# EVIDENCE OF A NORTHWARD MOVEMENT OF STOCKS OF THE PACIFIC SARDINE BASED ON THE NUMBER OF VERTEBRAE 

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## INTRODUCTION

Evidence on the movements of stocks of sardines along the Pacific Coast of the United States and Mexico has been derived from tagging, from counts of vertebrae, and from related data. The present study represents a second major attempt using numbers of vertebrae. Previous studies, reviewed below, have demonstrated an unknown but presumably significant amount of heterogeneity within the range of the sardine, as well as considerable intermingling of stocks between the regions of Punta Eugenia (in central Baja California), California, and the Pacific Northwest.

Tagging studies: An extensive tagging program, initiated in 1936 and carried on continuously until 1942, demonstrated that the sardine stocks intermingle considerably within the area from Pta. Eugenia to Central California and from Southern California to British Columbia (Hart, 1943; Clark and Janssen, 1945). Some fish tagged in Southern California were recovered along the west coast of British Columbia and some tagged in the latter region were recovered in Southern California. The tag-recoveries demonstrated a rather rapid migration : sardines tagged off Southern California in February and March were retaken off British Columbia in the following July ; others, tagged off British Columbia in July and August, were canght off San Pedro, Califormia, in the succeeding December and January (Hart, 1943). Associated with this rapidity of migration is a size relationship. Clark and Janssen (op. cit.) stated that, "The largest sardines may be expected to move quickly to distant fishing grounds whereas the smaller fish tend to remain longer in the locality where tagged or to make short migrations. These smaller fish reach distant grounds in later years when they have grown to larger sizes."

The one lot of sardines that was tagred south of Pta. Eugenia, in April, 1938, comprised 963 fish in Magdalena Bay. No recoveries were made from this lot, possibly because the number was too small to insure a return, or, as the authors suggested, because sardines from the area do not intermingle with the more northern fish.

Vertebral §tudies: Clark (1947) compiled the results of vertebral counts made by previous investigators in the United States and Canada-Hubbs (1925), Thompson (1926), Hart (1933), and Clark (1936). The 1947 data, when grouped by latitude, showed a rather definite trend from north to south, particularly

[^0]within the 0 and 1 age groups. No adults (2-year fish or older) were available from south of San Diego with the exception of a small sample of 31 fish from the Gulf of California. The areas treated ranged from Alaska to the Gulf of California and the years sampled from 1921 to 1941.

From the combined age-group data Clark (1947) reached a tentative conclusion that, "sardines found in southern Lower California and the Gulf of California constitute a separate population which rarely interminoles with the more northern population, but that a considerable, and perhaps variable, amount of interchange takes place throughout the range of the northern population from Alaska to Pta. Eugenia in central Lower Califormia.' 'The results of the tagging in the Magdalena Bay area, though somewhat inconclusive, recounted above, augmented Clark's interpretation of vertebral data from the area and strengthened the hypothesis that the stocks of fish in the area may well constitute a separate population that intermingles little if at all with the more northern stocks.

Grouth Studies: Felin (1954) attempted to assay the heterogeneity of the sardine populations from the standpoint of growth characteristics, using age and length data gleaned from samples of the commercial landings in Southern and Central California during the years 1942-1950. The following excerpts from her conclusions appear to be pertinent to the present study :

Complete intermixture and homogeneity in population of adult fish as sampled by the fishery in different regions is not evidenced from data on mean calculated lengths. The apparent cline in the growth characteristic . . . appears indicative of intraspecific populations in which there is limited intermingling, and suggests a series of overlapping coastal migrations of more than one stock.

Wolf and Daugherty (1960) have reported that two-year-old fish comprised the bulk of the Southern California eatch in the 1958-59 season (to be discussed later). These fish were unique in that they averaged 191 mm . ( 7.7 inches) in standard length, 12 mm . ( 0.5 inches) smaller than the previous recent minimum (1954-55), but not much smaller ( 3 mm . or 0.1 inch ) than the 1939 year-class as two-years-olds, an outstanding year-class. It has further been reported (Ibid., 1960) that the fish in Baja California averaged even smaller ( 162 mm ., 6.4 inches) -so much smaller as to suggest that the fishery there was not utilizing the same stocks of fish as was the Southern California
fishery. Also, the two-year-olds landed at Monterey were smaller than the San Pedro fish, indicating somewhat more population heterogeneity than usual (no samples from the Monterey landings were available for the present study).

These previous studies have all pointed either to a mixture of stocks, of phenotypic or genotypic origin, that intermingle more or less completely within the area from north and central Baja California to Southern California and from the latter area to British Columbia, or to more or less sporadic influxes of nonintermingling fish from other areas, presumably the south.

The present study attempts to cover essentially the same areas (Fig. 1) reported on by Clark, with the exception of Central and Northerin California, and provides a body of data well separated in time from any previous similar data. No samples were available from these northern areas, as it was not until the 1958-59 season that the sardines reappeared there in


FIGURE 1. Chart of areas discussed, showing the localities from which samples were secured in the present investigation and in that of Clark (1947).
sufficient numbers, since about 1950 , to warrant a fishery or a sampling program (Marine Research Committee, 1960). No samples were available for study from the 1958-59 central California fishery, although about 25,000 tons were landed at Monterey and San Francisco (Ibid., 1960). In general, the present data agree with Clark's findings only for the areas south of Pta. Eugenia. From there northward to San Pedro, California, the data show that a major portion of the
samples studied are characterized by a marked reduction in average number of vertebrae.

## METHODS

As age determinations were not available for samples from most of the localities treated, all age-groups are combined. Only the 1957-58 Ensenada and San Pedro samples were aged (by CalCOFI personnel, employing a subsample amounting to approximately 20 percent of each sample studied). In the other areas studied, aging would have been possible only by arbitrarily assigning an age to any given length frequency. This was not attempted as age-length composition studies have shown that adult sardines (2 years or older) vary in length from 1.5 to 2.5 inches in each age-group. Thus, an arbitrarily assigned age may result in an error of two or three years.

All fish, except one sample of 500 postlarvae from the Gulf of California, were X-rayed for determination of vertebral numbers. The postlarvae were stained with alizarin and cleared in glycerin before counting. All vertebrae were counted by the author. The urostyle was included in the count.

The nature of the data does not warrant detailed statistical analyses, and the study is not intended as a purely racial one. The real significance lies in the differences in average values, both in individual and in grouped samples, between the present body of data and that presented by Clark (1947) for the region north of Pta. Eugenia, Baja California.

Because of the rather small range in total numbers of vertebrae the standard deviations about the mean do not differ markedly. For the region north of Pta. Eugenia the range of deviations, including both Clark's and the present data, is 0.5980 to 0.6719 (ave., 0.6191 ). The range of standard errors of the means is 0.0006 to 0.0225 (ave., 0.0149 ). This large range in standard error values is due to the quite large variation in numbers of specimens used (Table 1).

An indication of the significance of the difference between means of Clark's and the present data, for the northern region, is the average difference of 0.23 , nearly one-fourth of a vertebra. In comparing this with the almost three-fourths of a vertebra that separates the Gulf of California fish (average mean, 51.00) from those reported by Clark for northern Baja California and northward (average mean, 51.70 ), elementary statistical treatment will provide odds of but one in hundreds of thousands of chances that the two sets of data comprise a single population or stock of fish. Such orders of significance do not, of course, pertain to the southern areas-from Pta. Eugenia southward and into the Gulf of Californiabecause of the striking similarity of the two sets of data in this southern region.

## RESULTS

Figure 2 is a plot of all samples embodied in the present data, arranged by area. Wherever the areas are closely comparable, Clark's 1947 data are also plotted. Each solid dot represents an individual sample of the present data, and each open circle repre-

TABLE I
vertebral numbers-all age groups


TABLE 1-Continued
VERTEBRAL NUMBERS-ALL AGE GROUPS



FIGURE 2. Frequency distribution of individual sample means and the mean of each area. Each solid dot (present data) or open circle (Clark's data) refers to an individual sample. The acufe triangles represent the area means.
sents a sample listed by Clark (1947). Table 1 summarizes the present data in Fig. 2 by year and month.

Clark's 1947 data, with all age-groups combined, indicate that prior to 1942 the mean vertebral values changed abruptly in the vicinity of Pta. Eugenia, Baja California: average values south of this point were markedly lower than those to the northward. The higher values to the northward formed the basis for Clark's statement that "The average number of vertebrae is approximately 51.7 for all sardines north of southern Lower California and about 51.2 for sardines from southern Lower California." These numerical values have since been considered to be
"standard" for sardines spawned under what has been thought to be "normal" oceanographic conditions. For Southern California alone Clark's average for all age groups combined was 51.73 . She reported on only five samples with a combined mean value of 51.62 , sampled from 1938 to 1940 from the Boundary to Pta. Eugenia-excluding Sebastián Viscaíno Bay samples, considered separately.
Whereas Clark's data from north of Pta. Eugenia comprised samples taken between 1921 and 1941, the present data stems from samples taken between 1950 and 1959. A distinct and significant change has taken place in the decade that separates the sampling ef-
forts (Fig. 2). The plotted mean values of all samples from each area and the area means for the present data show a rather marked reduction in areal mean values as well as a very great number of sample mean values that fall well below the lowest reported by Clark. It will be noted that this reduction persists from Southern California to Pta. Eugenia. Both sets of data are in excellent agreement from Pta. Eugenia southward and into the Gulf of California.

It is unfortunate that very few samples from the region, "Boundary to Pt. Eugenio," were available to Clark, as compared with the much larger number from Ensenada that are used in the present study. Clark's five sample means from this region all fall within the range of those from Ensenada, though they are distinctly on the high side. Clark's data from Sebastián Viseaíno Bay alone correspond very closely with those for the broad areal grouping from the Boundary to Pta. Eugenia. The higher averages appear to have persisted further south in 1921-41 than in 1950-59.

It is of considerable interest that so many sample means from the northern region should fall well below those reported by Clark. For areas south of Pta. Eugenia, excluding those of Cape San Lucas and the Gulf of California, very few samples in the present body of data (only 21 percent) have lower vertebral mean values than do those from Ensenada and Southern California (Fig. 2). Clark's data alone show 82 percent of the samples from these southern areas to have appreciably lower values than do the samples from Southern California reported on in 1947. This difference of 61 percent is striking evidence of the reduction in mean numbers of vertebrae between the two time periods in the samples from Southern California and northern Baja California. The populations, or stocks, of fish from areas south of Pta. Eugenia may intermingle to at least a small degree with those from the Gulf of California: of all samples from south of Pta. Eugenia, excluding those from the Gulf, about 23 percent have vertebral mean values similar to those reported from the Gulf (Fig. 2).

In contrast to the expected lower mean values for the areas south of Pta. Eugenia are the several relatively high values. The value of 51.795 for 78 fish (0 age-group), listed by Clark for the "Pt. Engenio to Pt. San Juanico', area, and the value of 51.669 for 127 fish (I age-group) from Magdalena Bay, are generally considered as typically "'northern" or "high" means. The present data includes one sample of limited significance (comprising only 22 fish) from the same area with a high mean of 51.68 . The reasons for these higher mean values are difficult to assess.

McHugh (1950) offered a possible explanation of these high values, which average 51.71. Postlarval sardines from southern Baja California, spawned in spring and summer, were found to have significantly different mean vertebral numbers of 51.54 and 51.21 respectively (as McHugh did not count the urostyle, his counts are increased by one to conform to those of the present study). The values of 51.79 and 51.17 for spring- and summer-spawned fish in samples from northern Baja California differ even more signifi-
cantly. Whereas Mcllugh's high value of 51.54 for postlarvae spawned in the spring in southern Baja California falls well below the average figure of approximately 51.71 for the older fish under consideration from these southern areas, it does indicate the possibility that environmentally induced meristic differences may result in abnormally high mean vertebral numbers in at least some samples from these areas, and, possibly, for all areas throughout the range. Of course the reverse situation may also occur as is shown by two samples taken near the San Benito Islands, about 15 miles west of Cedros Island. In 1946, 172 0-year fish furnished a mean vertebral value of 51.40 and in 1955, 143 fish (estimated at nearly two years of age) provided a mean of 51.87 vertebrae. This is all area that was quite "northern"' in the data presented by Clark, but considerably less so in the present data: the means are about 51.64 and 51.50, respectively.

Both Magdalena and Santa María Bays also show a tendency to produce some samples with relatively high mean vertebral numbers. Exeluding the two low mean values, 50.99 and 51.01 (Fig. 2, Table 1), raises the Santa María Bay average to 51.44, a figure notably higher than the combined average for the Bay and one that would appear to fit the plotted distribution of sample means (Fig. 2). It is reasonable to assume that as Santa María Bay is entirely open to the sea any migrating northern stock may readily enter. In contrast, the relatively enclosed Magdalena Bay is presumably less accessible to coastal migration and may be expected to harbor a more indigenous population. The number of samples from each bay is hardly adequate to resolve the question. Actually the highest mean value recorded for Magdalena Bay in each set of data exceeds any of the means for Santa María Bay. However, the high value of 51.68 listed in the present data is derived from a sample of only 22 specimens and may not be of great significance. The next highest value, 51.54 , is derived from 68 fish. It thus appears probable that higher values may oecur in the Bay. Clark's 1947 data includes a sample of 127 I-year fish which furnished the more significant mean value of 51.669 . Thus it is apparent that either migrations from the north may enter these bays or that local spawning conditions may occasionaliy be such that higher average vertebral numbers may result. It is also apparent that the same situation pertains to those samples having lower vertebral mean values comparable to those listed for the Gulf of California. From the standpoint of migration these bays may be considered to be more within the range of Gulf stock than those from more northern waters, particularly those from north of Pta. Eugenia.

As noted by Clark (1947) the Gulf of California may well harbor a separate population of sardines that intermingles little if at all with the northern populations, but that may mix to a degree with stocks occurring below Pta. Eugenia. The present data has strengthened Clark's conclusion, for the two sets of data are remarkably similar, considering both the time interval between the two sets of data and the total number of years involved. Whereas Gulf
samples consist of O fish or postlarvae, except for the 31 -fish sample of adults reported by Clark, affording a mean of 50.968 , all samples have provided mean values of about 51.00.

Year Class Data and the "Warm" Years: The occurrence of abnormally high ocean temperatures in 1957 and 1958, and the observed reduction in average numbers of vertebrae in samples from northern Baja California and Southern California, requires that some consideration be given to year classes comprising the present data. As a major portion of the samples were taken in 1957-58, particularly in these two areas, the age data are considered for these areas only.

Daugherty and Wolf (1960) show that, for the 1957-58 season in Southern California, the 1957 year class contributed only 1.3 percent to the conmercial catch. During the same period of the northern Baja California season (including Ensenada and Cedros Island landings) these authors show that the 1957 year classes contributed only 1.4 percent. The 1958-59 catch data for Southern California showed that 1957 fish comprised only 10.2 percent of the catch and in Baja California only 11.6 percent (Wolf and Daugherty, 1961).

Thus it is clear that the 1957 and 1958 year classes, presumably hatched in warmer water, were a minor constituent of the catches and the vertebral count samples. Therefore, the recent "warm water" can be almost completely discounted as contributing to the low vertebral numbers off Southern California and northern Baja California during the 1957-58 and 1958-59 fishing seasons.

## DISCUSSION

If the effect of the warm years may be discounted as being a major cause for the observed reduction in average vertebral numbers in the area of northern Baja California and Southern California, other hypotheses may be erected: (1) The environment had begun to change as early as 1950 and the change was reflected in the reduced average number of vertebrae (but there is no oceanographic evidence of such a change); (2) Micro-environmental changes affected the vertebral numbers and morphometry of the individual spawnings that were later sampled (such an event is, of course, always possible; however, there are great odds against the chance that such spawnings and samples make up the bulk of the present data) ; (3) Stocks of fish migrated northward from the southern areas, which are characterized by lower average numbers of vertebrae, accompanied by a reduction in the numbers of northern-type fish. This is the most attractive hypothesis.

Ahlstrom (1959) has reported that such a northward movement did occur in early 1954. Associated with this northward movement was an appreciable rise in water temperatures, particularly in the early spring. Clothier and Greenhood (1956) reported that 67,258 tons of sardines were landed during the 195455 season in contrast to the slightly more than 3,000 tons in 1953-54 and some 4,500 tons in 1952-53.

Unfortunately, the present data are not adequate to test whether or not this observed migration of sardines
into Southern California contributed to the lowering of the average number of vertebrae within the area in 1954, though they are suggestive. Only one sample of 37 fish, from San Pedro, was available for study. This sample afforded a mean of 51.49 (Table 1), quite characteristic of the recent period in the Southern California fishery, whereas the average for the earlier period reported on by Clark was 51.73.

That these 1954 fish, and those of subsequent and earlier samples to 1950, were probably not spawned in the area of capture during any warm period is evidenced by the following statement by Reid, Roden, and Wyllie (1958), "the period from 1949 to 1956 is distinguished from the previous 15 or 20 years by substantially coller waters in the first few months of the year."

The foregoing evidence of the period of 1949-1956 being colder than the previous 15 or 20 years adds further interest to the comparison of the two sets of data on vertebral numbers. If most specimens in the present study are presumed to have been spawned in waters colder than those in which Clark's must have been (all spawned prior to 1941), it could also be presmed that the average numbers of vertebrae would be higher than observed. This obviously is not the case in those samples studied from northern Baja California and Southern California; thus by every test the change in vertebral numbers is opposite that suggested by the environmental changes. There must, then, have been major changes in the stocks on the fishing grounds.

One question posed by the present body of data is, what happened to the "northern'" type of sardine? Temperature data indicate that sufficiently cold water was available to have produced high vertebral numbers. The number of samples studied would appear to afford an adequate representation of the fish available to the sampling techniques. It may be that the northern types were "somewhere else" and not available to the fisherman or the sampling techniques. It may also be that the influx of southern fish in 1954 continued and that interbreeding with the northern types has resulted in lower average numbers of vertebrae, or that the northern types were still present but in considerably reduced numbers.

In review, south of Pta. Eugenia there was no change in vertebral numbers between the earlier and later period, all counts being low. North of Pta. Eugenia, vertebral counts during the recent decade are lower than the earlier period, the average being intermediate between the stable southern àverage and the earlier northern average. Further, the direction of the change, i.e., a decrease, has been contrary to that expected to have resulted from the cooler environment during the recent period. Thus, there is good evidence that there has been a change in the "racial" composition of the stocks taken by the fishery in Southern California and northern Baja California.

The precise nature of the change is not so clear. There has been $a_{\text {s }}$ severe decline in the stocks available to those fisheries compared to the early period (Clark and Marr, 1955). This almost rules out the possibility that the lowering of the vertebral numbers was
caused only by an influx of southern fish. Rather, the change in vertebral numbers must have been associated with a reduction of the population of the northern, high vertebral number, 'race,' possibly, but not necessarily, accompanied by additional influx from the south.

## SUMMARY

1. The results of the summarized three widely differentiated earlier approaches to the problem of heterogeneity of sardine stocks throughout the range indicate the presence of more than one population, or stock, of sardines inhabiting the total range.
2. The present study demonstrates that a marked reduction in average numbers of vertebrae, for sardines sampled in northern Baja California and Southern California, has oceurred throughout the period from about 1950 through 1958. This reduction results in a much lower average value than that reported by Clark (1947), the respective values being 51.50 and 51.73 .
3. The plot of average numbers of vertebrae for each sample within a given area, and the area averages (Fig. 2), indicates that many of the samples taken in northern Baja California and Southern Califormia, in the period from 1950 to 1959, have sufficiently low values to have originated in the waters off Central or Southern California.
4. Year-class data for a major portion of these fish with low values indicate that only a small percentage of the total catch could have been spawned in the area of capture during the abnormally high ocean temperatures that began in 1957.
5. For the areas of southern Baja California (Pta. Engenia into the Gulf of California) the present data is in excellent agreement with that presented by Clark (1947). The two sampling efforts cover a period of time from 1926 to 1958 for this broad area. This fact indicates that these areas may harbor indigenous populations in that no apparent change in the average vertebral numbers has occurred in the 32year period.
6. It is concluded that the sardines caught in northern Baja Califormia between the years 1950 and 1959 were comprised of a different "racial" mixture than those taken prior to 1941, because the recent reduction in vertebral numbers is contrary to the phenotypic increases usually associated with cooler water. Concurrently, abundance has declined, so the change in vertebral number is most easily explained by postulating reduction in a northern "race," possibly accompanied by an influx of additional southern fish.

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