

ELECTROPHORETIC, MORPHOMETRIC, AND MERISTIC STUDIES OF SUBPOPULATIONS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*¹

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We investigated the population structure of northern anchovy found between southern Baja California and Newport, Oregon. We used electrophoretic, morphometric, and meristic methods in our studies, and the results indicate the presence of three distinct anchovy subpopulations.

INTRODUCTION

Hubbs (1925) and McHugh (1951) found subpopulations of the northern anchovy along the west coast of the United States and Mexico. For more effective management of the growing United States and Mexican anchovy fisheries, knowledge of the number of subpopulations and how they are distributed geographically is necessary, as is a feasible method of readily distinguishing the subpopulations. In this study we used electrophoretic methods to distinguish subpopulations and delineate their geographical range; morphometric and meristic comparisons were made between these subpopulations.

Transferrin Electrophoresis

Transferrin is the vertebrate blood serum protein responsible for binding iron. Transferrin polymorphism has been reported in a variety of teleost fishes by several authors including Creyssel et al. (1964), Moller (1966), Moller and Naevdal (1966), Barrett and Tsuyuki (1967), Fujino and Kang (1968), and Utter (1969).

Morphometrics

Hubbs (1925) found small morphometric differences in samples of *Engraulis mordax* collected from San Francisco to southern California. He also described a distinct subspecies, *Engraulis mordax nanus*, which he found inhabiting the brackish waters of San Francisco Bay. We were unable to collect the bay anchovy.

Meristics

McHugh (1951) found three subpopulations of northern anchovy: one off British Columbia to northern California, one off southern California and northern Baja California, and one off central and southern Baja California. He based his conclusion on the mean values he found in five different meristic characters. Hubbs (1925) found a distinct difference in vertebral numbers when he com-

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pared open ocean anchovies with bay anchovies from San Francisco Bay. He also found small differences in vertebral numbers between samples of open ocean anchovies from San Francisco to southern California.

MATERIALS AND METHODS

Transferrin Electrophoresis

Anchovies were collected from Newport, Oregon, to the southern end of Baja California (Table 1). Availability of samples was limited since the anchovies had to be kept alive until the blood samples were taken; dead or preserved fish could not be used. The samples came primarily from commercial live bait vendors and from short-duration surface hauls made with a midwater trawl. We tried to obtain 50 to 100 fish per sample, but this was frequently impossible. In a few cases, two smaller samples taken very closely together in time and space were combined into one; other samples which contained less than 35 readable transferrin types and could not be combined were not used in the population analysis.

TABLE 1. Sampling Data for Northern Anchovy Subpopulation Genetic Testing and Percent Occurrence of Transferrin Alleles in the Samples

Site	Location	Date	Number of fish	Percent transferrin alleles			
				Tf ^A	Tf ^B	Tf ^C	Tf ^D
Northern subpopulation							
1	Newport, Oregon	July 1969	84	81.6	8.3	5.4	4.8
2	Newport, Oregon	July 1970	66	78.0	13.6	5.3	3.0
3	Eureka, California	July 1970	38	77.6	14.5	5.3	2.6
4	Salt Point, California	July 1970	54	80.6	13.0	3.7	3.4
5	Monterey, California	November 1969	106	76.9	12.3	5.7	5.2
Central subpopulation							
6	San Francisco, California	April 1968	48	85.4	7.3	7.3	0
7	San Francisco, California	May 1968	64	72.7	16.4	10.9	0
8	Monterey, California	May 1968	87	76.4	13.8	9.8	0
9	Monterey, California	October 1967	54	82.4	7.4	10.2	0
10	Newport, California	August 1968	94	80.8	10.1	8.0	1.1
11	San Diego, California	July 1968	47	81.9	9.6	7.4	1.1
12	San Diego, California	July 1968	100	80.5	12.0	7.5	0
13	Ensenada, Mexico	May 1968	37	82.4	9.5	8.1	0
14	Ensenada, Mexico	July 1968	94	80.8	11.2	8.0	0
15	Todos Santos Is, Mexico	August 1969	48	83.3	11.5	5.2	0
16	30° 50.5'N	August 1969	43	82.6	11.6	4.7	1.2
17	30° 17'N	January 1969	67	84.3	11.9	3.7	0
18	30° 12'N	January 1969	70	84.3	10.0	5.7	0
19	30° 09'N	March 1968	43	84.9	7.0	7.0	1.2
20	29° 33'N	November 1967	36	80.6	11.1	8.3	0
Southern subpopulation							
21	28° 33.2'N	November 1967	83	91.1	4.8	4.2	0
22	27° 55.5'N	November 1967	64	90.6	5.5	3.9	0
23	27° 52.5'N	November 1967	87	87.9	6.3	5.8	0
24	27° 06.0'N	November 1967	75	88.7	6.7	4.7	0
25	27° 04.0'N	November 1967	72	87.5	6.9	5.6	0
26	24° 30.0'N	November 1967	72	88.2	6.2	5.6	0

We collected blood samples from live fish by inserting a heparinized capillary tube through the gill opening into the dorsal aorta. The tube was allowed to flow full of blood and then was sealed on the bottom with a bit of clay. Filled capillary tubes were then centrifuged at about 2000 *g* for 5 min. When samples were not electrophoresed immediately, they were frozen with dry ice and stored at 0° C.

When a sample was ready to be electrophoresed, the thawed capillary tube was broken off at the interface of the serum and red cells; the cells were discarded. A piece of absorbent paper was touched to the end of the capillary tube to absorb the serum until a column of liquid 33 mm long remained; this was equivalent to 25 μ l. The 25 μ l of serum were mixed with 10 μ l of radioactive Fe⁵⁹ and allowed to incubate for at least 10 min. A slot cut in the starch gel was filled with the mixture and electrophoresed for 1 h 40 min at 150 v in a horizontal, thin layer, starch gel apparatus. After electrophoresis was complete, we prepared autoradiographs of the gels using a modification of the method of Giblett, Hickman, and Smithies (1959).

We examined the hypothesis that each band represented a specific transferrin, controlled by a different autosomal allele at a single locus. First, we verified that "artificial heterozygotes" produced by mixing equal parts of sera from the appropriate homozygous types produced electrophoretic patterns indistinguishable from the natural heterozygous types. Secondly, we examined the statistical distributions of phenotypes in populations thought to be in equilibrium with respect to the alleles found.

The frequency of occurrence of the transferrin alleles in anchovy samples was calculated as $1/N (O_i + \frac{1}{2}\Sigma O_{ij})$, where *i* = A, B, C, D (representing alleles) and *j* \neq *i*. For example, O_{AA} is the number of phenotypes AA observed and *N* is the total number of fish in the sample. Allocation of samples to the subpopulations was determined by cluster analysis (Sneath and Sokal 1973) of the percentage distributions of alleles for each sampling site. The clustering sequence was obtained by identifying the two sites most alike, combine the two and clustering with the next most similar site, etc. The computer program used was BMDP2M written at the Health Sciences Computer Facility, University of California, Los Angeles. Clustering was by Euclidean distance (the square root of the sums of squares of differences between percent alleles).

Morphometrics

Morphometric measurements were made with a vernier caliper on formalin preserved anchovies which had been classified to subpopulation by transferrin gene frequencies. Head length, eye diameter, snout to post-orbital margin, head depth, and body depth were measured. Allometric regressions ($\ln y = a + b \ln x$) were calculated for each of the five morphometric measurements, where *x* is the standard length (SL).

Meristics

We took all meristic counts from formalin preserved samples which we had classified as northern, central, or southern subpopulation anchovies on the basis of transferrin gene frequencies. Counts were made from x-ray plates with the aid of a binocular dissecting microscope. Vertebrae, anal fin rays, and dorsal fin rays were counted. The vertebral counts did not include the basioccipital nor the hypural.

combinations of the T^P allele were grouped for the chi-square tests. The results of the chi-square tests for independence [$\Sigma(O-E)^2/E$] are as follows:

$$\text{North-central } X^2 = 61.99, \text{ d.f.} = 6; P < .005$$

RESULTS AND DISCUSSION

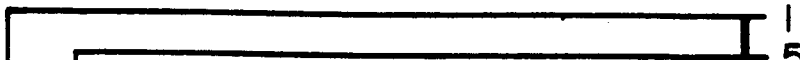
Transferrin Electrophoresis

We found that transferrin polymorphism in the northern anchovy originates in a genetic system of four co-dominant autosomal alleles, each controlling the formation of a single protein with a specific anodal migration rate when electrophoresed in starch gel. The four iron-binding protein bands were designated A, B, C, and D. The migration distance in a standard run was 23.4 mm for band A, 21.1 mm for band B, 19.0 mm for band C, and 16.2 mm for band D (Figure 1).

Northern (sites 1–5) and southern (sites 21–16) groups were clearly distinguished by cluster analysis (Figure 2) of the transferrin alleles' percentage of occurrence (Table 1). A central group (site 6 and sites 9–20) was also evident. However, samples taken at sites 7 (San Francisco) and 8 (Monterey) during May of 1968 were distinct from all groups. These samples were anomalous in that they were not intermediate between the major groupings but rather represented extreme levels for all alleles; thus a mixture of populations or interbreeding does not suffice as a rational explanation. These anomalies are believed to be due to occasional indistinct separation of the first three bands within the gel. The absence of the D allele separates these samples from the northern group and the relative frequencies of the B and C alleles separates them from the southern group; thus we included them within the central subpopulation. There is an overlap in the geographical range of samples attributed to the northern and central subpopulations; the southernmost sample from the northern subpopulation was taken in Monterey in November 1969, and the northernmost samples from the central subpopulation were taken from San Francisco Bay in April and May 1968, an overlap of about 70 nautical miles. This does not mean that the two subpopulations were necessarily present in these areas at the same time; instead, both subpopulations may tend to move north in the spring and summer and return toward the south in the fall and winter. Anchovy tagging studies conducted by California Department of Fish and Game support the north and south movements (Haugen, Messersmith, and Wickwire 1969).

The northern subpopulation was distinguished from the other two by the Tf^D allele which was not found in the southern subpopulation, was rare in the central subpopulation (0.2%), but occurred at a rate of 4.02% in the northern subpopulation (Table 2). The central subpopulation was distinguished from the southern one by the frequency of occurrence of Tf^A and Tf^B alleles. Tf^A occurred at a rate of 88.96% in the southern subpopulation compared to 81.17% in the central one; Tf^B occurred at 11.0% in the central subpopulation and only 6.07% in the southern one. Chi-square goodness of fit tests on observed numbers of phenotypes for the three subpopulations versus the expected numbers calculated from the Hardy-Weinberg equilibrium formula (Table 2) support the four-allele hypothesis.

Similarity or dissimilarity of the subpopulations was judged on the basis of the observed phenotypic distributions with northern-central and central-southern differences treated separately. We found the rare allele to be important in discriminating the northern subpopulation, whereas the predominant alleles provided the discriminatory power for the central and southern subpopulations (Table 3). To avoid difficulties with expectations in the statistical tests, all



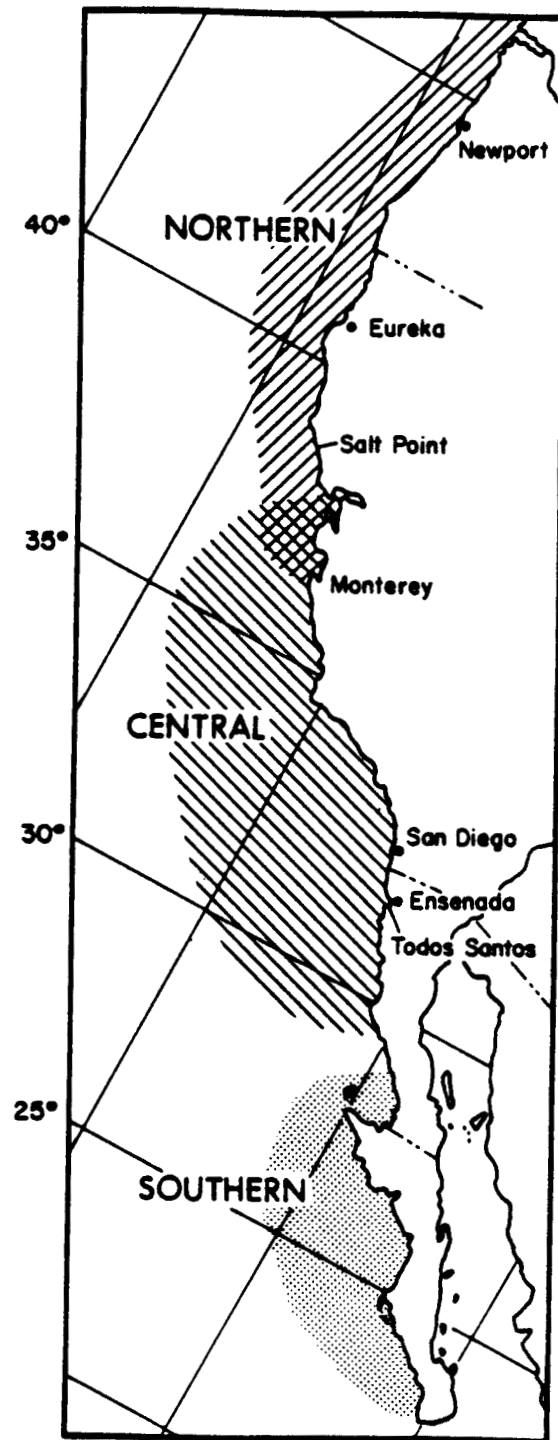


FIGURE 3. Distribution of three northern anchovy subpopulations based on transferrin allele frequencies.

TABLE 3. Observed and Expected Numbers of Phenotypes Assuming No Differences Between Subpopulations

		<i>Phenotype</i>							
		<i>AA</i>	<i>AB</i>	<i>AC</i>	<i>BB</i>	<i>BC</i>	<i>CC</i>	<i>AD+BD+</i> <i>CD+DD</i>	<i>Total</i>
Northern	O	215	67	30	4	4	0	28	348
	E	226.7	62.0	38.3	4.6	5.7	1.6	9.0	
Central	O	619	161	111	13	17	6	5	932
	E	607.2	166.0	102.7	12.4	15.3	4.4	24.0	
TOTAL		834	228	141	17	21	6	33	1280

		<i>AA</i>	<i>AB</i>	<i>AC</i>	<i>BB</i>	<i>BC</i>	<i>CC</i>	<i>AD+BD+</i> <i>CD+DD</i>	<i>Total</i>
Central	O	619	161	111	13	17	6	5	932
	E	658.8	140	100.9	10.1	14.1	4.73	3.4	
Southern.....	O	360	47	39	2	4	1	0	453
	E	320.2	68	49.1	4.9	6.9	2.3	1.6	
TOTAL		979	208	150	15	21	7	5	1385

Morphometrics

Morphometric measurements were taken on 613 fish (Table 4). Except for eye diameter, there was no evidence that the slope coefficients *b* differed among the subpopulations (Table 5) test for parallel lines. The slope for eye diameter in the northern group differed from those of the southern and central, but the latter two showed no statistical difference. Only body depth indicated direct proportionality, i.e., *b* was not significantly different from unity.

TABLE 4. Sampling Data for Northern Anchovy Morphometric and Meristic Testing

<i>Subpopulation</i>	<i>N</i>	<i>Mean standard length (mm)</i>	<i>Range</i>	<i>Standard deviation</i>
Northern	206	97.20	77-135	10.01
Central.....	225	104.47	70-136	15.39
Southern	182	90.11	50-116	13.65

Because the slope coefficients for eye diameter differed among subpopulations, no test for a common regression line was performed for eye diameter. All other tests for a common regression line, i.e., the same slope and intercept, were highly significant ($P < 0.01$). In each instance, the more similar of the two subpopulations were also tested for a common relationship. Body depth indicated no difference between the southern and central subpopulations. Otherwise all differences between subpopulations were significant at $P < 0.05$. The analysis of covariance is not entirely appropriate for morphometric data since both variates are subject to error, especially for field sampling where the size range of the samples is rarely the same and cannot be controlled. It is well to insist on a conservative level of statistical significance; therefore, we calculated the estimated morphometric measurements for a 70-, 100-, and 130-mm anchovy from each subpopulation (Table 6). Southern subpopulation anchovies showed a distinctly longer head, larger eye, and longer snout to post-orbit than did either central or northern ones. Northern subpopulation anchovies exhibited a deeper body, and northern and southern subpopulation anchovies showed a slightly deeper head than did those of the central stock. Average morphometric meas-

measurements calculated for 10-mm intervals from 70 to 120 mm show the consistent pattern of differences between the subpopulations at all sizes (Table 7).

TABLE 5. Covariance Analysis for the Three Northern Anchovy Subpopulations: SL = Standard Length

Subpopulation		Test for common regression line	Test for parallel lines
	<i>Head depth (hd)</i>		
Southern	$\ln L_{hd} = -1.637 + .967 \ln L_{sl}$	$F_{4,407} = 12.79^*$	$F_{2,407} = 0.10^{**}$
Central	$\ln L_{hd} = -1.661 + .968 \ln L_{sl}$		
Northern	$\ln L_{hd} = -1.570 + .955 \ln L_{sl}$		
	<i>Body depth (bd)</i>		
Southern	$\ln L_{bd} = -1.982 + 1.052 \ln L_{sl}$	$F_{4,407} = 16.00^*$	$F_{2,407} = .54^{**}$
Central	$\ln L_{bd} = -1.928 + 1.039 \ln L_{sl}$		
Northern	$\ln L_{bd} = -1.770 + 1.012 \ln L_{sl}$		
	<i>Eye diameter (ed)</i>		
Southern	$\ln L_{ed} = -1.551 + .753 \ln L_{sl}$		$F_{2,407} = 8.37^*$
Central	$\ln L_{ed} = -1.366 + .692 \ln L_{sl}$		
Northern	$\ln L_{ed} = -2.235 + .882 \ln L_{sl}$		
	<i>Snout to post-orbit (po)</i>		
Southern	$\ln L_{po} = -1.273 + .823 \ln L_{sl}$	$F_{4,407} = 125.04^*$	$F_{2,407} = 2.76^{**}$
Central	$\ln L_{po} = -1.313 + .816 \ln L_{sl}$		
Northern	$\ln L_{po} = -1.042 + .755 \ln L_{sl}$		
	<i>Head length (hl)</i>		
Southern	$\ln L_{hl} = -0.850 + .932 \ln L_{sl}$	$F_{4,407} = 158.92^*$	$F_{2,407} = 2.56^{**}$
Central	$\ln L_{hl} = -1.027 + .955 \ln L_{sl}$		
Northern	$\ln L_{hl} = -0.784 + .900 \ln L_{sl}$		

* Significant $P \leq .01$

** Not significant

TABLE 6. Estimated Morphometric Measurements of 70, 100, and 130 mm Standard Length Northern Anchovies Expressed as Percent of Standard Length

Length	Subpopulation	Head length	Eye diameter	Snout to post-orbit	Head depth	Body depth
70	Northern	29.8	6.5	12.4	17.2	17.9
	Central	29.6	6.9	12.3	16.6*	17.2
	Southern.....	31.9*	7.4*	13.2*	16.9	17.2
100	Northern	28.8	6.2	11.4	16.9	18.0*
	Central	29.1	6.2	11.5	16.4*	17.4
	Southern.....	31.1*	6.8*	12.4*	16.7	17.5
130	Northern	28.1	6.0	10.7	16.7	18.0*
	Central	28.8	5.7	11.0	16.2*	17.6
	Southern.....	30.6*	6.4*	11.8*	16.6	17.7

* Significant difference ($P \leq 0.01$) between subpopulations within length group.

Hubbs (1925) also reported longer head length (31.9% SL) for a San Francisco Bay subspecies *Engraulis mordax nanus* which also had a greater body depth (19.7% SL) than did the open ocean anchovies (18.1% SL).

Mais (1974) reported that southern subpopulation anchovies are much smaller than central stock anchovies. Of the 2,332 fish he measured from 96 samples collected in more than 5½ yr south of lat 28°30' N, less than 10% exceeded 106

mm total length (the minimum legal limit of the California anchovy reduction fishery), while 79% of the central stock anchovies were 106 mm or greater. Southern anchovies were significantly smaller than central ones at all ages and nearly attained their maximum length by age 3, while central subpopulation anchovies continued to grow for at least 3 more years.

TABLE 7. Average Morphometric Measurements (mm) in Three Northern Anchovy Subpopulations in 10 mm Intervals of Standard Length; N = Northern; C = Central; S = Southern Subpopulations.

Interval		Standard length	Body depth	Head depth	Head length	Snout-postorbital	Eye diameter	Number of observations
70-79	N							0
	C	75.5	12.8	12.4	22.4	9.2	5.2	24
	S	75.6	13.0	13.0	24.9	10.3	5.9	34
80-89	N	86.2	15.9	15.0	25.2	10.3	5.5	42
	C	84.0	14.9	14.6	24.9	10.1	5.5	3
	S	83.7	14.4	14.0	26.7	10.9	6.1	36
90-99	N	92.9	16.4	15.5	27.0	10.8	5.8	91
	C	95.4	16.7	15.8	27.7	11.1	5.9	62
	S	95.0	16.5	15.8	29.4	11.8	6.4	51
100-109	N	105.1	18.9	17.7	30.0	11.8	6.4	33
	C	103.6	18.2	16.8	29.7	11.6	6.3	51
	S	103.5	18.3	17.3	31.7	12.6	6.8	42
110-119	N	112.1	20.5	19.1	31.9	12.5	6.9	37
	C	114.2	20.1	18.9	33.1	12.9	6.8	37
	S	111.6	19.8	18.6	33.9	13.4	7.3	10

Meristics

Vertebrae

Northern subpopulation anchovies had the greatest mean number of vertebral centra (Table 8). The mean for the central subpopulation was significantly less than that of the northern subpopulation ($d = 0.46$; $F_{1,204} = 41.83$; $p < 0.001$). This was also the case for the southern subpopulation with regard to the northern one ($d = 0.43$; $F_{1,204} = 49.44$; $p < 0.001$). There was no significant difference between central and southern subpopulation mean number of vertebrae ($d = 0.03$; $F_{1,200} = 0.16$; $p < 0.25$).

Hubbs (1925) reported a mean number of 44.73 vertebrae for offshore northern anchovies off San Francisco, which is very close to the 44.75 we found for the northern subpopulation. When we partitioned McHugh's (1951, Tables 2 and 3) vertebral data into probable subpopulations (northern, central, or southern) merely on the basis of location of capture, we calculated his northern subpopulation samples to have a mean of 44.74 vertebrae, again in good agreement with ours. His southern subpopulation samples had a mean of 44.32 vertebrae, identical to ours.

TABLE 8. Meristic Analysis of the Three Subpopulations of Northern Anchovies: \bar{x} = Mean, S = Standard Deviation, and S_r = Standard Error of Mean

	No.	Range	\bar{x}	S	S_r
<i>Vertebrae</i>					
Northern subpopulation.....	206	43-46	44.75	0.6325	0.0441
Central subpopulation	200	42-46	44.29	0.7994	0.0565
Southern subpopulation.....	182	42-45	44.32	0.5734	0.0425
<i>Anal fin rays</i>					
Northern subpopulation					
Male.....	136	20-24	22.18	0.9043	0.0775
Female	70	20-25	22.20	0.9869	0.1180
TOTAL	206	20-25	22.19	0.9308	0.0649
Central subpopulation					
Male.....	94	19-25	22.43	1.1499	0.1186
Female	106	19-25	22.36	0.9481	0.0921
TOTAL	200	19-25	22.39	1.0456	0.0739
Southern subpopulation					
Male.....	109	20-25	22.53	1.0850	0.1039
Female	64	20-25	22.64	1.0445	0.1306
TOTAL	173	20-25	22.58	1.0686	0.0808
<i>Dorsal fin rays</i>					
Northern subpopulation					
Male.....	136	15-18	16.26	0.5962	0.0511
Female	70	15-17	16.43	0.6272	0.0750
TOTAL	206	15-18	16.32	0.6108	0.0426
Central subpopulation					
Male.....	94	15-18	16.46	0.6336	0.0654
Female	106	15-18	16.37	0.6666	0.0647
TOTAL	200	15-18	16.41	0.6512	0.0460
Southern subpopulation					
Male.....	110	15-18	16.35	0.6146	0.0586
Female	65	15-17	16.43	0.6116	0.0759
TOTAL	180*	15-18	16.37	0.6075	0.0453

* Includes five juveniles.

When we compared the central subpopulations, however, we calculated a mean of 44.88 vertebrae for his samples, which is 0.59 greater than ours. His data indicated a high degree of variability from month to month and year to year. For instance, his data for the mean number of vertebral centra in anchovy post-larvae off southern California (McHugh 1951, Table 4) was 44.21 in 1945, 44.69 in 1947, 44.84 in 1948, and 44.65 in 1949.

Anal Fin Rays

McHugh (1951) reported strong evidence for sexual dimorphism in the number of anal fin rays, with those of males exceeding those of females by 0.13 rays. Our data did not indicate such dimorphism. When all of our samples were

combined according to sex, fin rays of females exceeded those of males by only 0.02 rays. When each subpopulation was tested separately for sexual dimorphism, the greatest difference found (Table 8) was in the southern subpopulation where females exceeded males by 0.11 anal fin rays, which was not significant ($F_{1,171} = 0.43$; $p > 0.25$).

When we compared both males and females combined for each of the three subpopulations, we found that the northern subpopulation had a mean anal fin ray count 0.20 less than that of the central subpopulation; the difference was significant ($F_{1,404} = 4.18$; $p < 0.05$). The mean number of anal rays for the northern subpopulation was 0.39 fewer than that for the southern subpopulation, which was highly significant ($F_{1,379} = 14.33$; $p < 0.001$). Central and southern subpopulations differed by 0.19 rays, which was not significant ($F_{1,373} = 2.93$; $p < 0.10$).

When we partitioned McHugh's (1951) anal fin ray data into their probable subpopulations on the basis of locality, we found his mean anal fin ray count for the combined northern subpopulation samples to be only 0.03 fewer than ours. His southern subpopulation mean ray count was only 0.16 fewer than ours, but, as with vertebrae, there was a large difference in the central subpopulation, with his mean count being 0.36 greater than ours (Table 9).

TABLE 9. Mean Numbers of Anal Fin Rays From McHugh (1951, Table 11, 12 and 13) Compared with Those of This Study: N = Number, \bar{x} = Mean

		McHugh (1951)			This study	
		Adult males	Adult females	Young	Combined total	Combined total
Northern subpopulation	N	105	87	105	297	206
	\bar{x}	22.21	21.94	22.28	22.16	22.19
Central subpopulation	N	284	418	404	1,106	200
	\bar{x}	22.81	22.66	22.79	22.75	22.39
Southern subpopulation	N	41	49	100	190	175
	\bar{x}	22.83	22.55	22.18	22.42	22.58

Dorsal Fin Rays

McHugh (1951) noted a probable sexual dimorphism in mean dorsal fin ray counts; males had a grand mean difference of 0.12 count greater than that of females. Males in our samples averaged fewer dorsal rays than did females in both northern and southern subpopulations but more rays than did females in the central subpopulation (Table 8). Since the differences between the sexes were not significant and were not consistent in direction, we concluded that the variations were random and we might combine the data for males and females when comparing the three subpopulations.

Central subpopulation anchovies had the largest mean number of dorsal fin rays, 0.09 greater than that of the northern stock and 0.04 greater than that of the southern stock, but these differences are not significant (northern vs. central: $F_{1,904} = 2.27$, $p > 0.10$; northern vs. southern: $F_{1,384} = 0.83$, $p > 0.25$; central vs. southern: $F_{1,378} = 0.33$, $p > 0.25$).

SUMMARY AND CONCLUSION

We found three distinct subpopulations of northern anchovies inhabiting the coastal waters between Newport, Oregon and the southern end of Baja California, Mexico: northern, between Newport and Monterey; central, between San Francisco and lat 29° N and southern, south of; lat 29° N. There was an overlap of about 70 nautical miles for the northern and central subpopulations (Figure 3). Our conclusion was based on our transferrin electrophoresis study, and supports McHugh's (1951) conclusion of three subpopulations. Our morphometric and meristic work also supports our genetic findings.

Given a sample of anchovies from the southern subpopulation range, our studies showed that it could be identified as such if the mean head length, snout length, and eye diameter were greater than those of the northern and central subpopulations, and if the mean standard length of the sample (at all ages) were significantly less than that of the other two subpopulations. A sample of anchovies from the northern subpopulation range could be identified as such if it had i) a greater mean number of vertebrae and fewer anal fin rays than either central or southern subpopulation anchovies, and ii) if the mean head depth were greater than that of central subpopulation anchovies. However, any conclusion on subpopulations involving meristic counts should take into consideration McHugh's (1951) work showing a high degree of variability in these parameters from year to year and even from month to month.

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REFERENCES

- Barrett, I., and H. Tsuyuki. 1967. Serum transferrin polymorphism in some scrombroid fishes. *Copeia*, (3):551-557.
- Creysse, R., P. Silberzan, G. Richard, and Y. Manual. 1964. Etude du serum de carpe (*Cyprinus carpio*) par électrophoreses en gel d' amidon. *Bull. Soc. Chim. Biol.*, 46:149-159.
- Fujino, K., and T. Kang. 1968. Transferrin groups of tunas. *Genetics*, 59:79-91.
- Giblett, E. R., C. G. Hickman, and O. Smithies. 1959. Serum transferrins. *Nature*, 183:1589-1590.
- Haugen, C. W., J. D. Messersmith, and R. H. Wickwire. 1969. Progress report on anchovy tagging off California, March 1966 through May 1966. *Calif. Dept. Fish and Game, Fish. Bull.* (147):75-86.
- Hubbs, C. L. 1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. *Calif. Dept. Fish and Game, Fish. Bull.*, (8):1-23.
- Mais, K. F. 1974. Pelagic fish surveys in the California Current. *Calif. Dept. Fish and Game, Fish. Bull.*, (162):1-79.
- McHugh, J. L. 1951. Meristic variations and populations of northern anchovy (*Engraulis mordax*). *Scripps Inst. Oceanogr. Bull.*, 6(3):123-160.
- Moller, D. 1966. Polymorphism of serum transferrin in cod. *Fisk. Dir. Skr. HavUnders.*, 14:51-60.
- Moller, D., and G. Naevdal. 1966. Serum transferrins of some gadoid fishes. *Nature*, 210: 317-318.
- Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy: The principles and practice of numerical classification. W. H. Freeman and Co., San Francisco, 573 p.
- Utter, F. M. 1969. Biochemical polymorphisms in the Pacific hake (*Merluccius productus*): a, esterase polymorphism in vitreous fluids; b, lactate dehydrogenase isozymes; c, transferrin variants. Dissertation. Univ. Calif., Davis. 60 p.