POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

BY FRANCES E. FELIN

FISHERY BULLETIN 86

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The possibility of heterogeneity in stocks of *Sardinops caerulea* along the Pacific coast of the United States and Canada is examined through evidence from growth and vital statistics of the fished population(s). Growth characteristics of six year-classes sampled in Canada are compared with those from San Pedro. Significant difference in predicted size indicates lack of homogeneity in populations of adults as sampled by the fishery in Canada and in San Pedro.

Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and southern California.

Bimodality in length composition of certain year classes is evidence that pilchard populations are not homogeneous. Large, long-ranging pilchard may arise from spawning stocks off California while more southern stocks, smaller in size, more short-lived, have limited migration.

In view of indications of heterogeneity in growth types of fished stocks of pilchard, whether genotypic or phenotypic in origin, it appears desirable that their population dynamics be studied not only for the coast as a whole but also by geographic areas.

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POPULATION HETEROGENEITY IN THE PACIFIC PILCHARD

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In the course of routine examination of scales of the Pacific pilchard (*Sardinops caerulea*) several investigators working together had for a long time noticed the consistent occurrence of distinctively small individuals among the 5-year olds. This suggested the possibility that this species might be composed of more than one population, each having common and genetically distinct attributes. One of these attributes appeared to be growth rate; others might include habits, distribution, anatomy, and physiology. Possibly also these populations would have differing rates of birth and death. If this hypothesis should prove true, then the characteristics of each population must be taken into account in any study involving population dynamics.

To examine the proposition that the species *Sardinops caerulea* is a complex of different populations, distinguishable by peculiarities in growth rate, we undertook an intensive study of the growth characteristics as recorded on pilchard scales, and we analyzed these data in the light of certain pertinent vital statistics. The following paper is a report of that study.

The materials for this study are scales, and age and length data from pilchard sampled by State and Federal agencies. These were collected in as nearly random a fashion as possible from the catches at major ports along the Pacific coast where fishing was carried on during each fishing season from 1941–42 through 1949–50. Since validation of scale-reading techniques for Pacific pilchard (Walford and Mosher 1943a and 1943b), the age and length composition of these samples have provided the vital statistics from which may be estimated the annual accrual to the stocks by recruitment and growth, and the losses due to fishing and natural mortality and/or unavailability of fish to the fishery.

The assistance of the Fisheries Research Board of Canada, the Washington Department of Fisheries, the Oregon Fish Commission, the California Department of Fish and Game, and of the many persons who have made possible the continued cooperative program of sampling the catch, is gratefully acknowledged. I wish also to thank Dr. L. A. Walford, O. E. Sette, and J. C. Marr for their constructive criticism and encouragement; Dr. G. S. Myers, Stanford University, for his review of the manuscript; and T. M. Widrig for his assistance in preparing the statistical data.

AVERAGE GROWTH DATA

Growth curves of a given year class of pilchard may be constructed from the mean observed lengths of that year class in successive seasons (Phillips 1948). Such growth curves fluctuate in level from year to year because of the differential migration of the fish of different size (Clark and Janssen 1945) and age, and because of within-season and between-season variations in distribution of the population. Observed lengths, however, provide a useful check on back calculations of lengths, which are based on the proportionality of growth of scale to growth of fish.

DETERMINING LENGTHS BY THE DIRECT-PROPORTION METHOD

For calculating lengths of pilchard a direct proportionality is tentatively assumed in this study, so that

$$\frac{l_n}{l_t}=\frac{s_n}{s_t}$$

where l is length of fish, s is length of scale, n represents any given age, or annual ring on the scale, and t is total length of fish or scale. The scale, of course, is not formed when the fish is 0 mm. long. The extrapolated curve of the linear regression of fish length on scale length may show for adult fish of a given year class, a positive, a zero, or a negative y-intercept and since the scale cannot be laid down at a minus length of fish, the absolute value of the y-intercept can not be said to have a biological meaning. Regressions of pilchard length on scale length appear to be satisfactorily described by a linear equation over the range of ages 1- through 5-ring (Landa 1950). When the y-intercept differs significantly from zero, the percentage error in estimated length introduced by the assumption of direct proportionality will, of course, decrease with increasing age.

A variety of factors renders the calculated growth for the first year of life, or to the first ring on the scale, only an approximation. The amount of the first growth increment differs geographically, which is partly explained by the northward shift of spawning as the season progresses. Spawning also continues for some length of time at a given locality. There is consequent inequality in duration of the initial period of growth, so that the length of the first year, from the time spawned until the formation of the first winter annulus, depends upon the place and date of spawning. The time periods represented by the l_1, thus are not entirely comparable with those represented by other growth increments (l_n). Furthermore, there is least clarity in appearance of the first ring on pilchard scales and greater difficulty in locating it than is found with subsequent annuli, so that less reliability is associated with the mean value of the first growth increment, $\bar{l}_1$.

Average observed lengths at each age of all the year classes sampled in the commercial catch over nine seasons in five regions along the Pacific coast are given in table 1. The means given for each age in each region were obtained by assigning equal weight to each year-class average. These means were then taken as representative of a mean curve of growth for each area of catch. (See also Phillips 1948, p. 7.)

TABLE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length
British Columbia:		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
1934													40	245
1935											80	241	12	242
1936									237	236	51	244	39	250
1937							307	230	92	239	100	246	27	247
1938					142	216	104	230	148	239	93	245	45	250
1939			255	193	313	215	287	234	204	242	95	247	32	254
1940	10	175	84	204	89	226	117	239	67	245	26	250	30	253
1941					20	231								
1942			37	195	38	225	10	241	17	250				
1943	14	183	29	211			15	243						
Mean	24	179	405	201	602	223	840	236	765	242	445	246	225	249
Pacific Northwest:[1]														
1934													62	248
1935											112	242	12	242
1936									331	236	53	244	40	249
1937							483	229	95	239	104	245	27	247
1938					294	215	111	231	164	239	93	245	53	250
1939			680	191	390	215	322	233	204	242	122	249	61	255
1940	35	166	91	203	101	225	117	239	86	247	83	253		
1941	(*)				20	231	(*)		19	253				
1942	(*)		37	195	44	225	22	244						
1943	14	183	29	211	10	236								
1944	(*)													
Mean	49	174	837	200	859	224	1,055	235	899	243	567	246	255	248
San Francisco:														
1935											(*)		12	240
1936									44	220	86	231	33	241
1937							186	217	256	227	93	239	132	248
1938					862	209	736	222	348	232	403	244	28	253
1939			1,186	199	1,346	216	959	228	896	241	55	247	12	255
1940	21	180	205	208	574	223	665	236	78	240	(*)			
1941	(*)		51	206	185	223	80	222	(*)					
1942	48	173	313	212	191	222	16	238						
1943	46	182	147	210	13	234								
1944	(*)		14	209										
1945	18	168												
Mean	133	176	1,916	207	3,171	221	2,642	227	1,622	232	637	240	217	247

See footnotes at end of table.

TABLE 1.—*Average length of pilchard in the commercial catch of five Pacific-coast areas, by year class and age group*—Con.

Year class	1-ring		2-ring		3-ring		4-ring		5-ring		6-ring		7-ring	
	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length	Number of fish	Average length
Monterey:		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
1935											(*)		11	232
1936									36	218	55	231	18	237
1937							164	215	161	229	98	235	44	245
1938					903	206	700	220	367	230	163	242	15	247
1939			2,487	195	1,684	214	1,167	226	537	239	58	247	16	254
1940	447	175	641	205	949	221	470	234	71	236	21	243		
1941	137	164	255	198	352	219	150	219	43	237				
1942	570	164	1,379	204	320	210	77	234						
1943	450	170	255	209	135	232								
1944	73	172	83	207										
1945	324	184												
Mean	2,001	172	5,100	203	4,343	218	2,728	225	1,215	232	395	240	104	243
San Pedro:														
1935											11	223		
1936									43	212	15	215		
1937							140	212	58	214	22	223		
1938					1,090	202	448	210	97	219	31	231		
1939			1,756	194	1,301	206	443	213	178	224	14	224		
1940	419	179	1,373	198	834	206	415	213	44	218	(*)			
1941	476	181	1,112	196	1,141	206	151	213	26	222	11	237		
1942	485	180	1,060	204	242	206	59	220	45	237	(*)			
1943	546	187	337	200	186	213	83	228	9	219	(*)			
1944	105	182	283	205	161	219	33	213	28	212				
1945	397	195	281	210	99	210	61	208						
1946	195	169	407	199	210	206								
1947	59	187	253	198										
1948	75	189												
Mean	2,757	183	6,862	200	5,264	208	1,833	214	528	220	104	226		

[1] Includes samples from waters off Washington and Oregon.
*Less than 10 fish sampled.

TRANSFORMATION OF GROWTH CURVES

When such growth curves of means-of-average observed lengths for each area are transformed, using Walford's (1946 a) plot of l_{n+1} on l_n, figure 1 results. These transformations show marked deviation from the linearity characteristic of this plot for more homogeneous groups of fish (or of other animals). They are illustrative, however, of growth characteristics of different areas. As defined by Walford, these are (1) the slope of the regression, k, representing the rate of deceleration of growth; and (2) the predicted ultimate size, $l_\infty = \frac{y\text{-intercept}}{1-k}$. Pilchard landed at Monterey and San Francisco show growth characteristics intermediate between those of catches landed in the south at San Pedro and in the Pacific Northwest off Oregon, Washington, and British Columbia.

Growth data on European pilchard (*Sardina pilchardus*) assembled from various sources by De Buen (1937) are plotted similarly (as transformations) in figure 2 for different geographical areas. These curves are based on back calculations of length obtained for the most part by the direct-proportion formula. Differing growth types, possibly representing clines (or gradients) of growth, are indicated from north to south, extending from waters off England through the southern European Atlantic to the Mediterranean. In figure 2, solid symbols represent transformations of growth curves of pilchard off Cornwall, Plymouth, and Northumberland; various crosses and parts of crosses show growth transformations of pilchard from the English Channel off Boulogne, from other waters south along the French and Spanish coasts as far as Cadiz and the Azores; and open symbols represent pilchard growth types from the Mediterranean. As early as 1913 Fage suggested, on the evidence of growth, that two distinct races of sardines exist, one in the Atlantic and another in the Mediterranean. He also noted (1920) that the relative dwarfism of Mediterranean races is not peculiar to the sardine, but has also been noticed in the anchovy and other species common to the two seas.

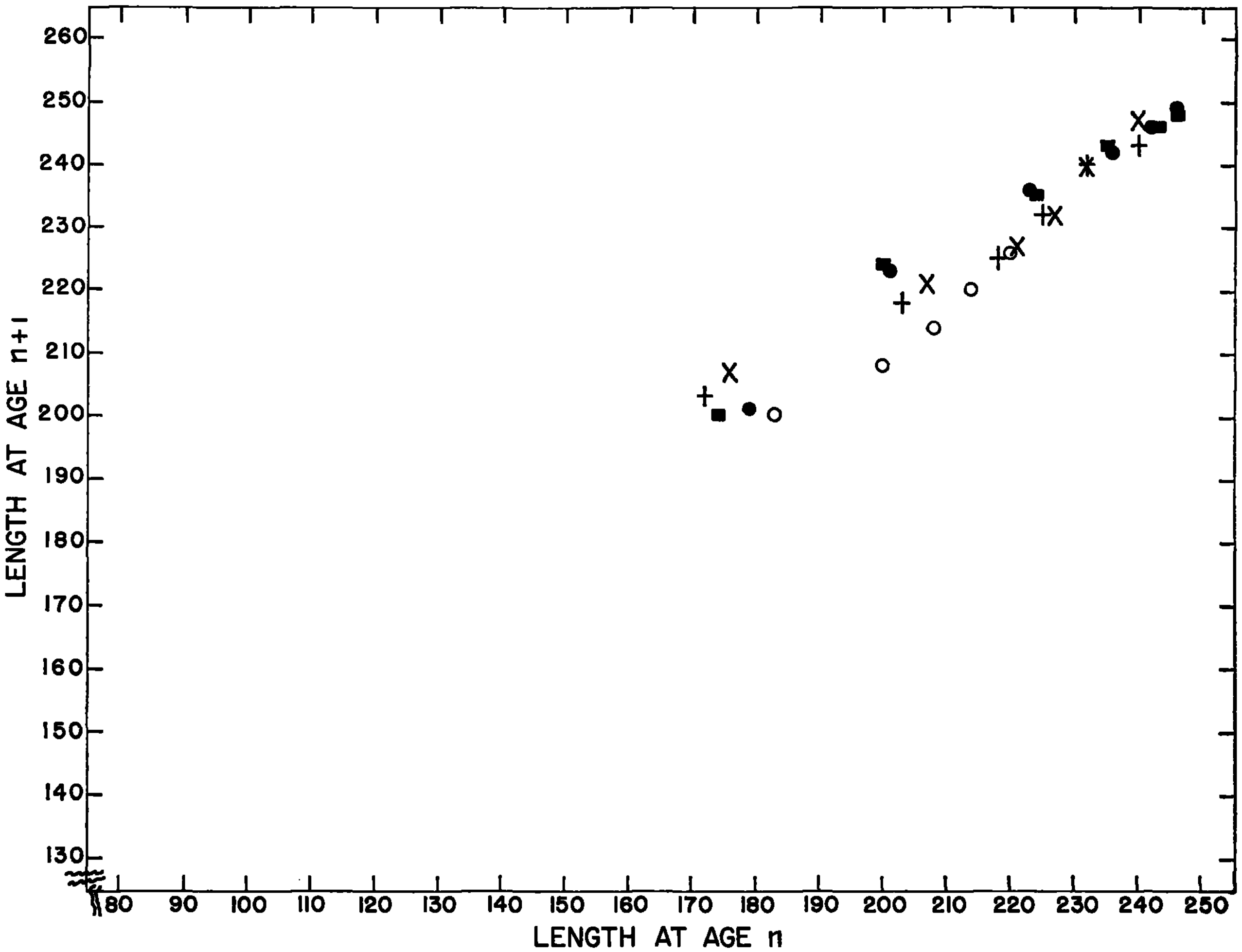

FIGURE 1.—Transformations of 9-season averages of observed lengths of Pacific pilchard at each age in five regions of catch. British Columbia averages represented by dot, Pacific Northwest by solid square, San Francisco by cross, Monterey by plus, San Pedro by circle.

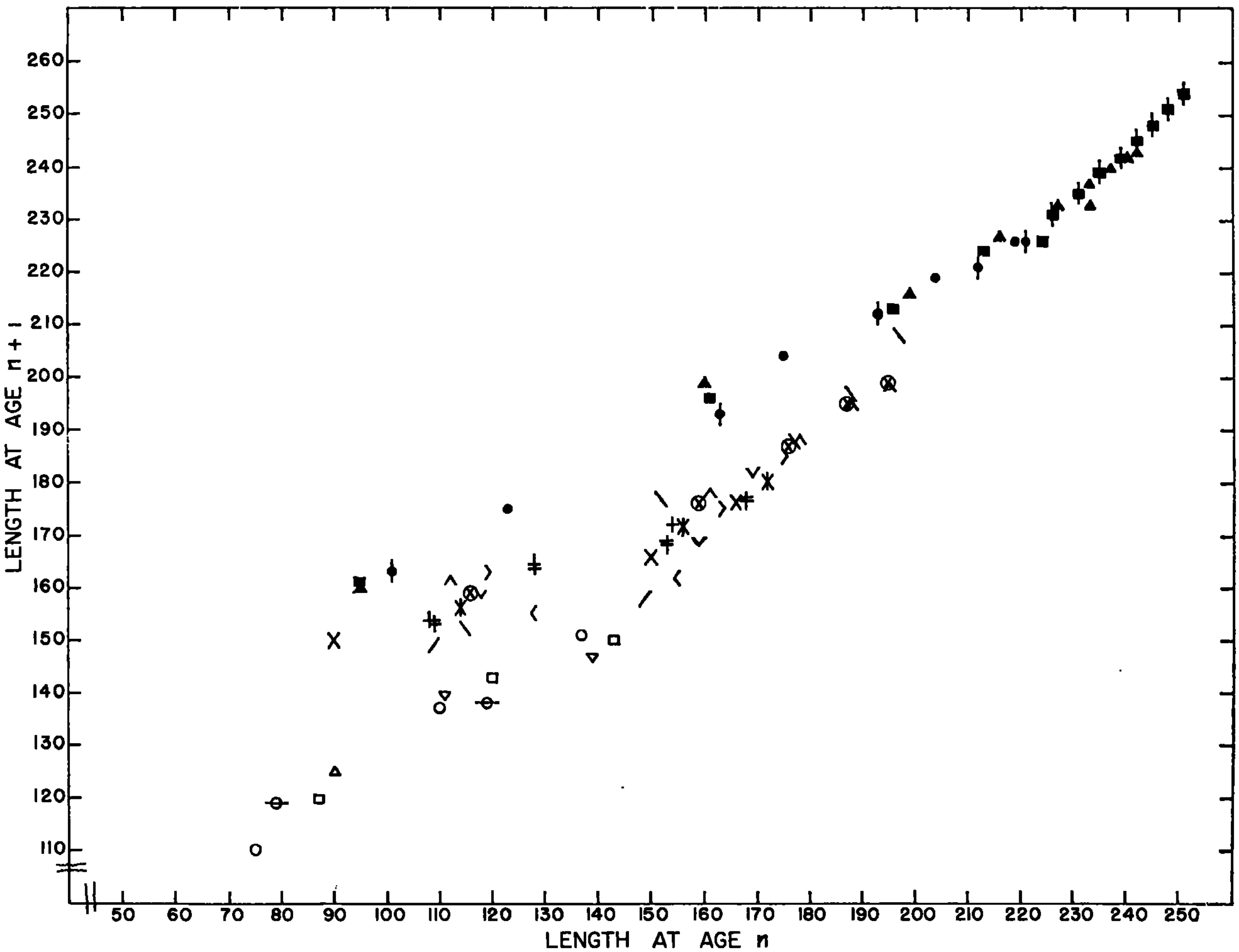

FIGURE 2.—Transformations of growth curves of European pilchard from different regions of catch. Solid symbols represent pilchard caught off England, various crosses and parts of crosses those off the French and Spanish coasts, open symbols those from the Mediterranean. (Data from De Buen 1937.)

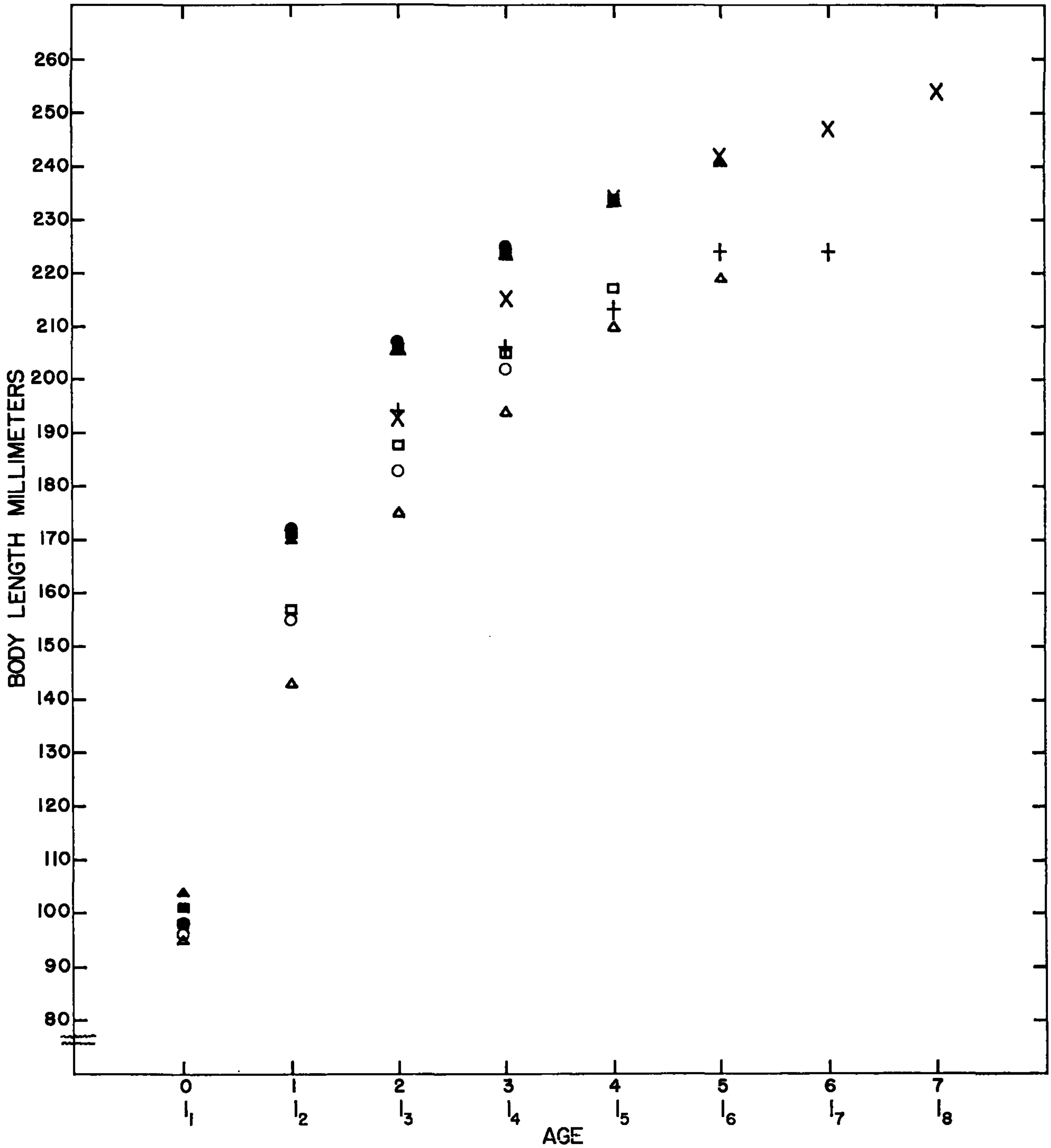

FIGURE 3.—Growth of pilchard of the 1939 year class taken in Canada and in San Pedro. Mean observed lengths of fish taken in Canada are shown by crosses, those in San Pedro by pluses. Mean calculated lengths of 4-, 5- and 6-ring fish are shown by circles, squares, and triangles, solid symbols for Canada, open symbols for San Pedro.

GROWTH CURVES OF 1939 YEAR CLASS

Utilizing mean calculated lengths (table 2) for a given year class of Pacific pilchard taken in the most northern region of catch, Canada, and in the most southern, San Pedro, we may compare growth curves derived from mean calculated lengths with those derived from mean observed lengths for each year class throughout its life in the fishery. An advantage in the transformation plot is graphically illustrated by figures 3 and 4. It is not readily apparent from the conventional growth curves of the 1939 year class (fig. 3) that the crosses delineating the growth curves derived from mean observed lengths of the year class in successive seasons express the same rate of deceleration of growth as do the mean back calculations of length for 4-ring, 5-ring and 6-ring fish (circles, squares, and triangles) of this 1939 year class. Solid symbols represent northern calculated-length data, open symbols the southern. These same curves transformed (fig. 4) show the relative constancy of slope (k) as well as level (y-intercept) of the regressions for northern and southern populations, whether plotted from observed or calculated length data.

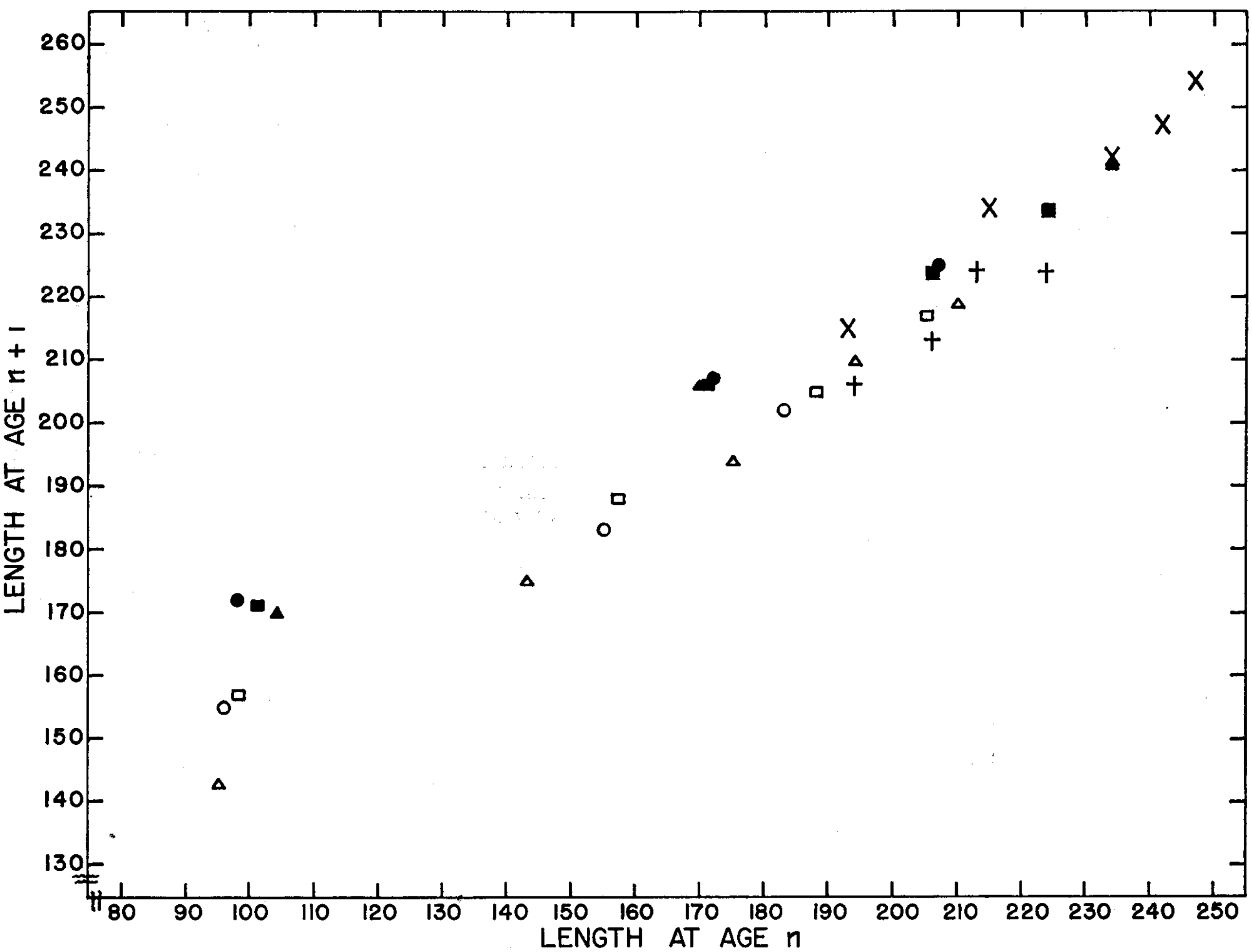

FIGURE 4.—Transformations of the growth curves of the 1939 year class shown in figure 3.

TABLE 2.—*Average calculated lengths* ($\bar{l}$) *of year classes at 4-ring and older, sampled in the commercial catch of pilchard, British Columbia and San Pedro*

[Parentheses indicate average based on 13 5-ring fish from Washington brackets, fish from Oregon; asterisks, 9 fish sampled]

Year class and calculated length ($\bar{l}$)	British Columbia			San Pedro		
	4-ring	5-ring	6-ring	4-ring	5-ring	6-ring
1937:						
$\bar{l}_1$	118	113	112	105	102	109
$\bar{l}_2$	175	173	172	161	156	161
$\bar{l}_3$	206	208	205	192	184	187
$\bar{l}_4$	223	225	223	205	197	202
$\bar{l}_5$	--------	236	234	--------	207	211
$\bar{l}_6$	--------	--------	241	--------	--------	218
1938:						
$\bar{l}_1$	103	107	110	96	98	103
$\bar{l}_2$	169	173	172	162	161	161
$\bar{l}_3$	203	206	205	188	188	191
$\bar{l}_4$	218	222	222	201	201	208
$\bar{l}_5$	--------	232	233	--------	211	217
$\bar{l}_6$	--------	--------	240	--------	--------	225
1939:						
$\bar{l}_1$	98	101	104	96	98	95
$\bar{l}_2$	172	171	170	155	157	143
$\bar{l}_3$	207	206	206	183	188	175
$\bar{l}_4$	225	224	224	202	205	194
$\bar{l}_5$	--------	234	234	--------	217	210
$\bar{l}_6$	--------	--------	241	--------	--------	219
1940:						
$\bar{l}_1$	108	112	112	103	105	--------
$\bar{l}_2$	179	178	182	156	158	--------
$\bar{l}_3$	213	211	211	185	184	--------
$\bar{l}_4$	230	228	227	202	200	--------
$\bar{l}_5$	--------	238	238	--------	211	--------
$\bar{l}_6$	--------	--------	246	--------	--------	--------
1941:						
$\bar{l}_1$	--------	(116)	[112]	100	107	--------
$\bar{l}_2$	--------	(186)	[179]	156	166	--------
$\bar{l}_3$	--------	(219)	[214]	187	195	--------
$\bar{l}_4$	--------	(236)	[231]	204	207	--------
$\bar{l}_5$	--------	(248)	[241]	--------	216	--------
$\bar{l}_6$	--------	--------	[248]	--------	--------	--------
1942:						
$\bar{l}_1$	107	95	[108]	116	109	--------
$\bar{l}_2$	183	166	[170]	174	170	--------
$\bar{l}_3$	213	211	[208]	198	203	--------
$\bar{l}_4$	232	231	[230]	211	219	--------
$\bar{l}_5$	--------	242	[244]	--------	230	--------
$\bar{l}_6$	--------	--------	[254]	--------	--------	--------
1943:						
$\bar{l}_1$	111	[112]	--------	115	*116	--------
$\bar{l}_2$	172	[177]	--------	174	*163	--------
$\bar{l}_3$	205	[213]	--------	203	*190	--------
$\bar{l}_4$	229	[234]	--------	218	*202	--------
$\bar{l}_5$	--------	[247]	--------	--------	*211	--------
1944:						
$\bar{l}_1$	[129]	--------	--------	133	130	--------
$\bar{l}_2$	[196]	--------	--------	175	169	--------
$\bar{l}_3$	[228]	--------	--------	193	185	--------
$\bar{l}_4$	[246]	--------	--------	205	197	--------
$\bar{l}_5$	--------	--------	--------	--------	207	--------

CONSISTENCY OF GROWTH CURVES

Year classes 1937 through 1942 provide sufficient data for construction of curves of growth similar to those of the 1939 class (see tables 1 and 2). For the year classes 1937 through 1940, the estimates of means have greater reliability owing to more extensive sampling during seasons 1941–42 through 1944–45. A decline in catches coincided with curtailment of the sampling program so that from seasons 1945–46 through 1949–50 the estimates of mean lengths are based on fewer fish.

The transformations for year classes 1937, 1938, 1940, 1941, and 1942 are similar in growth characteristics to those of the 1939 year class (see table 3). From analysis of covariance, no significant difference was apparent in the mean slopes, k, of the transformations between each of these year classes in the two areas of catch, Canada and San Pedro. That slope, or rate of deceleration of growth, is the more stable of the two growth characteristics, and that, with relatively constant environments, slope is a physiological character of genetic meaning, is suggested from an experimental study of growth in *Platypoecilus maculatus* (Felin 1951).

For each of the year classes tested, two distinct y-intercepts, or levels, for transformations of mean calculated and observed lengths are maintained in the northern and southern areas. From the covariance tests, the differences are significant at the 1-percent level. Further translated into predicted ultimate size $\left(\frac{y\text{-intercept}}{1-k}=l_\infty\right)$, the range of the means for San Pedro is 220–236 millimeters standard length, and for Canada, 249–258 millimeters, with no overlap for those year classes tested (table 3).

TABLE 3.—*Growth characteristics in northern and southern areas of catch derived from regressions of means* l_{n+1} on l_n

Year classes	Rate of deceleration, slope (k)		y-intercept levels		Ultimate size (mm.) $\left(l_\infty=\frac{y\text{-intercept}}{1-k}\right)$	
	British Columbia	San Pedro	British Columbia	San Pedro	British Columbia	San Pedro
1937	0.57	0.54	108	102	251	222
1938	.55	.52	112	107	249	223
1939	.54	.59	115	94	250	229
1940	.52	.55	120	99	250	220
1941	.52	.56	123	101	256	230
1942	.53	.53	121	111	258	236

BIOLOGICAL SIGNIFICANCE OF DIFFERENCE IN GROWTH CHARACTERISTICS

Significant difference in level, or the growth characteristic l_∞, may represent phenotypic response of a plastic genotype to varying hydrographic environments. It may be useful as an indicator, as suggested for vertebral counts in European pilchard (Ruivo 1950) to separate homogeneous populations of certain fishing areas without implying genetic significance. The results of the covariance tests apply only to mean growth curves, and at present it seems probable that if significant difference were found in the growth characteristic k in certain individuals or segments of the population it would indicate genotypic difference.

There is some evidence that deviations from the straight-line regression for each area are greater for mean observed lengths of a year class in successive seasons of catch than for mean calculated lengths of a year class in one season. To compare transformations of mean observed lengths with those of mean calculated lengths is rather difficult since observed lengths are not obtained until the scales have one ring, or the fish are in their second year of life, when they have accomplished much of their growth; whereas, calculated lengths begin at 1-ring, and this first growth increment as already noted shows great variability. In San Pedro growth curves for the 1942 class, however, variance of mean observed lengths alone about the regression is 10 times the variance for calculated lengths only. Such irregularities suggest that greater shifts in populations of a given year class may occur from season to season than within one season. Small deviations from the transformations of mean calculated lengths of the 4-, 5- and 6-ring pilchard of each year class indicate that within a single fishing season the populations at each port are more homogeneous.

North-south migration of larger fish

Tagging of fish along the Pacific coast by some of the agencies engaged in pilchard research gives evidence of extensive migrations (Hart 1943a). It is the larger fish within a group tagged in the south that are caught first farthest to the north (Clark and Janssen 1945, pp. 19–20). That some of the larger pilchard cover great distances is likewise indicated in the apparent shift at older ages in central California and San Pedro toward the level of regression of northern growth types as shown in transformations of the 9-year averages of observed lengths (fig. 1).

If, however, the migration course for the entire population were of great seasonal regularity from south to north and return, one would expect with increasing age of fish a tendency toward homogeneity of growth types along the coast. If populations of older fish became more homogeneous in their growth characteristics, a given year class at 5- or 6-rings would show a tendency for the level of northern and southern growth types to shift toward a single norm of oceanic migratory sardines common to all areas of the fishery, or at least to shift toward a level and slope other than the one consistently associated with a particular area of catch. This shift does not so far occur in transformations of mean calculated length data. At 4-, 5-, and 6-rings the levels of these regressions remain distinct for northern and southern sardines (*cf.* fig. 4).

Complete intermixture and homogeneity in populations of adult pilchard in different regions of catch is not evidenced from available data on mean calculated lengths. The distinct levels of the growth transformations which are maintained in northern and southern populations, however, do not controvert the evidence from tagging that there is migration of larger fish toward the north. As is shown from tagging results, growth data also indicate migration of northern pilchard into southern waters. That larger fish of older ages enter the southern catches is demonstrated not only from the 9-year averages of observed length data (fig. 1), but likewise for a single year class as it passes through the fishery (*cf.* table 1). For San Pedro the increase in mean observed lengths for certain individual year classes at 5-ring and older is reflected in a sharp rise at this stage in their length-on-time curves of growth. Similarly, an apparent departure from an expected asymptote of length is observable in Phillips' (1948, p. 7) curve of average observed length of sardines at each age over a 6-year period at San Pedro. Such irregularity in the San Pedro growth curves must be explained by an influx onto southern fishing grounds of large, old fish differing in their growth pattern from the smaller fish up to 4-ring age which are caught in San Pedro. Conversely, in certain other year classes, there has been an actual decrease in observed lengths as a year class reached older ages and was caught off San Pedro. This indicates an influx of smaller fish of more southern growth characteristics onto these grounds. The extent of the seasonal north-south migration and the extent of season-to-season variability in interchange of northern and southern populations are as yet not determined.

Possibilities of inshore-offshore migrations of pilchard are in the main unexplored and, short of the use of radioactive markers, may be difficult to determine. Hart (1943a, p. 178), however, records tagged fish moving into inlets on the west coast of Vancouver Island and remaining there throughout the winter. Such winter fish, according to Hart, "are occasionally captured during the winter herring fishing season and . . . they sometimes provide early in-shore fishing before the main pilchard shoals approach the Vancouver Island coast in the summer."

North-south variation in growth characteristics

The variation in growth of pilchard from north to south may prove to be a physiological characteristic of clinal significance. The study of intraspecific clines in fishes is, of course, complicated by what Mayr (1944, p. 135) terms the "strong and only rather recently appreciated phenotypical plasticity of many species." It seems likely that the greater size of fish in northern waters is not entirely explained by northern migration of the larger individuals of each year group. These northern pilchard may represent a separate stock grown to larger sizes rather than only a sorting out of larger fish from a whole coastal population. It may be that such growth differences from north to south can be explained in part by geographical gradients in environmental factors associated with gradients in morphological and physiological characters, or clines, within the range of a species.

It seems probable from existing evidence on growth characteristics of the fish in different geographical regions that there may be season-to-season fluctuations in the size and the location of optimum living areas associated with fluctuations in marine climate. Such fluctuations may largely determine what part of the sardine population will be available for capture in each area. Illustrative of between-season shifts in populations are the apparently greater deviations in mean observed lengths than in mean calculated lengths of a year class from its rectilinear transformation. But it also seems evident from back calculated lengths that there is, for a given year class, a persistent cline in growth characteristics from north to south, and that populations, although fluctuating in distribution from season to season and somewhat migrant, may be more discrete and limited latitudinally than has been supposed from the evidence of vertebral counts (Clark 1936, 1947) and tagging (Hart 1943a; Clark and Janssen 1945).

McHugh (1950) has reported on latitudinal variation in three species of clupeoids of the North Pacific. Parallel gradients in hydrographic and meristic characters and consequent homogeneity or heterogeneity of populations with respect to certain characters are discussed. For the northern anchovy (*Engraulis mordax*) and Pacific sardine, McHugh found clines in anal fin-ray counts and significant heterogeneity among several populations. He notes close parallelism in meristic counts of anal fin rays in anchovy and sardines and likewise in vertebral counts of both species. From his more complete study of meristic characters in anchovy, McHugh concludes (p. 58) that "clines in numbers of dorsal, anal and pectoral fin rays are in the opposite direction to that shown for gill-rakers, and all four fail to correspond with the distribution of mean vertebral number."

McHugh considers it probable that in the Pacific Northwest the fixation period for sardine fin-ray counts occurs during a period of warmer water temperatures, while in southern California water temperatures average lower at this period of development. Thus the usual inverse relation between meristic count and temperature follows for counts of fin rays as well as of gill rakers, and to a lesser degree of vertebrae.

Lack of significant differences in vertebral counts between samples of sardines from British Columbia to southern California (Clark 1936, 1947), and the heterogeneity in populations according to fin-ray counts, McHugh attributes to close dependence of each meristic character on coexistent physical factors in the environment at the time of fixation of the character. Since spawning occurs within a rather narrow temperature range, phenotypic variation could likewise be narrow for a character, such as vertebral number, with an early fixation period, whereas with a later, perhaps longer, fixation period there could be greater concomitant variability in environmental factors and heterogeneity of populations as indicated by these other meristic characters.

McHugh's results on vertebral counts thus agree with Clark's; and he concludes (p. 110)—

> Since the number of vertebrae drops very sharply with decreasing latitude off Baja California, it is assumed that these fish belong to a distinct race that has different temperature requirements.[1] It is also concluded that the number of vertebrae is not a particularly critical measure of population segregation in pelagic spawning species.

McHugh further suggests that—

> intermingling between populations may not be random with respect to meristic or other characters. If this is so, wandering of individuals, as shown by tag returns, may not necessarily indicate movements of the population as a whole. Experimental verification of these deductions is much needed . . .

The apparent cline in growth characteristics suggests the presence of intraspecific populations in which there is limited intermingling. Rather than a general coastwise migration pattern, a series of overlapping coastal migrations of more than one stock appears more consonant with observed data on growth.

Growth characteristics determined by origin

There is increasing reason to suppose that the geographic origin of sardine populations may be widely variable from season to season. Evidence from spawning studies demonstrates that there were, during 1949 and 1950, two centers of spawning; one, early in the year, around and to the south of Cedros Island off central Lower California, and another, somewhat later and farther offshore, off southern California. It is also reported (California Cooperative Sardine Research Program 1950, p. 37) that "In the waters separating these two spawning centers very little spawning has been encountered during either season, and this little has been confined to a coastal strip . . ." During these two seasons there was little indication of northern spawning. In 1940, however, an unusual abundance of young fish of the 1939 year class was reported (Walford and Mosher 1941) in north Pacific waters off Oregon, Washington, and British Columbia. The probable occurrence of northern spawnings of lesser magnitude is suggested by the presence in other seasons of small, presumably 1-ring, pilchard in British Columbia waters recorded by Hart (1943b). The growth characteristics of northern and southern populations may thus be early determined by their origins.

Whether the populations sampled by northern and southern fisheries have genetically distinct components has not been demonstrated. The significantly different levels of their mean growth transformations may indicate only phenotypic differences in growth ascribable to differing environmental conditions at time and place of spawning or in later life or both. These differing conditions of growth must largely be maintained, however, in each area and in each population sampled, since the mean levels of growth transformations characteristic of each geographic region have remained relatively constant and distinct as shown from calculated length data for 4-, 5-, and 6-ring sardines of each of six year-classes over the seasons of study. This appears to point to the conclusion that there may be a southern spawning center which contributes more heavily to the southern California stocks and that although some of the more southern growth types migrate into central California, they are found rarely in the Pacific Northwest.

The existence of an area of intense spawning off central Lower California was not realized until the expanded sardine research program under the California Marine Research Committee made possible the collection of eggs and larvae in this spawning center as well as in the better known area of more widespread spawning off southern California. In both areas, times of spawning vary between seasons and appear to be associated with conditions of favorable temperature and upwelling. (See California Cooperative Sardine Research Program 1950, p. 39.) The varying importance of the contributions of the two areas to the present sardine fisheries is suggested in differing prevalence of southern or of northern growth types in the catches. It appears to be a reasonable hypothesis that the spawning grounds off central Lower California give rise to the southern components found in the catches off San Pedro (and to a lesser degree in catches off central California), while the large northern fish originate off southern California and to the north in years favorable for northern spawning. It is not yet known whether spawning populations in the two main centers are or are not distinct, i. e., genetically isolated in space and time.

[1] From data obtained in the California Cooperative Sardine Research Program in 1949 and 1950, the spawning requirements, so far as temperature is concerned, have been closely similar in what at present appear to be the two main centers of spawning (1) off central Lower California and (2) southern California.

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Fish in the northern part of the range of the fishery are perhaps distinguishable as large, long-ranging individuals, while southern stocks may be characterized by smaller size and more limited migration routes. These stocks appear to overlap in their distribution on fishing grounds as evidenced from the length-frequency data accumulated over a long period of years by the California Department of Fish and Game and later by the State agency in cooperation with the United States Fish and Wildlife Service. Over the period of study of age composition of the catch for which length composition by age is also available, it is evident that the smaller sizes of each year class are rarely caught north of central California.

Ronquillo (1949, p. 29) found that the sizes of pilchard in the Pacific Northwest during most months of fishing did not differ significantly from those caught off central California, but that fish from both these regions showed significant differences from those taken off San Pedro. Over three seasons, from 1945–46 through 1947–48, in all age groups there was a significant difference in size between fish landed at San Pedro and Monterey. During the first 2 years of life sardines taken at San Pedro were significantly larger; in older age groups those landed at Monterey were larger than those at San Pedro. Ronquillo (op. cit., p. 25) also found that the coefficient of variation fluctuated more at San Pedro than at other localities which indicated greater heterogeneity in those samples. He found this measure relatively constant in the Pacific Northwest and therefore indicative of homogeneity within the samples.

The tendency for smaller sizes to remain in the southern part of the range of the species is illustrated also by tagging results (Clark and Janssen 1945, p. 22). They found a southward migration of some of the sardines released in central California and note—

> a greater proportion of the smaller sizes have made this southward migration. For the group tagged in 1940, 72 percent of the recoveries in southern California during the first season after tagging were less than 19 cm. when tagged. For the same season in central California only 50 percent of the recoveries were of these smaller sizes. During the second season after tagging, 74 percent of the southern California recoveries were less than 19 cm. when tagged but only 43 percent of the central California recoveries were composed of these smaller sizes.

Recoveries of sardines tagged off central Lower California have been almost entirely in California. Approximately 78 percent were recovered in southern California, 15 percent in Monterey, 7 percent in San Francisco and less than half of 1 percent (represented by one tag) in Washington (Janssen 1948). Concerning the absence of recoveries in Lower California, Janssen (p. 7) states as follows:

> No tag recoveries have been reported from reduction plants in Lower California. Facilities for recovering tags were in operation there for only a brief period and the quantity of sardines processed in Mexico is small in comparison with other localities along the coast.

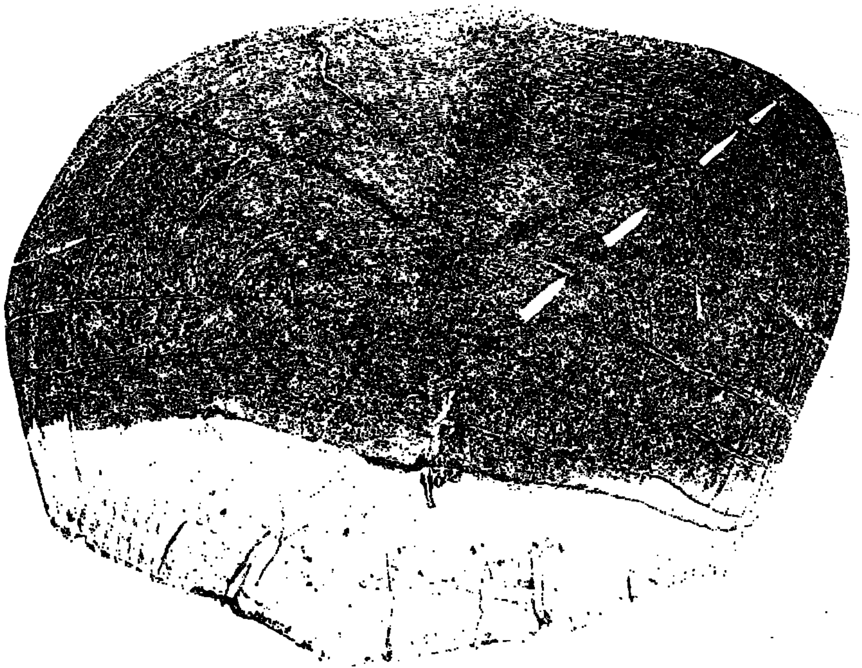
Considering the total number of tags recovered without regard to area of recovery, only 10 percent of tags put out off Mexico were recovered, while off southern California 23 percent and off central California 25 percent were recovered (according to Janssen's adjusted percentage recovery figures, p. 9). The Mexican taggings further indicate the tendency for the southern fish to remain in southern waters.

The larger pilchard of a year class, on the other hand, commonly are caught on any of the usual fishing grounds from the Pacific Northwest to southern California. Whether the significant difference in attained ultimate size, l_∞, of southern as opposed to northern growth types arises by reason of primary difference either in location of spawning centers or in location of nursery grounds, or both, and whether in turn difference in origin of stocks also represents genetic difference await further data from spawning studies and determination of how discrete are the areas of spawning and of spawning stocks.

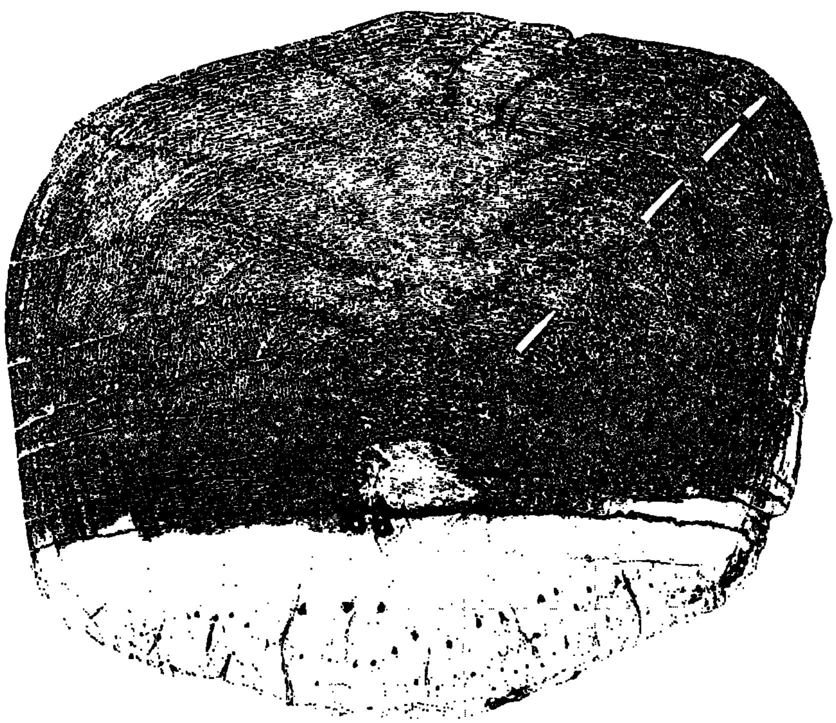
The apparent differences in growth characteristics in populations along the coast suggest the desirability of study of population dynamics not only for the coast as a whole but also for geographic areas, e. g., for the Pacific Northwest, central California, southern California, and further subdivisions of areas off Lower California not yet clearly delineated.

SCALE AND GROWTH PATTERNS OF INDIVIDUAL FISH

That the fished stocks of the Pacific Northwest and southern California have, for practical purposes, some independence seems indicated from further lines of evidence.



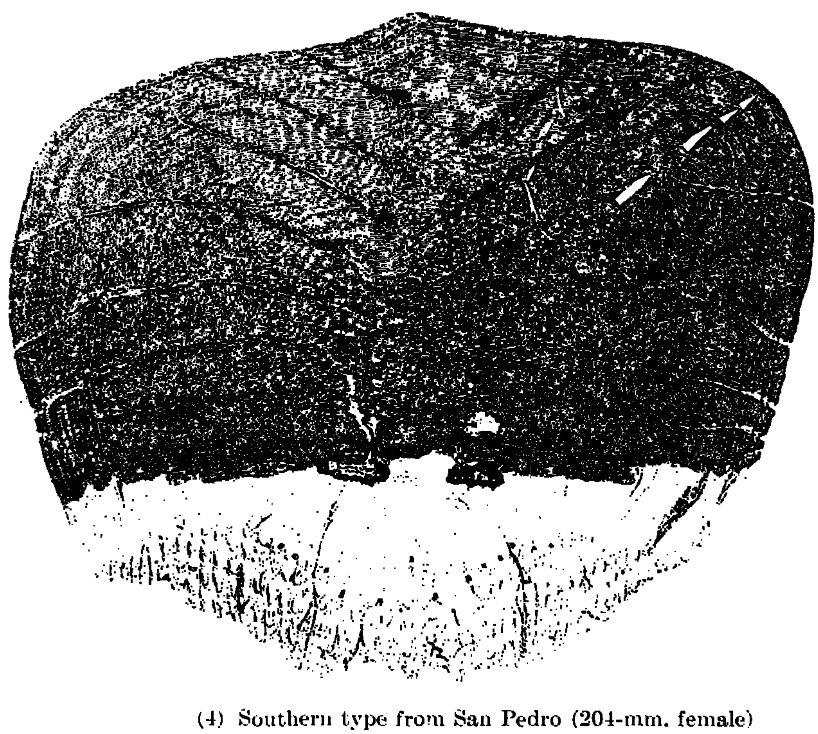
(1) Northern type from Canada (249-mm. female)



(2) Northern type from San Pedro (241-mm. female)

FIGURE 5a.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show the well-defined annual rings of large fish caught commonly in the north, but also entering the southern fishery. They have a proportionately small first-growth increment and a rapid rate of deceleration in growth.

(3) Southern type from San Pedro (206-mm. male)



(4) Southern type from San Pedro (204-mm. female)

FIGURE 5b.—Growth types of Pacific pilchard at 4-ring stage as shown in scale patterns. These scales show fainter year marks common among smaller fish in southern catches, rarely caught in the north. The proportionately large first-growth increment is common to both; (3) shows slow deceleration, (4) fast deceleration.

Early in the examination of scales for age determination, qualitative differences were noticed in the scale patterns of pilchard from different regions of catch. An attempt was made to establish criteria for separating ring types somewhat as had been done in herring by Norwegian investigators (Runnstrøm 1936). Although scales collected in the Pacific Northwest showed predominantly heavily marked winter rings of the northern type associated with sharp cessation of growth (*cf.* fig. 5a), and those from the San Pedro fishery showed, as a rule, the faintly marked annuli suggesting milder winters (*cf.* fig. 5b), the presence of intermediate ring types in central California made the separation too subjective for quantitative treatment.

Further attempts to separate the varying growth patterns in individual fish were made using transformation values (calculated by the method of semiaverages) asymptotic length (l_∞) and rate of deceleration of growth (k) for individuals caught in four geographical regions. For the 1939 class, the regression of the values l_∞ on k gave scatter diagrams (fig. 6) for Canada (N=286, dots) and San Pedro (N=433, circles). Even though there is overlapping in the scatter of individuals caught in the two areas, a large proportion of 4-ring sardines of the growth type caught in San Pedro are outside the scatter for the Pacific Northwest. This type was characterized by relatively steep slope, or slow rate of deceleration, and small calculated ultimate size. We interpreted this to mean that there was in turn a large proportion of San Pedro 4-ring fish that would never have been caught in the Pacific Northwest. Likewise, a smaller proportion of Canadian fish were outside the San Pedro scatter and might never be caught in southern California.

Scatter diagrams (fig. 7) of San Francisco (N=514, symbolized by x) and Monterey (N=783, symbol ǫ) show many fish of the northern type. Numerous individuals from Monterey catches also fall within the scatter of characteristically San Pedro type (*cf.* fig. 6). San Francisco shows few of the latter but a large proportion of types common to Canada; namely, with relatively rapid deceleration rates and greater asymptotic lengths.

These regressions of l_∞ on k for 1939-year-class pilchard caught in the 1943–44 season were curvilinear as in the aquarium fish *Platypoecilus maculatus*, and some individuals with improbably high calculated asymptotes [2] were found as in platies (Felin 1951).

Similar regressions for individual pilchard of the same year class were plotted at the 6-ring stage (fig. 8). By this time, individuals of an unlikely predicted ultimate size were not represented in the catches anywhere along the Pacific coast and calculated asymptotes were well within the probable range of size for the species. As a result of the disappearance of these types, the regressions appear linear.

The scatter for 6-ring pilchard at all four ports included 194 individuals. Of these, 10 percent were entirely outside the main scatter of all fish. This group showed southern growth characteristics. Out of 70 from Canada only 1 percent were of this type with slow deceleration rate and low predicted size. Of 54 fish from San Francisco, 11 percent were of this type; of 57 in Monterey, 7 percent; and out of the small number, 13, of this older age caught at San Pedro, 62 percent had the typically southern growth characteristics.

The high percentage of these fish in San Pedro is in agreement with the appearance of predominantly southern-type annuli in San Pedro scales. Many scale samples taken from sardines off southern California and a few collected off Lower California show faint winter marks and wide zones of summer growth; the yearly increments decrease very slowly in size, illustrative of their slow deceleration in growth. (See figure 5b.) These fish are characteristically of small size for their age compared with northern types (see fig. 5a), and so far have not been observed to attain as great age as the large northern pilchard. Their position in this respect appears similar to that of the warm-water Mediterranean pilchard when compared with North Sea types (*cf.* fig. 2).

From the few available samples of Mexican fish taken off northern Lower California there is also indication of another southern growth type characterized by a low k value (the slope is even less than that for northern types), and by a small calculated ultimate size. (See figure 5b.)

The pilchard scales were photographed by means of infrared plates. This method was used by Roper (1936), to bring out year rings as distinct

[2] J. L. Hart (personal communication) recorded a standard length of 351 mm. for a pilchard caught off the west coast of Vancouver Island and landed at Nootka.

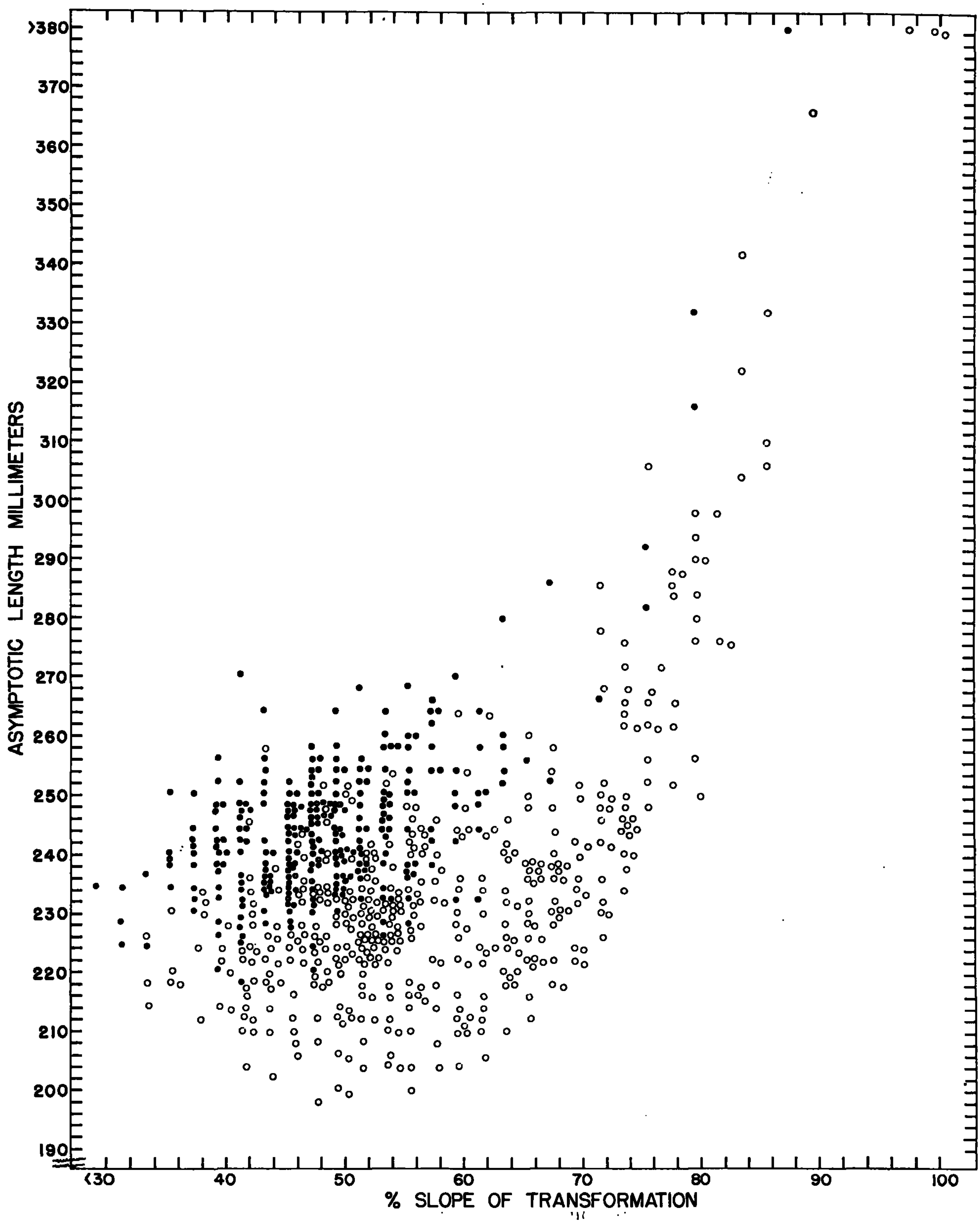


FIGURE 6.—Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage, asymptotic length (l_{∞}) on rate of deceleration of growth (k). Dots represent fish taken in Canada, circles in San Pedro.

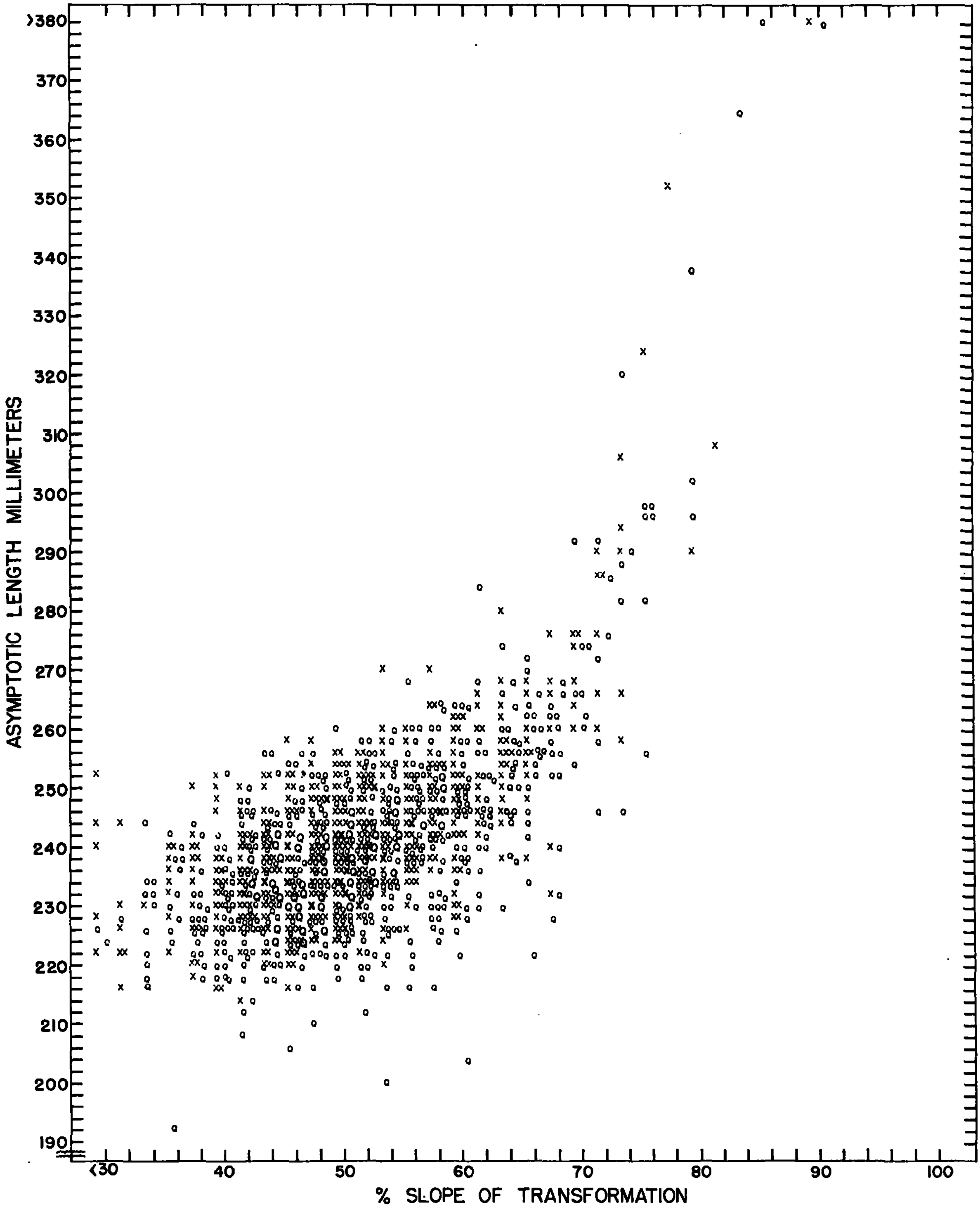


FIGURE 7.—Regression of transformation values calculated for individual pilchard of 1939 class caught at the 4-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Symbol x represents fish taken in San Francisco, symbol Q in Monterey. Larger symbols represent values for five fish, smaller for a single individual.

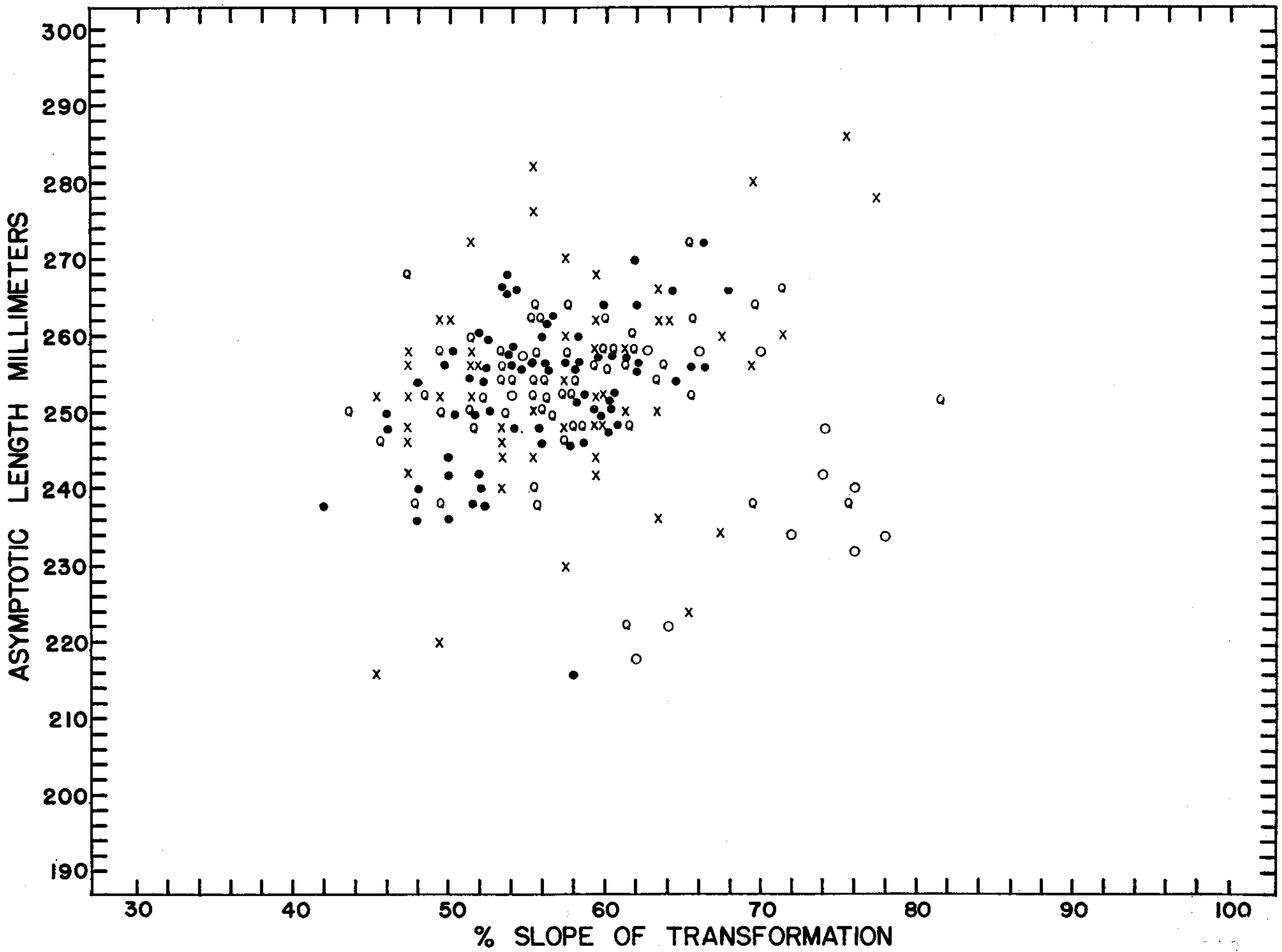


FIGURE 8.—Regression of transformation values calculated for individual pilchard of 1939-class caught at the 6-ring stage, asymptotic length (l_∞) on rate of deceleration of growth (k). Dots represent individuals taken in Canada, circles San Pedro, symbol x San Francisco, symbol Q Monterey.

from false rings in opercula of perch, and appears a satisfactory means of photographing pilchard scales.

Hessle (1925) gives illustrations of scale types which show differing growth patterns in various races of Baltic herring. The autumn-spawning herring which spawn in coastal waters (never inside archipelagoes) show rapid growth during the first 3 years and subsequent rapid falling off in growth increments. This is likewise the growth pattern of the somewhat smaller, spring-spawning sea herring of the Baltic in the same region. (The pattern corresponds to pilchard growth with a low k value, or rapid rate of deceleration in growth.) The fjord herring, on the other hand, also spring spawners, are sometimes quite isolated and show great variability in size with some dwarf and some giant forms. Hessle notes (p. 37) that "these two herring forms [dwarf and giant] show a striking similarity as regards actual mode of growth." He figures (p. 40) the "even growth" typical of all the fjord herrings as contrasted with the "stagnant growth" (pp. 17, 33) of sea herring of the Baltic. He also found (p. 45) ice herring in the Gulf of Bothnia with a growth pattern and spawning habits similar to the fjord herring. He concludes that—

> mode and rate of growth seems . . . to be very like that of the most rapid-growing fjord-herrings of the Middle Baltic. It is therefore natural to suppose that these spring-spawners of the Gulf . . . are closely related to the fjord-herring of the Middle Baltic.

The even-growth pattern of Hessle corresponds to the southern growth type of the Pacific sardine with a high k value, or slow deceleration in growth.

CONTRACTION OF FISHED STOCKS

Recent catch data may be pertinent also to the problem of populations. The abrupt decline in landings of pilchard in recent seasons reached a low of 130,000 tons in 1947–48, the lowest in the history of the fishery on the Pacific coast since 1923–24 (Anonymous 1948). To account for this decline, a number of explanations have been offered by pilchard investigators, all of which may affect in varying degrees the fished population(s): (1) Lowered recruitment of young fish, (2) reduced availability of fish to the fisherman, (3) increased natural mortality, and (4) increased fishing mortality.

The decline in catches in central California and in the Pacific Northwest have been almost entirely responsible for the sudden decline in total catch of the coast as a whole. In all these ports there has been poor fishing since the 1945–46 season and in the Northwest there were no landings during the 1949 and 1950 seasons.

In southern California, however, the total catch did not fall off conspicuously up to 1950–51, and in this season San Pedro recorded the largest tonnage of sardines ever taken there. The catch per unit-of-effort did fall in 1947–48 (Clark and Daugherty 1950, 1952), but for no other recent season has it differed greatly from previous average lunar months. Concentration of sardines on southern grounds has been used as argument by representatives of the industry to obtain legal extension of Monterey grounds 70 miles to the south (Monterey Herald, May 14, 1951).

Contraction of areas of good fishing and apparent contraction of spawning areas may be dependent on hydrographic changes, and centering of the available population in the southern part of the range thus may have produced a series of southern year classes.

DISTINGUISHING SOUTHERN AND NORTHERN YEAR CLASSES

To detect early in its life in the fishery a year class that is likely to be primarily southern, some measure of its relative strength in northern and southern areas of catch is desirable. One measure of strength of a year class in the fishery has been the numbers of pilchard in the 3-ring stage caught at all ports (Walford 1946b). Although availability and degree of recruitment at earlier ages are more variable, another measure of early strength of a year class in any region is the number of 1-ring or 2-ring fish caught at any port. At this age presumably, migrating pelagic sardines would be less widely dispersed throughout their possible habitat and nearer their point of origin.

San Pedro is considered the port nearest centers of spawning. Early strength of a year class at this port may be taken as a measure of spawning success in the south. Figure 9 shows ratios of catch per boat-month (using California catch-per-unit data, Clark and Daugherty 1950) at San Pedro to catch per boat-month [3] for the coast as a whole for 1-ring (dot) and 2-ring (circle) sardines of each year class over the period of comparable sampling (1941–49). The year-class strength for the Pacific coast as measured by catch per boat-month at the 3-ring stage is also figured (symbol x). (There is rather close correspondence between year-class strength at 2-ring and at 3-ring. For the 1947 year class, the number caught at 2-ring is figured, by symbol +, as an approximation of its probable strength in the following season.)

When the ratio of San Pedro 2-ring fish to the Pacific-coast total was low, as in the 1939 year class, the total year-class strength for the whole coast was well above average. The 1940 year class was slightly above average strength; the ratio San Pedro to Pacific coast was somewhat above 1.0 at 1-ring, somewhat greater at 2-ring. The 2-ring age group usually dominates at San Pedro. The 1941 class, however, was the dominant age group as 3-ring at San Pedro in 1944–45, showed a high ratio to the rest of the coast, was somewhat below average in year-class strength, and was relatively below normal numbers in northern ports throughout its life in the fishery. By these criteria, the 1939 year class may be called a successful year class with early strength in the northern fishery, the 1941 class relatively

[3] When estimates of total numbers of sardines caught, by year class, are used instead of those adjusted for fishing effort the results correspond closely.

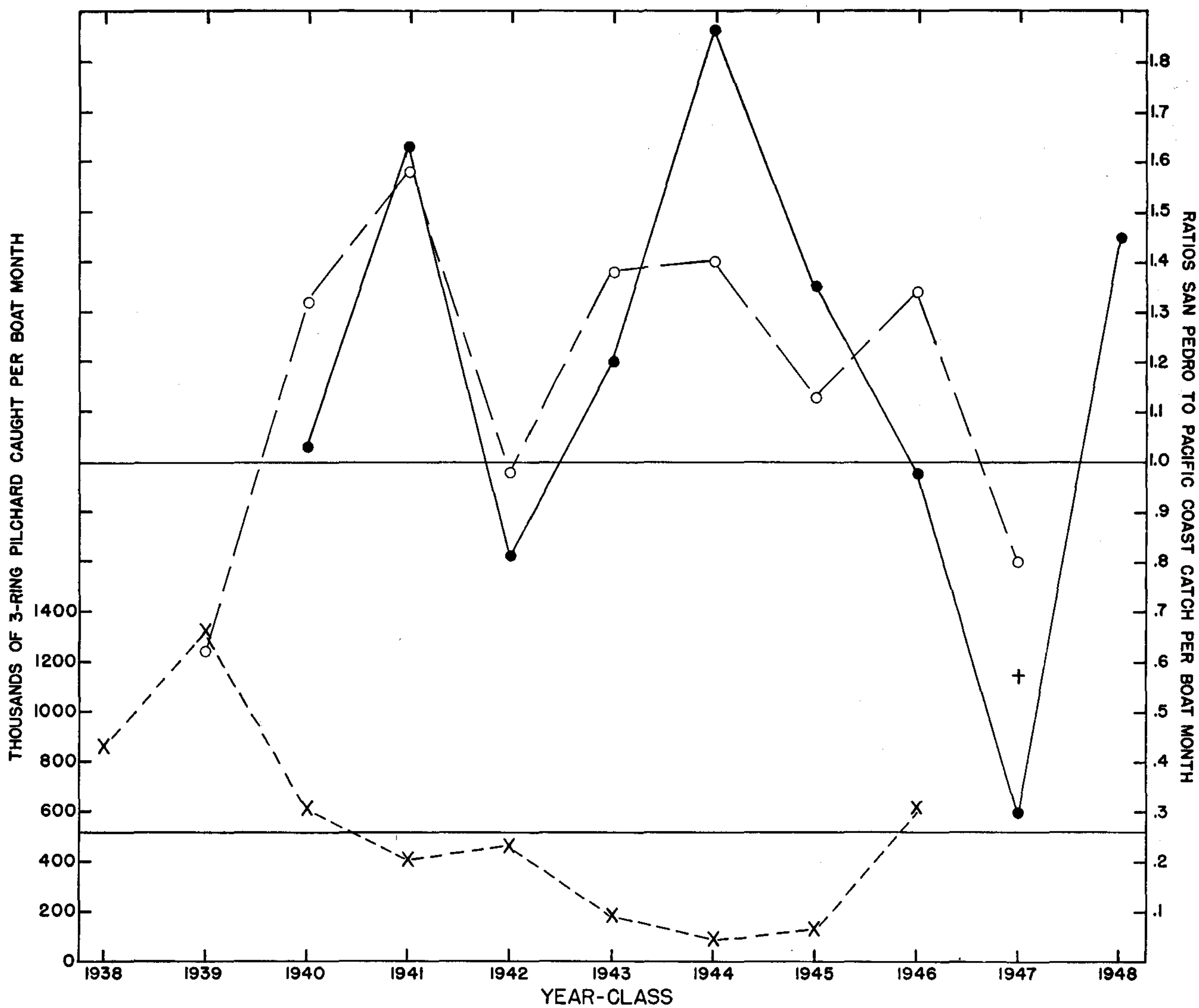


FIGURE 9.—Ratios of numbers of pilchard of each year class taken per unit-of-effort at San Pedro to those taken along the whole Pacific coast as 1-ring (dot), as 2-ring (circle). Numbers of fish of each year class taken per unit-of-effort at the 3-ring stage are shown (symbol x) as relative measures of year-class strength.

less successful and primarily a southern year class.[4] The 1942 class was of about average strength and the San Pedro-Pacific coast ratio indicated probable northern origin. The year classes 1943, 1944, and 1945 were below average strength and showed early dominance at San Pedro as compared with the rest of the coast. The 1946 year class was above average strength and the San Pedro-Pacific coast ratio was below 1.0 at 1-ring, although comparatively in greater numbers as 2-ring at San Pedro. The 1947 class appears the most successful of any year class since that of 1939, and it shows a low San Pedro-Pacific coast ratio.

From these data the existence of southern and northern year classes seems indicated. Early northern strength, or a low ratio, may prove indicative of a widespread spawning and a relatively successful year class. There also are indications that a strong southern year class, such as those of 1941, 1946, and probably 1948, can make such significant contributions to southern catches that their year-class strength when measured by numbers caught along the whole coast at 3-ring still can be considerable. It is nevertheless only those year classes 1943, 1944, and 1945 which appear predominantly southern, by these criteria, that so far have been much below normal strength.

The San Pedro to Pacific coast ratios at 1-ring may be a better measure of relative year-class strength by region than ratios at 2-ring. There are apparent wide variations in availability, as well as in recruitment, of pilchard at 1-ring as shown in total numbers of this age class caught during each season at each port (*cf.* Felin and Phillips 1948: Mosher et al. 1949; Felin et al. 1949; Felin et al. 1950; Felin et al. 1951). Such wide variations are likely to be associated with the origins of each year class. By the time sardines have reached 2-ring they may be more widely dispersed and their origins more obscure. Hart (1943a, p. 174), for example, noted that two fish, probably of the 1939 year class, tagged at Monterey by the California Bureau of Marine Fisheries, were taken off the Canadian coast early in 1941, presumably at the 2-ring stage.

In general, the assumption that 1- and 2-ring fish have not traveled great distances is substantiated by the behavior of tagged sardines of these approximate sizes. Data from Janssen (1938) and Clark and Janssen (1945) show that recoveries to the north of fish from the southern California tagging area are at first of larger sizes than commonly would occur in the 1- and 2-ring age classes. It is also evident from Phillips' (1948, p. 7) average length-on-time growth curves for the Pacific Northwest, central California, and southern California, that for the 6-season period (somewhat subsequent to the tagging data) the mean observed lengths at 1- and 2-ring are greater for San Pedro fish than for those caught in the Pacific Northwest. In central California, 1-ring fish average smaller than those in the other two areas. At 2-ring, central California sardines begin to exceed the sizes at San Pedro. At 3-ring the sizes of Pacific Northwest pilchard begin to exceed those caught in the other two areas. These data indicate that few large 1- and 2-ring fish have left the southern California area.

Further evidence that the larger 1-ring and 2-ring sardines have not migrated far from the southern grounds is provided by calculated length data (table 4). At 1-ring the mean calculated first growth increment, $\bar{l}_1$, is greater at San Pedro than at Monterey for all the year classes over the 9-year period of study. At 2-ring, for nearly all year classes the $\bar{l}_1$ still is greater in the southern area. By the time the year classes have reached 3-ring the situation has reversed and the calculated first growth increments are nearly all greater in central California, indicating a strong influx of southern fish with large $\bar{l}_1$ into the area. For nearly all year classes at 4- and 5-rings of age the average calculated first growth increment continues to be greater at Monterey than at San Pedro.

Ronquillo (1949, p. 12) found statistically significant difference in mean observed lengths of 0- and 1-ring fish in San Pedro and Monterey and concluded that "fish reared in these two areas do not intermingle at this age." Since the commercial fishery is carried on in the winter off California when growth is minimal and the first ring will soon

[4] William T. Miller (ms.) found that temperature conditions in the spring of 1941 were unusually warm in the area off Lower California during February and March, and that according to United States Hydrographic Office records, water temperatures were higher than those normally associated with pilchard spawning. His charts suggest that during this season temperatures favorable for spawning were restricted both in space and time, namely to the area off southern California. He contrasted the 1941 season with the 1939, an unusually cold spring, and showed that during the latter season temperatures off Lower California were favorable for spawning over a wide area in February, March, and April. Water temperatures suitable for the widespread northern spawning known to have taken place in 1939 were also recorded. The relative scarcity of fish of the 1941 year class in northern catches might thus be attributed to contraction of areas and time of spawning.

TABLE 4.—*Calculated mean first growth increments* ($\bar{l}_1$) *for pilchard year classes from 1- to 5-ring caught at San Pedro and Monterey, 1936–48*

Year class	1-ring				2-ring				3-ring				4-ring				5-ring			
	San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey		San Pedro		Monterey	
	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$	Number of fish	$\bar{l}_1$
1936	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	47	104	42	104
1937	------	------	------	------	------	------	------	------	------	------	------	------	160	105	193	107	53	102	159	108
1938	------	------	------	------	------	------	------	------	1,169	98	1,054	100	453	96	672	101	100	98	351	102
1939	------	------	------	------	1,707	93	2,512	94	1,293	92	1,581	95	424	96	1,146	97	174	98	534	103
1940	256	121	313	118	1,287	109	554	107	807	106	934	110	413	103	470	108	44	105	71	107
1941	332	115	69	98	1,069	103	253	100	1,134	98	350	103	151	100	153	101	26	107	43	111
1942	386	108	563	96	1,042	98	1,376	96	242	102	319	103	60	116	81	109	46	109	------	------
1943	523	105	446	104	335	101	254	107	189	107	140	115	83	115	------	------	10	116	------	------
1944	106	114	74	107	259	128	96	110	161	126	------	------	33	133	------	------	27	130	30	131
1945	370	143	327	117	281	139	100	99	99	131	23	114	60	133	62	132	------	------	------	------
1946	195	109	357	107	407	112	59	103	209	117	172	116	------	------	------	------	------	------	------	------
1947	59	123	613	104	242	121	503	101	------	------	------	------	------	------	------	------	------	------	------	------
1948	71	140	14	133	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------

appear, the observed length at 0-ring is comparable to the calculated length at 1-ring, and observed length of 1-ring fish is comparable to the calculated length at 2-ring.

Tagging and growth data thus both appear to indicate a tendency for larger fish to migrate farther north, but there is apparently not a great deal of emigration of the large 1- and 2-ring sardines from the southern California grounds so that these early ages may be used as reasonably good indices of early year-class strength in one geographical area.

ANOMALIES IN YEAR-CLASS CATCH CURVES

Vital statistics of the fishery show that new sources of fish were unexpectedly available in season 1949–50 (Felin, Daugherty, and Pinkas, 1950 and 1951). The overavailability of certain ages is reflected in certain anomalies in year-class catch curves at all California ports. At all three ports there was a marked deviation from the previous trend of total mortality rate for 1944 and 1945 year classes, as 4- and 5-ring fish. In central California ports, the 1943 and 1946 year classes also showed increase in availability (as defined by Marr 1951).

BIMODALITY IN LENGTH-FREQUENCY COMPOSITION

There are also indications of bimodality in length-frequency composition of the 1944 year class caught during the 1949–50 season in California ports (Felin, Daugherty, and Pinkas, 1950).

Study of growth transformations from calculated lengths of individual fish of the 1944 year class showed that coincident with the unexpectedly large catches of this year class as 5-ring fish in 1949–50 there were many small-sized individuals of this age caught in San Pedro and Monterey. Some of these 5-ring fish were smaller than sardines of the same year class as 4-ring so that their presence in the catches could not be accounted for as small fish remaining after the exodus of larger migrants going north. Their presence must rather be explained as an influx, probably from the south, of small fish into the southern and central California fishing areas. That this appears to be a strongly southern year class is indicated in figure 9. The average observed lengths of the 1944 year class as 5-ring at San Pedro and Monterey also show a decrease as compared with the same year class caught as 4-ring fish in the previous season.

An appearance of bimodality has also been observed in the length composition of other year classes in previous seasons (*cf.* Felin and Phillips 1948), and is further evidence from growth that pilchard caught along the Pacific coast do not constitute a single homogeneous population.

SUMMARY AND CONCLUSIONS

1. The question whether the fished stocks of the Pacific pilchard, or sardine, along the Pacific coast are homogeneous is considered in the light of evidence from growth studies and other vital statistics.

2. The direct proportionality of growth of scale to growth of fish is used to obtain approximations of mean calculated lengths of sardines.

3. Walford's (1946a) transformation plot is applied to mean observed length data and mean calculated length data sampled in different regions.

4. Comparison is made of growth characteristics, k (slope of the regression, or rate of deceleration of growth) and l_∞ $\left(\frac{y-\text{intercept}}{1-k}\right.$, or calculated ultimate size$\Big)$ of six year classes sampled in the most northern region of catch, Canada, and the most southern, San Pedro.

5. From analysis of covariance no significant differences are evidenced in the mean slopes, k, of the transformations between each of these six year-classes in Canada and San Pedro.

6. For each year class tested, two distinct y-intercepts, or levels, of mean transformations are maintained in the northern and southern areas, and from the covariance tests the differences are significant at the 1-percent level. The growth characteristic l_∞ thus differs significantly in the northern and southern catches.

7. The use of the straight-line transformation as a method of expressing growth differences not readily apparent in conventional length-on-time growth curves was noted by Walford (1946a). The applicability of the usual statistical tests of significance to such regressions of l_{n+1} on l_n is now also apparent. Possible meanings of significant difference in k and l_∞ as physiological characters are discussed.

8. Complete intermixture and homogeneity in populations of adult fish as sampled by the fishery in different regions is not evidenced from data on mean calculated lengths.

9. The apparent cline in the growth characteristic l_∞ appears indicative of intraspecific populations in which there is limited intermingling, and suggests a series of overlapping coastal migrations of more than one stock.

10. The recent discovery of an area of intense spawning off central Lower California, more or less discrete from the widespread spawning area off southern California, points to the tentative hypothesis that spawning grounds off Lower California give rise to the southern components found in catches off San Pedro (and to a lesser degree off central California), while the larger fish originate off southern California and occasionally to the north.

11. Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and southern California.

12. The decline in catches in central California and the Pacific Northwest has been almost entirely responsible for the sudden decline in total catch of the entire coast. It is suggested that the centering of the available population in the southern part of the range may have produced a series of southern year classes.

13. Ratios between year-class strength of 1- or possibly 2-ring fish taken at San Pedro and taken along the coast as a whole may prove a useful index in determining whether a year class is primarily southern or has more northern components.

14. The measure of year-class strength used by Walford (1946b), i. e., the number of 3-ring pilchard caught at all ports, is compared with the San Pedro–Pacific coast ratios of 1- and 2-ring fish. To date only those year classes which appear predominantly southern by these criteria have been much below normal strength.

15. Vital statistics of the fishery which indicated that new sources of fish became unexpectedly available in the 1949–50 season appear to be explained at least in part by an influx, probably from the south, of small fish onto the southern and central California fishing grounds.

16. Bimodality in length-frequency composition is further evidence from growth that pilchard caught along the Pacific coast do not constitute a homogeneous population.

17. Whether heterogeneity in growth characteristics is the expression of genotypic difference or a phenotypic response of a species to its environment is not yet determined.

18. In view of differences in stocks on the various fishing grounds along the Pacific coast, the study of population dynamics not only for the coast as a whole but also by geographic areas appears desirable.

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