francisco Bay herring mature, in part at least, at the age of two years.

The California sardine (Sardinia caerulea) apparently shows a very slight and irregular decrease toward the south in vertebra number. The difference between central California and southern California sardines in this respect, however, is less than the fluctuation of the average at one locality. This difference may or may not be due to annual variation. The problem of the racial distinctness or identity of the sardine of central and southern California can not be regarded as finally solved by the data here presented.

The California anchovy is divisible into two sharply-defined races, here regarded as subspecies: The ocean anchovy (Engraulis mordax mordax) of general distribution along the coast, and the San Francisco Bay anchovy (Engraulis mordax nanus). The latter is a typical brackish-water race analogous to the Baltic race of the Atlantic herring (Heincke, 1898), being characterized by its accelerated development, small size, reduced number of vertebrae, and a large head and deep body. The ocean race, like the sardine, exhibits a very slight and highly irregular southward decrease in average segment number. The differences between central California and southern California samples, however, are much less than the fluctuation at one locality and therefore are not of proved racial significance. Individuals hatched out earliest in the season, at the coldest average temperature, develop the lowest average number of vertebrae.

6. VI. LITERATURE CITED

Davidson, George. 1886 . The temperature of the water of the Golden Gate. Bull. Cal. Acad. Sci., 1, pp. 354–357.

Fage, Louis. 1911 . Recherches sur la Biologie de l'Anchois (Engraulis enchrassicholus Linné) races—age—migrations. Ann. Inst. Oceanog., 2, No. 4, 37 pp.

1920 . Engraulidae, Clupeidae *in*: Rept. Danish Oceanog. Exp. 1908–1910 to Mediterranean and adj. Seas, (Biol.), 2, 140 pp.

Heincke, Fr. 1989 . Naturgeschichte des Herings, Teil I. Die Lokalformen und die Wanderungen des Herings in den Europäischen Meeren. Abh. deut. Seefishcherei-Vereins, Band 2, Heft 1.

Hubbs, Carl L. 1922 . Variations in the number of segments in fishes correlated with the temperature of the water during development. Amer. Nat., 56, pp. 360–372.

1924 . Seasonal variations in the number of vertebrae in fishes. Papers Mich. Acad. Sci., Arts and Letters, 2, 1922, pp. 207–214.

McEwen, George F. 1912 . The distribution of ocean temperatures along the west coast of North America deduced from Ekman's theory of the upwelling of cold water from the adjacent ocean depths. Int. Rev. ges. Hydrobiol. Hydrog., 5, pp. 243–286.

1916 . Summary and interpretation of the hydrographical observations made by the Scripps Institute for Biological Research of the University of California, 1908 to 1915. Univ. Calif. Publ. Zool., 15, pp. 255–356.

Schmidt, Johs. 1917 . Racial investigations. I. Zoarces viviparus L. and local races of the same. Comptes-rendus Trav. Lab. Carlsberg, 13, pp. 279–397.

Sumner, Francis B. et al. 1914 . A report upon the physical conditions in San Francisco Bay, based upon the operations of the United States Fisheries Steamer "Albatross" during the years 1912–1913. Univ. Calif. Publ. Zool., 14, pp. 1–198.

Thompson, William F. 1917 . A contribution to the life-history of the Pacific herring: its bearing on the condition and future of the fishery. Rept. Brit. Col. Comm. Fish., 1916, pp. 39–87.

7.

Engraulis nanus was described as a distinct species by Girard in 1858, but currently is quoted as a synonym of E. mordax.