THE CENTRAL STOCK OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) IS NOT A RANDOMLY MATING POPULATION

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ABSTRACT

Allozyme variation at ten polymorphic loci is reported for a total of 2,628 northern anchovies from 32 midwater trawl samples of the central stock taken by the CalCOFI spawning biomass survey cruises of December 1982, and the winters of 1983, 1984, and 1985. Frequencies of genotypes at these loci conform to those expected on the basis of random mating, according to the Hardy-Weinberg (HW) principle and goodness-of-fit tests. Yet goodness-of-fit tests have low power for detecting failure of the HW principle or its assumptions and are here contradicted by evidence for significant heterogeneity of allelic frequencies among stations within years and within the total sample. Wright's F_{ST} statistic, a relative measure of allele-frequency variance among stations that ranges from 0.005 to 0.020, indicates little differentiation and relatively high gene flow among stations. Absolute total variance of allelic frequency among stations, however, is twice as large as the binomial sampling variance for a single, randomly mating population. Moreover, chi-square contingency tests of allele-frequency homogeneity among stations are highly significant over all loci for each of the four years. These results falsify the hypothesis that the central stock is a randomly mating population.

Several lines of evidence suggest that the genetic heterogeneity of the central stock is geographically unpatterned, or "chaotic," giving no indication of spatially distinct panmictic units. The loci that contribute to heterogeneity differ from year to year. Allelic frequencies are correlated weakly or not at all with latitude (CalCOFI line coordinate) or distance offshore. Spatial autocorrelation of allelic frequencies is weak among age subsamples within stations and declines to nonsignificant levels within 100 km. Correlations among genotypes at different loci, which can be nonzero in mixtures of genetically differentiated populations, are not significantly different from zero. Finally, cluster analysis of genetic distances among all 32 stations joins samples from different years and disparate latitudes at high levels of similarity.

Variation in allelic frequencies is significantly correlated with morphometric variation but not with measures of condition or reproductive state, suggesting that observed genetic heterogeneity is associated with substantial, perhaps heritable, morphological variation within the central stock. Genetic and morphometric variance may be generated by processes governing reproductive success, larval survival, and recruitment to first schools. How this variance is maintained through the adult stages is a matter for speculation, but it does permit natural selection to act among groups as well as among individuals.

[Manuscript received March 3, 1994.]

RESUMEN

Se reporta la variación de alocimos en diez loci polimorfos de 2,628 anchovetas norteñas del stock central obtenidas de 32 arrastres a media agua. Las muestras fueron obtenidas por el programa "CALCOFI" en los cruceros de evaluación de la biomasa de ponedores en diciembre de 1982 y los inviernos de 1983, 1984 y 1985. La distribución de frecuencias de los genotipos en estos loci se ajusta a las frecuencias esperadas en base a una suposición de apareamiento aleatorio, de acuerdo al principio Hardy-Weinberg (HW) y de acuerdo a pruebas de bondad de ajuste. Sin embargo, las pruebas de bondad de ajuste tienen poca potencia para detectar las fallas del principio HW o sus suposiciones. Y estas pruebas son contradichas por evidencia significativa de heterogeneidad de frecuencias de alelos tanto entre estaciones para un mismo año, como dentro del total de las muestras. El estadístico Wright $F_{ST,}$ que es una medida relativa de varianza de frecuencia de alelos entre estaciones con rango de 0.005 a 0.020, indicó poca diferenciación así como alto flujo genético entre las estaciones. Sin embargo, la varianza total absoluta de la frecuencia de los alelos entre las estaciones es el doble de la varianza de muestreo binomial para una sola población con apareamiento aleatorio. Aun mas, la prueba de contingencia Ji-cuadrada de homogeneidad de frecuencia de alelos entre estaciones es altamente significativa en todos los loci para cada uno de los 4 años. Estos resultados falsan la hipótesis que el stock central es una población con apareamiento aleatorio.

Varios indicios sugieren que la heterogeneidad genética del stock central carece de un patrón geográfico o que es "caótica", sin mostrar indicios de unidades en estado de panmixia separadas espacialmente. Los loci que contribuyen a la heterogeneidad difieren de año a año. La correlación entre las frecuencias de los alelos con la la-

titud (transectos de CALCOFI) o la distancia hacia mar adentro son bajas o nulas. La autocorrelación espacial de frecuencias de alelos es baja entre las submuestras de edad dentro de las estaciones y declina a niveles no significativos en un rango de 100 km. Las correlaciones entre los genotipos en loci distintos, que pueden ser diferentes de cero en mezclas de poblaciones diferenciadas genéticamente, no son estadísticamente diferentes de cero. Por último, un análisis de agrupamiento de distancias genéticas entre las 32 estaciones agrega muestras de años diferentes y latitudes distantes en niveles de similitud altos.

La variación de frecuencias de alelos está correlacionada significativamente con la variación morfométrica, mas no con medidas de condición o estados reproductivos, lo que sugiere que la heterogeneidad genética observada está asociada con variación morfológica importante, quizá hereditaria, dentro del stock central. La varianza genética y morfométrica podrían estar generadas por los procesos que gobiernan el éxito reproductivo, la sobrevivencia de larvas y el reclutamiento inicial al "primer" cardúmen. El cómo se conserva esta varianza en los estadíos adultos es motivo de especulación, mas esta varianza permite que la selección natural actúe entre grupos así como entre individuos.

INTRODUCTION

> In trying to identify and measure the causes of fluctuations in the abundance and distribution of a species of fish, it is essential that the number and identity of subpopulations, if any, within the species be established, since each subpopulation may have its own characteristic distribution, fecundity, natural mortality rate, growth rate, etc. This statement is axiomatic in the field of fisheries biology; and yet, there is some misunderstanding arising in part from semantic difficulties and in part from the lack of agreed definitions of problems. (Marr 1957)

On the basis of meristic and morphometric data and frequencies of electrophoretically detectable allelic forms of the serum protein transferrin (McHugh 1951; Vrooman et al. 1981), the northern anchovy *Engraulis mordax* Girard is considered to comprise a northern subpopulation spawning primarily in summer in the Columbia River plume, a central subpopulation spawning primarily in winter and spring in the Southern California Bight, and a southern subpopulation spawning off of Punta Eugenia and in Magdalena Bay, Baja California Sur, Mexico. The central subpopulation ranges from just north of San Francisco Bay (38°N) to Punta Baja (29°N) in northern Baja California (MacCall et al. 1983); it overlaps geographically but not temporally with the northern subpopulation in north central California (Vrooman et al. 1981) and perhaps likewise with the southern subpopulation in northern Baja California. Anchovies belonging to the southern subpopulation are morphologically distinguished from those in the central subpopulation by their smaller maximum sizes, longer heads, and larger eyes (Mais 1974; Vrooman et al. 1981; Parrish et al. 1985).

The central subpopulation of the northern anchovy has been regarded as both a stock, or unit of fishery management (MacCall et al. 1983), and a population of individuals that interbreed more or less at random with each other, and not at all or only infrequently with individuals from the other two subpopulations (Vrooman et al. 1981). Tagging studies show that adult anchovies can certainly traverse the range of the central subpopulation (Haugen et al. 1969). Frequencies of transferrin electrophoretic alleles are statistically homogeneous among samples from the central subpopulation, and proportions of transferrin phenotypes in the total subpopulation conform to those expected under random mating, according to the Hardy-Weinberg principle (Vrooman et al. 1981). Whether this is sufficient evidence that the central stock of northern anchovy is indeed a randomly mating population is an important practical and fundamental question.

On the practical side, assumption of random mating justifies application of the egg production method for estimating northern anchovy spawning biomass (Lasker 1985). In its most basic form the egg production method assumes that there is one true sex ratio, one true fraction of spawning females, and one true batch fecundity in the central stock. In practice, modifications of the basic method are necessary to account for regional variation in life-history characteristics and the catchability and vulnerability of spawning adults (Picquelle and Stauffer 1985; Smith and Hewitt 1985) and interannual variation in batch fecundity (Hunter et al. 1985). The demography of natural populations, however, is a complex summation of underlying, genetically heterogeneous, individual life histories (e.g., Brooks et al. 1994), so that finer-scale spatial and temporal heterogeneity within the central subpopulation might be confounded in estimates of spawning biomass. In a companion paper we demonstrate a surprising degree of spatial and interannual variation in the morphology and life history of northern anchovy within the central subpopulation (Nelson et al. 1994). In this paper, we present evidence that genetic heterogeneity among individual northern anchovies in the central stock is greater than that expected within a randomly mating population.

Previously, we reported significant heterogeneity of allelic frequencies among samples collected from within the range of the central subpopulation by the winter 1982 CalCOFI spawning biomass cruise (Hedgecock et al. 1989). Here we present comparable allozyme data for anchovies collected in four subsequent cruises. Samples collected in 1984 and 1985 were larger and were ana-

lyzed not just for genetic variation but for variation in morphometric and life-history traits as well. A preliminary analysis of a portion of the 1985 data was made by Hedgecock (1991), but we now present a complete analysis of correlation of morphometric, life history, and environmental variation with allozyme variation.

MATERIALS AND METHODS

Samples

Samples were collected at a total of 32 midwater trawl stations in December 1982, and early 1983, 1984, and 1985, by CalCOFI survey cruises 8212, 8302, 8403, and 8502 of the NOAA Southwest Fisheries Center, La Jolla, California. Localities, sample details, and alphabetic symbols for the 1984 and 1985 stations are given in figure 1A and table 1 of Nelson et al. (1994); comparable information for the 1982 and 1983 stations is given in table 1. With exceptions noted in these tables, sample sizes per station were 48 in the first two years and 120 in the last two years. Altogether 2,628 individuals were studied. Whole fish were frozen individually aboard ship at −70°C and then shipped in plastic bags by air to the Bodega Marine Laboratory, where they were held at −70°C until dissection.

Measurements

Specimens were partially thawed a few at a time and held on ice until measured and dissected. For the 1982 and 1983 samples, standard length (from snout to end of hypurals) was measured to the nearest mm with a mounted rule; more extensive morphological measurements were made on the 1984 and 1985 specimens, as described by Nelson et al. (1994). We dissected out tissues for electrophoresis, and otoliths for aging, and recorded the sex of each fish. Methods for determining ages from otolith followed those of Collins and Spratt (1969), as described by Hedgecock et al. (1989) and Nelson et al. (1994).

Allozyme Electrophoresis

Electrophoretic methods were described by Hedgecock et al. (1989). Eye, heart, liver, and skeletal (epaxial) muscle tissues were dissected from specimens, kept chilled during dissection, then stored at −70°C for no more than several days before electrophoresis. Tissue samples were thawed the day before electrophoresis, homogenized on ice in equal volumes of 0.5 M Tris-HCl, pH 7.1 buffer, and refrozen at −70°C overnight. Electrophoretic protocols for the ten polymorphic loci used for this study—*Est-5* (esterase), *Fum* (fumarate hydratase), *Gpi* (glucose-6-phosphate isomerase), *Hbdh-1* (3-hydroxybutyrate dehydrogenase), *Idh-1* (isocitrate dehydrogenase), *Ldh-1* (lactate dehydrogenase), *Lt-1* (leucyl-tyrosine dipeptidase), *Lgg* (leucyl-glycyl-glycine tripeptidase), *6pgdh* (6-phosphogluconate dehydrogenase), and *Pgm* (phosphoglucomutase)—are given in table 1 of Hedgecock et al. 1989. Two loci were dropped from this study: *Hbdh-2* because of the electrophoretic artifacts described previously (Hedgecock et al. 1989) and *Xdh* because of difficulty in scoring its closely migrating allozymes. All gels were scored independently by D. Hedgecock and G. Li or E. Hutchinson, and discrepancies resolved by joint re-examination and consensus.

Analysis

Individual genotypes were coded as paired alphabetical characters and analyzed with the BIOSYS-1 program (Swofford and Selander 1981; release 1.7 for the PC, Swofford 1989), to yield estimates of allelic frequencies, tests of Hardy-Weinberg (HW) equilibrium genotypic proportions, Wright's (1978) *F*-statistics, and Nei's (1972) minimum genetic distance in pairwise comparisons among all 32 stations. Fit to HW-expected proportions was tested by an exact probability method, after pooling of alleles into common and rare categories. Because most polymorphisms comprised two major alleles (see appendix tables A–D), there appears to be little loss of information by pooling. Comparable results were obtained by chi-square goodness-of-fit tests—with Levene's (1949) correction for small sample sizes—for loci with an expected number of at least 1.0 in each genotypic class. Log-likelihood analyses of allelic frequencies cross-classified by sex and age within locality (Fienberg 1980) were used to evaluate the homogeneity of station samples. The significance of contingency chi-square tests of locality × allele-frequency independence was evaluated for each locus by the pseudo-probability method and algorithm of Zaykin and Pudovkin (1993). We used minimum genetic distance and the unweighted pair-group method for cluster analysis of all stations.

We analyzed a subset of the 1985 samples, the six stations considered by Hedgecock (1991)—i.e., H, I, K, L, O, P in table 1 in Nelson et al. 1994—for evidence of population mixture. Using the methods and computer program PANMIX described by Waples and Smouse (1990), we calculated genotypic correlations (gametic phase disequilibria) for all pairwise combinations of loci studied in these samples and tested the null hypothesis that all interlocus correlations were zero. This was done both for individual and pooled stations, after collapsing all loci to two-allele cases.

Because morphometric measurements varied among ages, both within and among stations, Nelson et al. (1994) treated age classes within stations as independent subsamples of the 1984 and 1985 midwater trawl collections. For analysis of the 1984 and 1985 genetic data, we likewise selected 31 subsamples having more than 24

TABLE 1
Collection Localities and Samples of Northern Anchovy

Coll. no.	Date	CalCOFI Line; Station	Age (*N*>12) range	*N*	Standard length (cm) Mean	SD	Percent female*
A. 1982 cruise 8212							
4520	12/14	56.2; 50.0	0	19	8.31	1.65	54.5
			1	25	10.69	2.00	52.4
			0–2	48	9.73	2.16	51.4
4518	12/12	61.7; 52.0	0	14	8.09	0.91	54.5
			1	30	8.67	0.67	55.2
			0–3	48	8.61	0.91	51.2
4515	12/11	65.0; 50.5	1	36	8.43	0.78	37.1
			0–3	48	8.28	0.99	38.1
4522	12/15	73.8; 49.8	0	32	9.65	0.61	41.4
			0–2	48	10.41	1.40	50.0
4523	12/15	74.4; 49.3	0	20	9.74	0.92	73.3
			1	20	10.06	0.86	50.0
			0–3	48	9.91	0.95	58.6
4524	12/15	74.8; 49.0	0	16	10.26	0.79	25.0
			1	26	10.13	0.57	46.2
			0–2	48	10.28	0.76	41.7
4510	12/05	75.0; 49.0	1	28	11.97	0.99	64.3
			2	13	12.58	0.66	76.9
			0–3	48	11.93	1.12	68.8
B. 1983 cruise 8302							
4532	02/06	75.0; 49.0	0	41	8.95	0.71	46.2
			1	22	10.08	1.04	57.1
			0–3	72	9.67	1.36	50.7
4538	02/10	80.0; 53.0	1	18	10.81	0.82	33.3
			2	14	12.22	0.75	50.0
			0–4	48	11.23	1.11	37.5
4546	02/16	85.0; 51.0	0	22	9.90	0.47	71.4
			1	13	10.12	0.75	69.2
			0–3	48	10.36	0.96	69.8
4573	03/17	94.1; 34.0	0	24	9.00	0.42	70.8
			1	24	9.30	0.45	91.7
			0–1	48	9.15	0.46	87.0
4576	03/18	95.8; 38.0	0	15	9.93	0.41	26.6
			1	31	10.18	0.60	61.3
			0–2	48	10.15	0.68	52.1
4582	03/22	100.0; 36.0	0	13	10.02	0.45	69.2
			1	24	10.50	0.66	78.3
			0–3	48	10.71	0.95	74.5
4584	03/24	101.7; 34.0	0	40	9.10	0.53	55.0
			0–2	48	9.16	0.53	56.2
4586	03/28	105.0; 34.0	0	15	9.38	0.48	26.7
			1	33	9.30	0.57	36.4
			0–1	48	9.32	0.54	33.3
4590	03/30	110.0; 35.0	0	27	9.27	0.57	29.6
			1	18	9.92	0.72	38.9
			0–2	48	9.64	0.82	33.3

*Percent female is 100 times the number of females divided by the total number of fish with identifiable sex. Sex could not be determined for 27.0%, 10.4%, 12.5%, 8.3%, 39.6%, 0%, and 0% of fish collected in seven 8212 stations, respectively. Sex was indeterminate for only 1% of fish collected on cruise 8302.

individuals each. Subsamples were similarly selected from the 1982 and 1983 collections, although smaller sample sizes per station required a less stringent criterion: 25 subsamples with 11 or fewer fish (weighted mean = 4.6) were omitted, and 29 subsamples with 13 or more fish (weighted mean = 23.1) were retained.

The BMDP multivariate statistical software package (Dixon et al. 1988) was employed for additional analyses. Principal components analysis (PCA) was done without rotation on arcsine-square root transformed frequencies of the most common allele at each locus, for both stations and subsamples. Allele-frequency data for the 1982 and 1983 cruises were combined and analyzed separately from data for the 1984 and 1985 cruises, which had larger mean sample sizes and accompanying morphometric data. Correlations of genetic PCA factors with CalCOFI line coordinates, age, mean standard lengths, and—for the 1984 and 1985 samples—mean

measures of size, condition, gonadosomatic index, and five morphometric PCA factors were also obtained from BMDP (Nelson et al. 1994). We used autocorrelation (Rossi et al. 1992) of genetic factor scores (GII) for paired 1985 subsamples classified into distance categories to examine the spatial scale of genetic heterogeneity and to compare it with the spatial scales of variation in morphometric and life-history traits (Nelson et al. 1994).

RESULTS

Goodness-of-fit to Hardy-Weinberg Genotypic Proportions

Goodness-of-fit between observed numbers of genotypes at each of ten polymorphic allozyme loci and those expected under the Hardy-Weinberg principle for randomly mating populations was tested for each station sampled in each of the four surveys. Of the grand total of 313 exact probability tests, only 9 showed discrepancies significant at a nominal 5% significance level, fewer than the 16 expected by chance alone. The 9 significant tests, indicated by superscripts in the F_{IS} column of table 2, are spread over six loci, with *Est-5*, *Hbdh-1*, and *Ldh-1* accounting for two each and *Fum*, *Idh-1*, and *Lgg*, one each. Likewise, the 9 discrepancies are distributed across seven stations. Adjusting levels of significance for simultaneous testing of the hypothesis of random mating at ten loci per station (Cooper 1968; Rice 1989) leaves only one test significant at the 5% level (*Lgg* in 1984, station 4660). Agreement of observed and expected genotypic proportions is also evident for pooled data from each cruise. Means for Wright's (1978) F_{IS} statistic, which can be interpreted as a measure of average departure from random mating, fluctuate closely around zero, indicating no departure (table 2), and no significant departures from HW genotypic proportions were detected by exact probability tests for each locus in pooled cruise data.

Heterogeneity among Sexes and Age Classes within Stations

Loglinear models were fit to allele-frequency data tabulated by sex and age class for each of the 32 stations to determine whether these three factors were independent. Each of eight possible loglinear models (Fienberg 1980) were fit to the 190, frequency × age × sex, 3-way tables. Sex was found to be independent of age in 17 of 32 station samples but was significantly dependent on age in the remaining 15 stations; females were on average older than males at 11 stations. Allelic frequency was independent of sex and age, whether or not there was interaction of sex and age, in 174 (91.6%) of the 3-way tables.

In 16 cases, loglinear models involving interactions of allelic frequency with age or sex or both provided the best fits to the cross-classified data. Over all samples, dependence of frequency on age, and dependence of frequency on sex were each found in 9 stations. Because a model of frequency independent of age but conditional on sex fit data for two loci in one station (*Fum* and *Pgm* in station L, 1985), three subsamples for this station were considered in further analyses of allelic frequencies and morphometrics: age 0 females, age 1 females, and age 0 males. Interactions of allelic frequency with sex or age were spread over eight of the ten allozyme loci, led by *Pgm* with six; followed by *Est-5*, *Fum*, and *Ldh-1* with three each; *Hbdh-1* and *Lt-1* with two each, and *Idh-1* and *Lgg* with one each.

Heterogeneity among Stations

Allelic frequencies for 10 loci in each of 32 stations are given in appendix tables A–D. Heterogeneity of allelic frequencies among stations within years is measured by Wright's (1978) F_{ST} statistic, which standardizes the variance of allelic frequencies among samples against the maximum variance that would obtain if localities were fixed for alternate alleles in proportion to the mean allelic frequency for the total population. The F_{ST} values given in table 2 suggest that, relative to this maximum variance, genetic variance among stations ranges from less than 1% in 1984 and 1985 to 2.0% in December 1982. Combining all stations from the four cruises into a hierarchical analysis of genetic diversity, we find that standardized variance among stations within cruises, F_{SC}, is equal to variance among stations within the total, F_{ST} = 0.006, and that variance among cruises, F_{CT}, is zero.

Nevertheless, divergence of allelic frequencies among stations is highly significant for each of the four population surveys, as shown by the summed chi-square tests of heterogeneity (table 2). In each of the four surveys, four of ten loci yield significant heterogeneity chi-square values; but which loci are heterogeneous varies from year to year, resulting in a distribution of significant chi-square values over loci as follows: *Est-5*, 4; *Fum*, 1; *Gpi*, 3; *Hbdh-1*, 3; *Idh-1*, 0; *Ldh-1*, 1; *Lt-1*, 1; *Lgg*, 2; *6pgdh*, 1; *Pgm*, 0. Eight of the ten loci are significantly heterogeneous in at least one survey, and only two loci are homogeneous in all four surveys.

There is no correspondence of loci showing departures from Hardy-Weinberg genotypic proportions and loci showing heterogeneous allelic frequencies among localities; four loci with significant departures from random mating within stations show heterogeneity of allelic frequencies among stations, but five other loci with departures show no such heterogeneity (table 2). Likewise, loci showing interactions of allelic frequency with sex or age within station are not those showing spatial heterogeneity in the 1982, 1983, and 1984 surveys, although three of four loci showing spatial heterogeneity in the

TABLE 2
F-Statistics and Contingency Chi-Square Analyses for Northern Anchovy Samples from Four NMFS Cruises

Locus	F_{IS}[a]	F_{IT}	F_{ST}	No. of alleles	Heterogeneity among samples: Chi-square	d.f.	P[b]
A. December 1982 (8212); 7 samples							
Est-5	0.073[1]*	0.137	0.069	6	98.996	30	0.000*
Fum	0.000	0.014	0.014	3	18.116	12	0.092
Gpi	0.014	0.023	0.010	5	38.207	24	0.032*
Hbdh-1	0.094	0.102	0.009	5	39.860	24	0.019*
Idh-1	0.033	0.056	0.024	6	31.466	30	0.347
Ldh-1	−0.015	−0.008	0.007	2	4.772	6	0.573
Lt-1	0.152	0.155	0.004	5	20.584	24	0.808
Lgg	−0.065	−0.042	0.022	4	37.881	18	0.001*
6pgdh	0.020	0.031	0.011	3	14.656	12	0.251
Pgm	−0.057	−0.040	0.016	4	21.577	18	0.226
Mean	−0.006	0.014	0.020	Sum	326.115	198	0.000*
B. February–March 1983 (8302); 9 samples							
Est-5	0.020	0.074	0.055	5	72.176	28	0.000*
Fum	0.012	0.025	0.013	3	16.851	16	0.330
Gpi	−0.062	−0.035	0.025	4	43.254	21	0.009*
Hbdh-1	0.014	0.027	0.012	6	63.069	40	0.009*
Idh-1	−0.008	0.025	0.033	4	20.219	24	0.471
Ldh-1	0.016[1]*	0.022	0.005	2	4.961	8	0.762
Lt-1	−0.069	−0.059	0.009	5	37.256	32	0.222
Lgg	0.028	0.037	0.009	4	34.811	24	0.075
6pgdh	0.060	0.075	0.016	4	42.710	24	0.010*
Pgm	0.078	0.087	0.010	5	31.567	32	0.471
Mean	0.020	0.035	0.015	Sum	367.858	256	0.000*
C. February–March 1984 (8403); 7 samples							
Est-5	0.074	0.090	0.017	6	55.042	30	0.008*
Fum	−0.049[1]*	−0.047	0.002	4	18.615	18	0.398
Gpi	−0.016	−0.011	0.005	5	46.207	24	0.006*
Hbdh-1	0.063	0.067	0.004	7	32.952	36	0.596
Idh-1	0.007[1]*	0.010	0.003	6	31.898	30	0.316
Ldh-1	−0.072	−0.051	0.020	3	26.896	12	0.003*
Lt-1	−0.031	−0.019	0.011	7	78.057	36	0.000*
Lgg	−0.034[1]*	−0.028	0.006	4	23.470	18	0.164
6pgdh	−0.003	0.001	0.004	5	19.636	24	0.753
Pgm	−0.014	−0.002	0.012	4	25.556	18	0.094
Mean	−0.024	−0.015	0.008	Sum	358.330	246	0.000*
D. January–March 1985 (8502); 9 samples							
Est-5	0.034[1]*	0.041	0.007	7	68.397	48	0.023*
Fum	0.062	0.068	0.007	6	55.591	40	0.025*
Gpi	−0.034	−0.031	0.003	5	34.171	32	0.344
Hbdh-1	0.062[2]*	0.068	0.007	7	64.558	48	0.030*
Idh-1	−0.012	−0.008	0.003	5	34.233	32	0.326
Ldh-1	−0.022[1]*	0.024	0.002	4	18.612	24	0.892
Lt-1	−0.036	−0.033	0.003	6	35.073	40	0.726
Lgg	0.012	0.017	0.005	6	53.513	40	0.047*
6pgdh	0.021	0.025	0.004	6	47.741	40	0.150
Pgm	−0.050	−0.043	0.006	6	43.660	40	0.298
Mean	0.014	0.019	0.005	Sum	455.548	384	0.007*

[a]Superscripts with asterisks in the F_{IS} column indicate number of significant deviations from random-mating genotypic proportions.
[b]Asterisks in P column indicate significant among-sample heterogeneity χ^2 values.

1985 survey—*Est-5*, *Fum*, and *Hbdh-1*—show interactions with sex or age for stations I, L, and O. Finally, six 1985 stations that differed substantially in mean standard length and allelic frequencies (Hedgecock 1991) were tested for evidence of population mixture. Genotypic correlations between pairs of loci (gametic phase disequilibria), either for individual-station or pooled-station data, were not significantly different than zero.

Principal Components Analysis (PCA) of Allelic Frequencies

Using frequencies of the most common alleles at ten allozyme loci, we performed two PCAs of data from the 1982 and 1983 surveys—one for the 16 stations and the other for 29 age-class subsamples. The station data yielded four factors with eigenvalues greater than 1.0, accounting cumulatively for 69.5% of total variance in allelic frequencies. The subsample data yielded five factors with eigenvalues greater 1.0, accounting cumulatively for 74.1% of total variance. The patterns of contributions by individual loci to factors were quite different for the two analyses. Factor 2 for the station data (accounting for 18.5% of total variance) resembled factor 1 for the subsample data (accounting for 21.1% of total variance) in having high positive loadings by *Pgm* (≈0.7) and high negative loadings by *Idh-1* (≈−0.6); however, the latter was also positively loaded by *Gpi* and *Hbdh-1* (both >0.6), whereas the former was positively loaded not by these loci but by *Fum* (0.69). The third factor extracted in the subsample PCA, which accounted for 14.1% of total variance and later yielded correlation with age (see below), was loaded positively by *Fum* (0.83) and negatively by *6pgdh* (−0.51).

A comparable PCA for the 31 age-class subsamples selected from the 1984 and 1985 collections yielded four factors with eigenvalues greater than 1.0, accounting cumulatively for 67.3% of total variance in allelic frequencies. Factor 1, which accounted for 23.9% of total variance, was loaded positively (>0.7) by *Idh-1* and *Hbdh-1* and negatively by Gpi (−0.7). Factor 2, which accounted for 20.3% of variance, was loaded positively but weakly (≈0.5) by *Lgg*, *Fum*, and *Est-5* and negatively by *6pgdh* (−0.65) and *Lt-1* (−0.56).

Correlation of Genetic, Morphometric, and Environmental Factors

For the 1982 and 1983 data, genetic factor scores could be correlated with CalCOFI line coordinate, mean standard length, and—for subsamples—age (table 3). For the station data, only one of eight correlations, that between GII factor scores and CalCOFI line, was significant (r = 0.814, 14 d.f., $p < 0.01$). For the subsample data, two of 15 correlations were significant—GI factor scores vs CalCOFI line (r = 0.457, 27 d.f., $p < 0.05$) and GIII factor scores vs age (r = −0.478, 27 d.f., $p <$ 0.01). Mean standard length and age were not correlated with CalCOFI line, but age was positively correlated with mean standard length (r = 0.638, 27 d.f., $p < 0.01$), as expected (table 3).

For the 1984 and 1985 data, subsample scores for four genetic factors were correlated with subsample means for a total of 15 morphometric, life-history, and environmental variables: five morphometric factors (characterized as body depth, jaw length, anal-fin-base length, body depth, and orbit/preorbit length); a consensus measure of size; condition factor; gonadosomatic index (GSI); the coefficient from the regression of gonadosomatic index on ln(somatic wet weight) or GSI slope; distance of station from shore; CalCOFI line coordinate of station; year of capture; sea-surface temperature at capture; depth of bottom at station; and year class or estimated year of birth (see Nelson et al. 1994 for details). No correlation was observed among any of the genetic factors and condition, GSI, GSI slope, distance offshore, CalCOFI line, year of capture, sea-surface temperature, or year class. Single correlations between a genetic factor and each of the seven remaining variables—the five morphometric factors plus size and depth of bottom—exceed the critical significance value of 0.355 for $\alpha_{0.05}$ and 29 d.f. (table 4). The observation that 7 of 60 correlations are significant at the $\alpha_{0.05}$ level differs significantly from the expectation that 3 correlations might be significant by chance (χ^2 = 5.614, 1 d.f., p = 0.018); one correlation significant at the $\alpha_{0.01}$ level—0.456—is not different from the 0.6 expected by chance.

TABLE 3
Correlations of Genetic Factors with CalCOFI Line, Age, and Mean Standard Length for 1982 and 1983 Northern Anchovy Samples

	Stations		Subsamples		
	Line	Length	Line	Age	Length
Line	1.000		1.000		
Age	—	—	−0.131	1.000	
Length	0.047	1.000	0.024	0.638*	1.000
GI	0.131	−0.397	0.457*	−0.113	−0.068
GII	0.814*	0.065	−0.074	−0.057	−0.317
GIII	0.036	0.065	0.347	−0.478*	−0.221
GIV	0.384	0.167	−0.035	−0.113	0.036
GV	—	—	−0.049	−0.142	−0.046

Stations and subsamples (within-station age classes having 13 or more fish) are listed in table 1. Line is the CalCOFI coordinate for the station; length is the mean standard length for station or subsample; and age is the otolith age class. GI through GV represent principal components of allelic frequencies at ten allozyme loci; only four genetic factors were extracted from station data. *Correlations exceeding critical values for significance at the 5% level.

Spatial Pattern

Autocorrelation of 1984 and 1985 subsample scores for factor GII declines with distance, from a within-station r of 0.452 (N=16), significant only at the $\alpha_{0.05}$ level for a one-tailed test, to nonsignificant r values of 0.140 (N=61), −0.153 (N=103), 0.100 (N=133), and −0.078 (N=120) for distances of up to 100, 200, 300, and >300 km, respectively. This spatial pattern resembles that found for the morphometric factors body length, jaw length, and anal-fin-base length (Nelson et al. 1994).

TABLE 4
Correlations of Genetic Factors with Morphometric Factors and an Environmental Variable for 1984 and 1985 Northern Anchovy Samples

	Body length (MI)	Jaw length (MII)	Anal-fin-base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	Size	Depth of bottom
GI	0.023	0.091	−0.080	0.193	−0.124	0.438*	0.170
GII	−0.471*	0.409*	0.121	−0.363*	−0.010	−0.224	−0.424*
GIII	−0.024	0.289	−0.069	−0.095	0.379*	−0.130	−0.056
GIV	−0.102	0.138	−0.399*	−0.079	0.266	−0.129	0.002

Morphometric factors are described by Nelson et al. (1994). MI through MV are mean subsample scores for principal components of variation for 11 morphometric traits; size is a consensus measure based on these 11 traits. Depth of bottom is at station. GI through GIV represent genetic factor scores for 32 subsamples described by Nelson et al. (1994).
*Correlations exceeding the critical value for significance at the 5% level.

DISCUSSION

Is the Central Stock a Randomly Mating Population?

The central stock of the northern anchovy *Engraulis mordax* is commonly assumed, implicitly if not explicitly, to be a randomly mating population. This assumption is based primarily on long-term spatial and temporal distribution of eggs and larvae in CalCOFI samples (Kramer and Ahlstrom 1968; Hewitt 1980), recaptures of tagged adult fish (Haugen et al. 1969), meristic and morphometric studies (McHugh 1951; Vrooman et al. 1981), and agreement of transferrin genotypic frequencies with proportions expected on the basis of random mating and the Hardy-Weinberg (HW) principle (Vrooman et al. 1981). However, chi-square goodness-of-fit or exact probability tests of genotypic data have very low power to detect failure of the HW null hypothesis (Lewontin and Cockerham 1959; see review by Lessios 1992). In view of the potential significance of subpopulations for fishery biology and management so succinctly stated by Marr (1957), it may be important to question whether the assumption of random mating within the geographically defined central stock of northern anchovy has been sufficiently tested.

In our study of allozyme variation in 2,628 northern anchovies sampled at 32 stations within the range of the central stock, we too have found statistical agreement between observed distributions of genotypes at ten polymorphic loci and those expected according to the HW principle. Only 9 of 313 tests of agreement within stations showed discrepancies significant at a nominal $\alpha_{0.05}$ level; once significance is adjusted for simultaneous multiple testing of the hypothesis (Cooper 1968; Rice 1989), only one of these departures remains significant, which is expected by chance. Even after pooling data for all stations within each of the four survey cruises, we find no significant departures from HW genotypic proportions at any locus and no significant deviation of the mean fixation index from zero. Thus testing of HW genotypic proportions, either within or over all stations, offers no evidence against the assumption that the central stock of northern anchovy is a randomly mating population. Neither, however, does agreement with HW genotypic proportions prove the assumption true.

Having failed to reject the null hypothesis of random mating, we next examine evidence for heterogeneity of allelic frequencies among stations. The measure of population differentiation most often employed by population geneticists, Wright's F_{ST} statistic, ranges in this study from 0.005 to 0.020 over four survey cruises and was 0.032 in our previous analysis of data from an early 1982 cruise (Hedgecock et al. 1989). Such low values are typical for marine fishes (Gyllensten 1985), including the southern African anchovy, *Engraulis capensis*, for which mean F_{ST} was found to be 0.0015 (Grant 1985), and are generally regarded as indicative of only slight differentiation and relatively high rates of gene flow among localities. "Differentiation is, however, by no means negligible if F is as small as 0.05 or less" (Wright 1978).

In this case, the absolute variance of allelic frequencies among population samples, especially in comparison to the variance of sampling from a randomly mating population, is more informative than F_{ST} itself, which is among-population variance relative to its maximum value at complete fixation. For all ten loci and 32 stations sampled in this study, the expected binomial sampling variance of allelic frequencies is 0.00177. Absolute variance in allelic frequency among stations, which is obtained by subtracting the binomial sampling variance from total observed variance among stations, is 0.00131. Thus the total variance of allelic frequencies that we have measured among samples from the central stock is about twice what should have been observed were we sampling from a randomly mating population. That genetic differentiation among samples from this stock is not negligible is further demonstrated by chi-square tests of allele-frequency heterogeneity across all ten loci, in each of the four surveys (table 2). These tests consistently reveal highly significant heterogeneity of allozyme fre-

quencies, which is incompatible with the hypothesis that samples were drawn from a randomly mating population.

Our samples were drawn from a single, readily identified stock of northern anchovies living in a prescribed area of the California Current. If this stock is not a randomly mating population, then how should it be described? At the risk of becoming entangled in the "semantic difficulties" and "lack of agreed definitions" referred to by Marr (1957), we offer the following description. The central stock of northern anchovy is a geographic subpopulation which itself comprises a hierarchy of population units, the lowest ones in the hierarchy being the panmictic units within which mating is at random. Whether it is possible to partition this subpopulation into its individual panmictic units or to determine the causes of genetic heterogeneity within the central stock remain important questions.

Chaotic Spatial Pattern of Genetic Heterogeneity

Spatial patterning of allelic frequencies might suggest differential spatial distribution of panmictic units within the central stock. A number of lines of evidence indicate, however, that genetic heterogeneity within the central stock of northern anchovy is geographically unpatterned or "chaotic" (Johnson and Black 1982).

First, the loci contributing to heterogeneity differ from year to year. Including results previously reported for the early 1982 survey (Hedgecock et al. 1989), nine of ten polymorphic loci show significant heterogeneity of allelic frequencies in at least one of the five surveys taken, and all ten loci have homogeneous allelic frequencies in at least one survey. Moreover, the contributions of loci to factors extracted by various principal components analyses differ considerably from analysis to analysis. Comparing PCA factors for the 1982 and 1983 subsample data to those obtained for the 1984 and 1985 data, we find absolute loadings of loci, or the signs of the loadings, or both to be completely different. Comparing PCAs of stations vs subsamples for the 1982 and 1983 surveys, we find factor GII for stations to resemble factor GI for subsamples, in having positive loading by *Pgm* and negative loading by *Idh-1* and positive correlation with CalCOFI line coordinate (see below); nevertheless, there are major differences between the two factors in loadings by other loci. The contributions of particular loci to genetic heterogeneity are not consistent over groupings (station vs subsamples) or between years.

Second, although significant correlations between CalCOFI line coordinate and genetic factors from the 1982 and 1983 station and subsample PCAs suggest a cline in allelic frequencies with latitude, this correlation accounts for only a small percentage of allele-frequency variance for any one locus. In the station analysis, for example, correlation with CalCOFI line explains 66% of the variance in GII (table 3). This factor, in turn, explains only 18.5% of total variance in allelic frequencies and at most 55% of the variance contributed by any one locus (i.e., the squared loading of GII by *Pgm*, the largest contributor to that factor). Thus correlation of GII with CalCOFI line coordinate explains only 36.6% of among-station variance in the frequency of the Pgm^{100} allele. Correlation of CalCOFI line and GI from the subsample PCA (table 3) similarly explains only 10.7% of among-subsample variance in Pgm^{100} frequency; proportions of variance explained for other loci by this correlation are smaller still. Moreover, the direction of the cline implied by this correlation—increasing frequency of Pgm^{100} to the south—is opposite to the significant negative correlation between latitude and Pgm^{100} frequency reported for samples from early 1982 (Hedgecock et al. 1989). There is little evidence in these data for significant or persistent associations of allelic frequency with latitude.

Third, spatial autocorrelation of the second principal component, GII, for the 1984 and 1985 subsample data indicates that weak positive genetic correlation among ages within a station grades off to even weaker correlations among subsamples within 100 km.

Fourth, correlations of genotypes among loci (gametic phase disequilibria) are not significantly different from zero for six 1985 stations that differed obviously in mean standard length at age and allelic frequencies, providing no evidence that stations represent mixtures of genetically discrete populations (Waples and Smouse 1990).

Finally, a cluster analysis of minimum genetic distance among all 32 trawl samples shows collections from different years and diverse CalCOFI line coordinates joined at high levels of genetic similarity (figure 1). Heterogeneity of allelic frequencies in the central stock shows little spatial patterning, giving no indication of spatially distinct panmictic units.

Correlations of Genetic and Morphometric Traits

Having found heterogeneity of allelic frequencies both within and between station samples in 1982 (Hedgecock et al. 1989), we increased sample size per trawl collection and obtained data on 11 morphometric traits, age, sex, and reproductive status for each fish in the 1984 and 1985 surveys in order to look for morphological and life-history correlates of genetic heterogeneity. A preliminary analysis found a strong positive correlation of factor scores from a PCA of allelic frequencies at five loci with mean standard length for six 1985 stations (Hedgecock 1991). We have presented here, for 31 subsamples of the 1984 and 1985 trawl samples, a complete correlational analysis among genetic factor scores for ten loci and subsample means for 15 morphological, life-

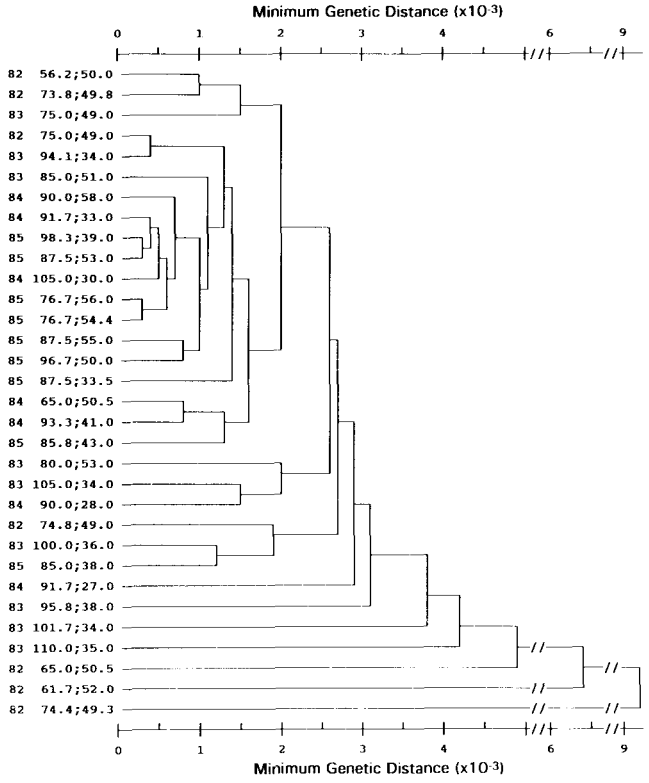

Figure 1. Cluster analysis of Nei's (1972) minimum genetic distance among 32 midwater trawl samples of northern anchovy. Samples are labeled with the year of collection (two digits, corresponding to CalCOFI cruises 8212, 8302, 8403, and 8502) followed by CalCOFI station coordinates. Samples from different years and disparate latitudes are joined at high levels of genetic similarity (low values of genetic distance).

history, and environmental descriptors (Nelson et al. 1994).

Four genetic factors (GI–GIV) were extracted by PCA of the frequencies of the most common alleles at ten loci in 31 age-class subsamples. Although no correlation was observed among any of the genetic factors and condition or gonadosomatic index—traits which may be involved in physiological responses to spatial patterns of productivity and temperature, respectively, in the California Current (Nelson et al. 1994)—each of these factors shows modest but significant correlation with at least one of six morphological variables, five morphometric factors (MI–MV), and a consensus measure of body size (table 4). Except for the correlation of GII with depth of bottom at station, none of the genetic factors is correlated with environmental variables, CalCOFI line coordinate, distance of station offshore, or sea-surface temperature at time of capture. The number of correlations significant at the $\alpha_{0.05}$ level, 7 out of a total of 60, is itself significant. GII is responsible for 4 significant correlations: with body size (MI), jaw length (MII), body depth (MIV), and depth of bottom. GI is correlated with size, GIII with orbit-preorbital length (MV), and GIV with anal-fin-base length (MIII). A correlation of GII with year class, $r = -0.325$, falls just short of the critical value of significance, 0.355.

Whereas no correlation was found between genetic factors for 1984 and 1985 samples and CalCOFI line coordinate, this correlation was significant for the 1982 and 1983 data. This may be attributable to the greater latitudinal range spanned by the 1982–83 collections, from 38°31.1'N to 29°47.3'N (effectively the entire range of the central subpopulation) compared to the more limited latitudinal range represented in the 1984–85 samples, 37°3.9'N to 30°49.2'N, which were also more concentrated in the Southern California Bight (see figure 1, Nelson et al. 1994). The nearly significant correlation of GII with year class in the 1984–85 data may be similar to the significant correlation of GIII with age in the 1982–83 data; loadings of several loci on these two factors are similar in size and sign: *Fum*, 0.51 vs 0.83; *6pgdh*, −0.65 vs −0.51; *Est-5*, 0.52 vs 0.35; and *Lt-1*, −0.56 vs −0.25, respectively. Finally, the correlation between a genetic factor and mean standard length reported in a preliminary analysis of six 1985 stations (Hedgecock 1991) appears to be subsumed in the subsample correlations of GI with size and of GII with MI, judging from the loadings of loci on the respective principal components.

The general conclusion that the central subpopulation is not a randomly mating population is reinforced by evidence of substantial morphological and life-history variation in the same samples (Nelson et al. 1994). Significant correlations between genetic and morphometric factors but not condition or reproductive state suggest that genetic heterogeneity is not a statistical artifact, but is associated with biologically meaningful, perhaps heritable, morphological variation. We wish to emphasize that we do not believe that these correlations are causal, i.e., that differentiation of the allozyme frequencies is directly responsible for the divergence of morphological traits. Rather, we regard the genetic-morphometric correlations as a reflection of spatial covariance between two sets of multivariate traits that show significant heterogeneity within the central stock of northern anchovy. How this heterogeneity arises and is maintained within a geographical area that is readily traversed by individual adults and is the major spawning ground for the species is unclear.

Causes of Heterogeneity within the Central Stock

One hypothesis for the genetic and morphological heterogeneity that we have observed within the central stock is that southern subpopulation fish migrated into the range of the central stock during the California El Niño of 1982–84. We believe that this hypothesis can be rejected on both genetic and morphological grounds. We observed similar among-station genetic heterogene-

ity in surveys taken before, during, and after the El Niño event, which commenced in late 1982 and lasted until summer of 1984. The southernmost samples taken in the winters of 1983 and 1984 at Cape Colnett and Punta Baja (CalCOFI lines 105 and 110) do not have distinctive allozyme frequencies, and cluster with more northerly samples of the central stock (figure 1). Moreover, the standard lengths of fish in these southerly samples, especially the age 0 and age 1 fish, are intermediate to those for other stations (table 1; table 1 of Nelson et al. 1994), not significantly smaller as would be expected if they had originated from the southern subpopulation (Mais 1974; Vrooman et al. 1981; Parrish et al. 1985). Likewise, fish sampled in 1984 are not appreciably smaller than those sampled in 1985 despite exposure to the elevated temperatures of El Niño (Nelson et al. 1994).

If we exclude immigration of the southern subpopulation into the Southern California Bight as the source of the genetic and morphological heterogeneity observed in the central subpopulation, we must then regard this heterogeneity as a property or feature of the central subpopulation itself. How does this heterogeneity arise within the geographical and oceanographical confines of what appears to be a single spawning stock?

Slight but significant genetic heterogeneity—chaotic genetic patchiness (Johnson and Black 1982)—embedded within broad areas of great genetic similarity has been observed of many marine animal species capable of planktonic or pelagic dispersal (Hedgecock 1994). This paradox may be resolved by the hypothesis that slight differences in allelic frequencies could arise as a consequence of variance in the reproductive success of spawning adults and subsequent sampling errors in the recruitment of larval fish to their first schools. That this may be the case for northern anchovy is suggested by significant correlations, in the 1982 and 1983 subsample data, of genetic factor GIII with age (table 3). Correlations, in the 1984 and 1985 subsample data, of genetic factors GII and GIII with morphometric factors MII (jaw length) and MIII (anal-fin-base length) respectively (table 4)—morphological features that may be established early in life (McHugh 1951)—are also consistent with this hypothesis. The pattern of spatial autocorrelation shared by MII, MIII, and GII—low within-station correlation grading off to insignificant correlation within the first 100 km—may reflect variation in larval or juvenile experience, not just among natal localities, but also among year classes from the same area that are later captured together. Within-station heterogeneity for these factors would imply low spawning-site fidelity and heterogeneity of origin of the different year classes at a station. These disparate year classes later come to resemble one another in size, body depth, condition, and reproductive state, possibly through common environment and assortative grouping (Nelson et al. 1994).

Despite the existence of some within-station heterogeneity, most of the genetic variance is among stations, as reflected by significant contingency chi-square values in all years (table 2) and correlations of genetic factors with CalCOFI line coordinates in the 1982–83 data and with morphometric factors that show spatial autocorrelation on a scale of 100–200 km (size and body depth) in the 1984–85 data (table 4; Nelson et al. 1994). Maintaining these differences among adult anchovy populations would appear to require one or more of the following: life-long fidelity to schools, assortative movements and grouping, or homing to natal spawning grounds. None of these behaviors is known for northern anchovies. Current understanding of the biology of this and other pelagic fishes is too rudimentary to specify alternative explanations of the phenomenon that we have recorded.

Finally, the similarity of our results to those of Altukhov et al. (1969) and Spanakis et al. (1989) for *Engraulis encrasicholus* indicates that genetic and morphological heterogeneity may be a general feature of anchovy populations. In some respects our data conform to the elementary population concept of Lebedev (1969). Variation in genetic and certain morphological traits may be linked to processes (variance in adult reproductive success) or environments acting early in the life of the northern anchovy, as required if "elementary populations are formed as 'intra-age' groups at the birthplaces of the young" (Altukhov et al. 1969). Unlike reports in the Russian literature on elementary fish populations, however, genetic, morphological, and life-history variation in northern anchovy appears not to be stable over time or space but chaotic in spatial pattern and ephemeral in its expression. The only feature that remains constant is the heterogeneity itself.

CONCLUSIONS

We can conclude only what the central stock of northern anchovy is not: it is not a randomly mating subpopulation. How genetic, morphological, and life-history variation are generated and maintained throughout the adult stages of this subpopulation are matters about which we can only speculate. The central stock appears to be a geographic subpopulation comprising "virtual" panmictic units, which produce cohorts of offspring that deviate in random fashion from the subpopulation's genotypic and phenotypic norms. These among-group deviations, which may be wholly or partially preserved through the lifetime of an individual cohort—either by homing to natal localites, assortative grouping with other cohorts on the basis of swimming speed or common experience, or both—are probably not transmitted to the succeeding generation, owing to substantial mixing and

gene exchange among cohorts spawning in the Southern California Bight. Although such variation cannot accumulate over generations, the processes that generate and sustain it may nevertheless play important roles in the adaptation and evolutionary potential of this subpopulation and perhaps other pelagic fishes as well. By continually generating greater phenotypic and genotypic variation than would otherwise be presented by a single, randomly mating population, the central subpopulation of northern anchovy permits natural selection to act not only among individuals but among groups as well.

ACKNOWLEDGMENTS

The authors thank R. D. Methot for obtaining the samples of anchovies used for this study, M. Simmons for help with data collection, and L. Stenzel for help with data organization and preliminary analysis. This research was funded in part by grants (R/F 82 and R/F 98) from the California Sea Grant College Program.

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APPENDIX

TABLE A

Allelic Frequencies in Seven Samples of Northern Anchovy from Cruise 8212

	Sample						
Locus	1	2	3	4	5	6	7
Est-5							
N	42	42	46	33	38	38	43
96	.000	.000	.011	.000	.000	.000	.000
98	.012	.036	.011	.030	.276	.026	.047
100	.917	.940	.870	.909	.684	.921	.919
101	.024	.000	.054	.045	.039	.013	.023
102	.048	.012	.054	.015	.000	.039	.012
103	.000	.012	.000	.000	.000	.000	.000
Fum							
N	48	48	48	48	48	48	48
96	.000	.000	.000	.000	.000	.010	.021
100	.469	.458	.458	.490	.594	.604	.510
104	.531	.542	.542	.510	.406	.385	.469
Gpi							
N	48	48	48	48	48	48	48
96	.000	.000	.010	.052	.010	.000	.000
98	.000	.000	.000	.000	.000	.021	.010
100	.938	.969	.979	.927	.948	.938	.948
103	.063	.021	.010	.021	.031	.042	.031
105	.000	.010	.000	.000	.010	.000	.010
Hbdh-1							
N	48	48	48	48	48	48	48
92	.021	.000	.000	.010	.021	.010	.000
94	.010	.031	.010	.042	.021	.000	.031
96	.010	.000	.010	.010	.000	.021	.021
100	.958	.927	.979	.938	.958	.969	.948
103	.000	.042	.000	.000	.000	.000	.000
Idh-1							
N	44	13	43	40	36	39	37
95	.000	.000	.012	.013	.014	.013	.000
100	.977	1.000	.965	.913	.903	.936	1.000
106	.022	.000	.012	.076	.084	.052	.000
118	.000	.000	.012	.000	.000	.000	.000
Ldh-1							
N	48	48	48	48	48	48	48
96	.177	.125	.125	.208	.188	.146	.135
100	.823	.875	.875	.792	.813	.854	.865
Lt-1							
N	48	48	48	48	48	48	48
94	.000	.000	.000	.000	.000	.000	.010
96	.000	.010	.010	.021	.021	.000	.000
97	.000	.000	.000	.000	.000	.000	.010
100	.958	.938	.958	.948	.969	.958	.938
103	.042	.052	.031	.031	.010	.042	.042
Lgg							
N	48	48	47	48	48	48	48
97	.010	.010	.011	.052	.052	.063	.010
100	.563	.781	.543	.563	.604	.635	.583
104	.396	.208	.404	.385	.302	.302	.385
107	.031	.000	.043	.000	.042	.000	.021
6pgdh							
N	48	48	48	48	48	48	48
98	.042	.063	.083	.031	.083	.031	.052
100	.948	.917	.917	.958	.875	.958	.948
104	.010	.021	.000	.010	.042	.010	.000
Pgm							
N	48	48	48	48	48	48	48
96	.010	.000	.000	.010	.000	.010	.010
100	.750	.750	.667	.760	.823	.813	.802
103	.240	.250	.333	.229	.167	.156	.177
106	.000	.000	.000	.000	.010	.021	.010

Key to samples: 1, 56.2;50.0. 2, 61.7;52.0. 3, 65.0;50.5. 4, 73.8;49.8. 5, 74.4;49.3. 6, 74.8;49.0. 7, 75.0;49.0.
N is the number of individuals sampled.
Idh-1^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE B
Allelic Frequencies in Nine Samples of Northern Anchovy from Cruise 8302

	Sample								
Locus	1	2	3	4	5	6	7	8	9
Est-5									
N	32	—	28	8	27	23	9	45	48
98	.047	—	.018	.063	.000	.000	.000	.011	.000
100	.891	—	.893	.938	.833	.957	1.000	.967	.885
101	.063	—	.036	.000	.167	.043	.000	.000	.000
102	.000	—	.054	.000	.000	.000	.000	.022	.115
Fum									
N	69	46	43	48	48	47	48	48	48
96	.007	.000	.000	.000	.000	.000	.000	.010	.000
100	.507	.478	.523	.531	.542	.638	.573	.583	.438
104	.486	.522	.477	.469	.458	.362	.427	.406	.563
Gpi									
N	60	46	43	12	48	44	—	47	43
98	.075	.000	.000	.000	.010	.000	—	.011	.000
100	.875	.967	.988	.958	.938	.943	—	.979	.965
103	.042	.033	.012	.042	.052	.057	—	.011	.035
105	.008	.000	.000	.000	.000	.000	—	.000	.000
Hbdh-1									
N	69	46	43	48	48	47	47	48	48
92	.000	.000	.000	.021	.000	.000	.000	.000	.000
94	.022	.000	.000	.031	.010	.000	.032	.010	.010
96	.022	.033	.035	.021	.021	.011	.053	.042	.000
98	.000	.000	.023	.000	.000	.000	.000	.000	.000
100	.935	.967	.930	.927	.958	.989	.915	.948	.990
103	.022	.000	.012	.000	.010	.000	.000	.000	.000
Idh-1									
N	39	42	30	—	29	24	—	39	48
95	.013	.000	.017	—	.000	.000	—	.000	.010
100	.974	.940	.900	—	.948	.958	—	.923	.865
106	.013	.048	.083	—	.052	.042	—	.077	.125
118	.000	.012	.000	—	.000	.000	—	.000	.000
Ldh-1									
N	69	46	41	48	48	47	48	48	48
96	.181	.130	.146	.146	.167	.181	.104	.115	.135
100	.819	.870	.854	.854	.833	.819	.896	.885	.865
Lt-1									
N	69	46	43	47	48	47	48	48	48
94	.000	.000	.012	.000	.000	.000	.000	.000	.000
96	.000	.000	.000	.000	.000	.000	.000	.010	.010
97	.022	.011	.035	.000	.000	.011	.010	.000	.000
100	.920	.978	.942	.936	.938	.947	.917	.917	.906
103	.058	.011	.012	.064	.063	.043	.073	.073	.083
Lgg									
N	69	44	43	46	48	46	37	48	46
97	.065	.011	.058	.022	.021	.076	.014	.031	.087
100	.514	.636	.535	.554	.635	.543	.635	.625	.630
104	.413	.352	.395	.380	.323	.359	.351	.344	.283
107	.007	.000	.012	.043	.021	.022	.000	.000	.000
6pgdh									
N	69	46	43	48	48	47	48	48	48
96	.014	.000	.000	.000	.010	.043	.000	.000	.000
98	.043	.022	.081	.031	.031	.032	.115	.083	.042
100	.920	.978	.907	.969	.948	.904	.885	.906	.958
104	.022	.000	.012	.000	.010	.021	.000	.010	.000
Pgm									
N	69	46	43	47	48	47	48	48	48
96	.000	.011	.000	.000	.000	.000	.000	.000	.000
98	.000	.000	.000	.000	.000	.000	.010	.000	.000
100	.775	.837	.837	.830	.802	.862	.740	.875	.854
103	.217	.152	.163	.170	.198	.138	.240	.125	.146
106	.007	.000	.000	.000	.000	.000	.010	.000	.000

Key to samples: 1, 4532, 75.0:49.0. 2, 4538, 80.0:53.0. 3, 4546, 85.0:51.0. 4, 4573, 94.1:34.0. 5, 4576, 95.8:38.0. 6, 4582, 1000.0:36.0. 7, 4584, 101.7:34.0. 8, 4586, 105.0:34.0. 9, 4590, 110.0:35.0.
N is the number of individuals sampled.
Idh-1^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE C
Allelic Frequencies in Seven Samples of Northern Anchovy from Cruise 8403

	Sample						
Locus	1	2	3	4	5	6	7
Est-5							
N	120	94	111	105	118	40	64
97	.000	.005	.023	.029	.034	.000	.000
98	.033	.011	.045	.005	.030	.013	.039
100	.929	.957	.847	.929	.860	.962	.930
102	.033	.027	.081	.033	.076	.025	.023
Other	.004	.000	.005	.005	.000	.000	.000
Fum							
N	120	120	120	120	120	48	72
96	.004	.000	.000	.025	.013	.010	.014
100	.575	.538	.525	.521	.546	.510	.556
104	.421	.463	.471	.450	.442	.479	.431
Other	.000	.000	.004	.004	.000	.000	.000
Gpi							
N	119	120	120	120	120	48	72
96	.000	.000	.000	.000	.000	.021	.000
100	.962	.962	.933	.967	.954	.948	.972
103	.034	.038	.067	.029	.046	.031	.021
Other	.004	.000	.000	.004	.000	.000	.007
Hbdh-1							
N	120	120	120	120	120	45	72
92	.013	.004	.004	.004	.008	.000	.000
94	.013	.004	.004	.017	.017	.022	.035
96	.013	.017	.025	.004	.004	.011	.021
100	.950	.971	.958	.962	.967	.967	.938
Other	.012	.004	.008	.013	.004	.000	.007
Idh-1							
N	120	77	117	120	119	43	65
95	.000	.006	.000	.004	.013	.023	.008
100	.942	.922	.940	.917	.937	.942	.908
106	.058	.071	.056	.071	.046	.035	.062
118	.000	.000	.004	.004	.004	.000	.015
Other	.000	.000	.000	.004	.000	.000	.008
Ldh-1							
N	120	120	120	120	120	48	72
96	.150	.125	.158	.108	.158	.115	.271
100	.850	.871	.842	.892	.842	.885	.729
Other	.000	.004	.000	.000	.000	.000	.000
Lt-1							
N	120	120	120	120	120	48	72
96	.000	.000	.042	.000	.000	.010	.000
97	.004	.017	.004	.004	.013	.021	.007
100	.929	.917	.896	.950	.946	.875	.951
103	.058	.067	.058	.029	.038	.094	.021
105	.004	.000	.000	.008	.004	.000	.014
Other	.004	.000	.000	.008	.000	.000	.007
Lgg							
N	117	118	117	120	120	48	72
97	.026	.042	.034	.042	.042	.010	.035
100	.547	.568	.560	.558	.512	.646	.597
104	.385	.386	.393	.387	.433	.302	.347
107	.043	.004	.013	.013	.013	.042	.021
6pgdh							
N	120	120	120	120	120	48	72
98	.063	.050	.050	.063	.063	.031	.035
100	.929	.942	.933	.929	.933	.969	.965
104	.004	.008	.017	.004	.004	.000	.000
Other	.004	.000	.000	.004	.000	.000	.000
Pgm							
N	120	120	120	120	119	48	72
100	.842	.796	.742	.825	.786	.875	.854
103	.154	.196	.254	.171	.214	.115	.146
Other	.004	.008	.004	.004	.000	.010	.000

Key to samples: 1, 4660, 90.0:58.0. 2, 4662, 91.7:33.0. 3, 4612, 65.0:50.5. 4, 4689, 105.0:30.0. 5, 4671, 93.3:41.0. 6, 4655, 90.0:28.0. 7, 4665, 91.7:27.0.
N is the number of individuals sampled.
Alleles with frequencies less than 0.01 in all stations are pooled as "other."
Idh^{106} is a composite category for alleles *104*, *106*, and *108*.

TABLE D
Allelic Frequencies in Nine Samples of Northern Anchovy from Cruise 8502

	Sample								
Locus	1	2	3	4	5	6	7	8	9
Est-5									
N	112	180	109	119	117	120	119	117	114
97	.000	.008	.018	.004	.004	.008	.008	.021	.013
98	.018	.022	.009	.004	.004	.017	.021	.021	.022
100	.938	.894	.899	.950	.919	.887	.945	.885	.921
101	.013	.017	.005	.017	.013	.004	.000	.038	.018
102	.027	.056	.064	.025	.056	.083	.025	.034	.022
Other	.004	.003	.005	.000	.004	.000	.000	.000	.004
Fum									
N	119	180	120	120	120	120	120	120	120
96	.008	.008	.004	.004	.000	.000	.000	.013	.004
100	.529	.519	.525	.521	.517	.496	.642	.492	.525
104	.462	.472	.467	.463	.483	.504	.354	.488	.471
Other	.000	.000	.004	.013	.000	.000	.004	.008	.000
Gpi									
N	119	179	120	119	120	120	120	120	120
96	.000	.003	.000	.000	.004	.013	.004	.004	.000
100	.958	.958	.971	.975	.958	.954	.938	.946	.946
103	.042	.039	.029	.021	.029	.033	.058	.050	.054
Other	.000	.000	.000	.004	.008	.000	.000	.000	.000
Hbdh-1									
N	120	180	120	120	120	120	120	120	120
92	.004	.011	.004	.000	.004	.004	.004	.000	.000
94	.017	.008	.013	.008	.017	.013	.004	.004	.004
96	.008	.011	.046	.008	.008	.021	.008	.038	.017
100	.958	.944	.929	.979	.954	.958	.983	.954	.979
103	.008	.022	.008	.004	.017	.004	.000	.004	.000
Other	.004	.003	.000	.000	.000	.000	.000	.000	.000
Idh-1									
N	116	178	114	120	115	118	120	120	116
93	.000	.011	.009	.004	.009	.008	.004	.008	.004
100	.905	.924	.943	.904	.922	.928	.938	.904	.931
106	.086	.062	.039	.092	.065	.064	.054	.067	.047
118	.009	.003	.009	.000	.004	.000	.004	.021	.017
Ldh-1									
N	119	180	120	120	120	120	120	120	120
96	.155	.139	.188	.142	.175	.142	.167	.158	.150
100	.845	.858	.813	.858	.825	.854	.833	.842	.846
Other	.000	.003	.000	.000	.000	.004	.000	.000	.004
Lt-1									
N	120	180	120	120	119	120	120	120	120
97	.017	.008	.004	.004	.013	.004	.017	.008	.000
100	.917	.933	.946	.917	.937	.938	.921	.958	.950
103	.058	.050	.046	.067	.042	.058	.050	.033	.046
105	.008	.003	.000	.013	.008	.000	.013	.000	.000
Other	.000	.006	.004	.000	.000	.000	.000	.000	.004
Lgg									
N	119	179	120	117	118	120	117	120	119
97	.059	.022	.042	.038	.034	.058	.021	.004	.050
100	.601	.570	.538	.590	.589	.525	.526	.525	.567
104	.328	.388	.383	.346	.352	.375	.423	.454	.366
107	.013	.020	.038	.026	.021	.042	.021	.013	.017
Other	.000	.000	.000	.000	.004	.000	.008	.004	.000
6pgdh									
N	120	180	120	114	120	120	119	118	120
98	.038	.047	.038	.026	.025	.021	.042	.017	.042
100	.950	.944	.950	.947	.967	.979	.954	.983	.946
104	.008	.008	.000	.018	.008	.000	.000	.000	.004
Other	.004	.000	.012	.008	.000	.000	.004	.000	.008
Pgm									
N	119	180	120	120	120	120	120	120	120
100	.832	.806	.825	.754	.837	.867	.796	.796	.808
103	.155	.183	.175	.242	.158	.121	.192	.192	.175
Other	.012	.012	.000	.004	.000	.012	.012	.012	.016

Key to samples: 1, 4708, 76.7:56.0; 2, 4766, 98.3:39.0; 3, 4725, 87.5:55.0; 4, 4729, 87.5:33.5; 5, 4707, 76.7:54.0; 6, 4763, 96.7:50.0; 7, 4719, 85.0:38.0; 8, 4722, 85.8:43.0; 9, 4726, 87.5:53.0.

N is the number of individuals sampled. Alleles with frequencies less than 0.01 in all stations are pooled as "other."

Idh^{106} is a composite category for alleles *104*, *106*, and *108*.