

VARIATION IN LIFE HISTORY AND MORPHOLOGY IN NORTHERN ANCHOVIES (*ENGRAULIS MORDAX*)

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ABSTRACT

Individual, geographic, and interannual variation in morphometric and life-history traits was examined and related to environmental variables. In the winters of 1984 and 1985, 1,836 otolith-aged northern anchovies (*Engraulis mordax*) were obtained from 16 California-northern Baja California stations. Life-history characters were age, size (mean of logs of 11 morphometric measures), condition, and gonadosomatic index (GSI). Principal components analysis of 11 log-transformed morphometric traits adjusted for size and sex revealed five factors that summarized variation in (1) length of body, (2) length of jaw and operculum, (3) length of anal-fin base, (4) body depth, and (5) length of orbit and preorbital region. Independent variables used in further analyses were age, sex, size, year of sampling, year-class, distance offshore, CalCOFI line, depth of bottom, and sea-surface temperature at station. Within-station age-classes containing more than 13 fish were treated as independent subsamples (a total of 37).

Morphometric factors, although independent of size, were found to reflect condition. Although GSI and condition were negatively correlated among ages within years, they were independent among subsamples. Only 0.7% of individual variation in GSI was attributable to sex. Although there was overall positive correlation of GSI and size, the allometric relationship of GSI with size within a subsample (GSI slope) was negatively correlated with subsample mean GSI, signifying individual variation in reaction-norm allometry.

Spatial heterogeneity was unexpectedly large for all life-history and morphometric characters. Two temperature-correlated, mesoscale spatial patterns were found: (1) of size, GSI, and GSI slope; and (2) of condition, body depth, and body length. Pattern 2 resembled published satellite images of a recurrent pattern of phytoplankton-pigment concentration, reflecting primary production. A third pattern of negative correlation of jaw length with condition and body depth was independent of temperature, year, and other independent variables. Year-class- and temperature-related differences between 1984 and 1985 samples suggested expected effects of the 1982-84 El Niño, but these were not cleanly

separable from the much larger contributions of geographic variation. Heterogeneity within and among subsamples, particularly in jaw and anal-fin-base lengths, suggested heterogeneity of early environment, both among ages from the same station and within certain subsamples.

RESUMEN

Se examinó la variación individual, geográfica e interanual de los caracteres morfométricos y de las fases de vida de la anchoveta norteña y se buscó relacionar esta variabilidad con variables ambientales. Se obtuvieron 1836 *Engraulis mordax* y se determinó la edad por medio de sus otolitos; los especímenes se obtuvieron en los inviernos de 1984 y 1985 en 16 estaciones de Baja California (México) y California. Los caracteres de la fase de vida que se consideraron fueron edad, tamaño (el promedio de los logaritmos de 11 medidas morfométricas), condición e índice gonadosomático ("IGS"). El análisis por componentes principales de 11 caracteres morfométricos ajustados por tamaño y sexo revelaron 5 factores que resumen la variación en (1) talla, (2) longitud del maxilar y opérculo, (3) longitud de la base de la aleta anal, (4) profundidad del cuerpo y (5) longitud de la región orbital y preorbital. Otras variables independientes que se analizaron fueron edad, sexo, tamaño, año de muestreo, clase anual de edad, distancia hacia mar abierto, transecto establecido por el programa "CalCOFI", profundidad, y temperatura del agua superficial por estación. Las estaciones donde las clases de edad incluyeron más de 13 especímenes fueron tratadas como submuestras independientes (resultando en un total de 37).

Los factores morfométricos reflejaron la condición, a pesar de que fueron independientes del tamaño. A pesar de que la correlación entre IGS y condición fué negativa entre las edades para los distintos años, estas variables fueron independientes entre las submuestras. El sexo sólo explica 0.7% de la variación individual del IGS. Hubo una correlación positiva entre IGS y tamaño. Sin embargo, hubo una correlación negativa entre la relación alométrica IGS—tamaño dentro de cada submuestra (pendiente del IGS) con el promedio del IGS por submuestra, lo que significa que hubo variación individual en la alometría de la norma de reacción.

La heterogeneidad espacial fué sorprendentemente alta para todos los caracteres morfométricos y de las fases de vida. Se encontraron dos patrones relacionados con la temperatura en la meso-escala: (1) de tamaño, IGS y pendiente del IGS, y (2) de condición, profundidad del cuerpo y talla. El patrón no. 2 se asemejó a imágenes de satélite ya publicadas de un patrón recurrente de un pigmento de fitoplancton que refleja la producción primaria. Un tercer patrón, correlación negativa entre longitud del maxilar con condición y profundidad del cuerpo, fué independiente de la temperatura, el año, y otras variables independientes. Debido a diferencias en las clases anuales así como en temperatura entre las muestras de 1984 y 1985, se esperarían efectos debidos al evento El Niño 1982–84. Sin embargo, estos efectos no se pudieron demarcar claramente de la contribución mas substancial de la variación geográfica. La heterogeneidad dentro y entre las submuestras, particularmente en la longitud del maxilar y de la base de las aletas anales, sugirió heterogeneidad del ambiente que los peces encuentran a edad temprana, tanto entre edades en la misma estación, como dentro de algunas submuestras.

INTRODUCTION

The responses of a species to changes in its environment determine where it can persist. A free-ranging animal such as a pelagic fish may encounter environmental variation with both temporal and spatial components, each with a wide spectrum of frequencies. Response to this variation may be behavioral, physiological, and morphological, with resulting modifications in life history. Certainly the most important among such norms of reaction (Schmalhausen 1949) are those to variations in temperature and food supply, including variation in growth rate and, in fishes, such reproductive traits as fecundity and age- and size-at-maturity (Miller 1979; Nelson and Soulé 1987; Nelson, 1993). In the marine coastal environment in particular, variations in water movements, temperature, and production are linked, although not in any simple way (references in Roesler and Chelton 1987). Responses of different morphological and life-history variables to such variations are also likely to be correlated with one another. Patterns of environmental correlation and effects upon population structure will be correspondingly more complex.

Anchovies are a characteristic and key forage species for other pelagic fishes in all eastern boundary current systems (Reid 1966). Because of CalCOFI, the northern anchovy (*Engraulis mordax*) and its California Current habitat are probably the best-known of these systems. Yet, how northern anchovy morphology and life history respond to spatial and temporal changes in the environment remains a mystery (cf. Fiedler et al. 1986).

Two subspecies of *Engraulis mordax* have been described (Hubbs 1925; cf. McGowan 1984): the wide-ranging nominate subspecies and another that inhabits San Francisco Bay and about which little is known. *Engraulis mordax mordax* Girard has been considered to be further subdivided into northern, central, and southern subpopulations, based on meristic, morphometric, and transferrin electrophoretic phenotypes (McHugh 1951; Vrooman et al. 1981). The central subpopulation was supposed to range from San Francisco Bay to northern Baja California, approximately the area shown in figure 1A. Vrooman et al. found electrophoretic evidence for a certain amount of geographic overlap with the northern subpopulation. Although the central and southern subpopulations were believed to be nonoverlapping, each may occupy an area off north central Baja California at a different time of year; anchovies belonging to the southern subpopulation are distinguished by their smaller maximum sizes (Parrish et al. 1985).

Previously, we found significant geographical heterogeneity for 5 of 11 electrophoretic allozyme loci among samples collected from the central subpopulation range by the 1982 CalCOFI winter (spawning biomass) cruise (Hedgecock et al. 1989); we have confirmed this with anchovies collected in four subsequent cruises (Hedgecock et al. 1994). In an attempt to understand the biological basis of this geographic variation, we expanded our study of 1984 and 1985 winter-cruise material to include much larger samples and analysis not just of allelic variation but also of morphometric and life-history variation. We report here the results of these latter analyses; the relationship of this variation to allozyme heterogeneity is presented elsewhere in this volume (Hedgecock et al. 1994). The different year classes represented in the material from the two winter cruises differ in the amount and ontogenetic timing of their experience of the 1982–84 major California El Niño event, and we sought in their morphological responses to that experience an “El Niño signature.” Such effects have been reported previously for anchovies (Fiedler et al. 1986; Butler 1989) and other fishes (references in DeMartini 1991).

Thus, the objectives of this study are to ascertain the relative contributions of interannual and geographic differences to individual variation in size, morphometrics, and somatic and reproductive condition, and to the covariation of these variables. We find unanticipated correlations of morphometrics with somatic condition, and of reproductive condition with size and reproductive allometry. For all variables, geographic variation is unexpectedly great but of variable spatial scale. Although there are signs of pervasive influence of temperature, evidence for an El Niño signature is equivocal.

TABLE 1
 Station Data for Northern Anchovy Collection

Year	Station ^a		CalCOFI coord.	n ^b	Percent female	Age, SD ^c	Standard length, SD
	Symbol	No.					
1984	A	4612	65:50.5	117	15.4	1.598, 0.901	111.5, 11.1
	B	4655	90:28	48	81.2	0.917, 0.539	100.3, 11.0
	C	4665	91.7:27	70	27.1	0.414, 0.551	84.1, 6.7
	D	4662	91.7:33	120	44.2	1.017, 0.389	104.7, 6.1
	E	4660	90:56	120	37.5	1.183, 0.518	118.3, 6.2
	F	4671	93.3:41	179	33.5	1.017, 0.326	107.3, 5.5
	G	4689	105:30	116	14.7	0.828, 0.622	101.4, 9.0
1985	H	4707	76.7:54	116	60.3	0.871, 0.880	96.0, 6.0
	I	4708	76.7:56	119	47.9	1.975, 1.298	98.9, 6.2
	J	4719	85:38	120	43.3	1.058, 0.781	103.9, 5.2
	K	4729	87.5:34	118	46.6	1.017, 0.795	95.9, 8.7
	L	4722	85.8:43	118	70.3	0.576, 0.821	117.0, 7.2
	M	4725	87.5:55	119	49.6	0.328, 0.489	105.9, 6.6
	N	4726	87.5:53	120	59.2	0.358, 0.515	109.3, 6.0
	O	4763	96.7:50	117	54.7	1.675, 0.981	118.9, 6.9
	P	4766	98.3:39	119	55.5	1.319, 0.882	108.2, 5.7
	Totals				1836	45.1	1.028, 0.872

^aLetter symbols and CalCOFI coordinates for stations as in figure 1A.

^bThe number of fish for which data were complete.

^cAge, SD is the average otolith score and its standard deviation.

MATERIALS AND METHODS

Samples

Samples were obtained at a total of 16 midwater-trawl stations in the winters of 1984 and 1985 by CalCOFI cruises 8403 and 8502 aboard the RV *David Starr Jordan* of the NOAA Southwest Fisheries Center (La Jolla). Localities are shown in figure 1A, and sample details are given in table 1; other station information including sea-surface temperature and depth of bottom are available on request. 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.

Specimens were partially thawed a few at a time and held under ice until measured. This procedure prevented undue warming of tissue samples removed subsequently for allozyme electrophoresis and minimized uncontrolled morphometric variation from differential thawing. All measurements and counts of any one type were made by the same person.

Measurements

Standard length (from snout to end of hypurals) was measured to the nearest mm with a mounted rule, and the following other morphometric characters were measured to the nearest 0.1 mm with vernier calipers: six lengths from the snout to (1) the anterior margin of the orbit (preorbit), (2) the posterior edge of maxilla, (3) the posterior edge of the operculum, (4) the supraoccipital border, (5) the dorsal fin origin, and (6) the vent;

followed by measurement of the anteroposterior orbit diameter, the maximum head width, the minimum body depth at pectoral girdle, and the length of the anal-fin base.

Total wet weight was recorded to the nearest 0.1 g. After removal of tissues for electrophoresis, otoliths were removed for ageing, and sex and gonad wet weight (to the nearest 10 mg in a tared dish) recorded. Gonads were oven-dried to crispness, reweighed, and the tare rechecked. Somatic wet weight was entered into the data set as total wet weight minus gonad wet weight.

Sagittal otoliths were cleared overnight in 2% KOH, rinsed in deionized water for one or more days, air-dried, and stored by pairs in individual gelatin capsules in envelopes labeled by station. Each pair was placed under water in a separate well (1 cm diameter, painted black) drilled in plexiglass. Otolith annuli (age) were counted under a binocular dissecting microscope with incident illumination, following the methods of Collins and Spratt (1969). Comparison of early counts with those by an experienced California Department of Fish and Game scorer showed 92% overall agreement, dropping to 75% for a selected sample of older fish (Allen Grover, pers. comm.). Anchovies with age = 0 are approaching one year old; a derived variable—year class—was calculated as (year of sampling) - (age + 1).

Analysis

The BMDP multivariate statistical software package (Dixon et al. 1988) was employed for all analyses. Screening of outliers was done with bivariate plots of

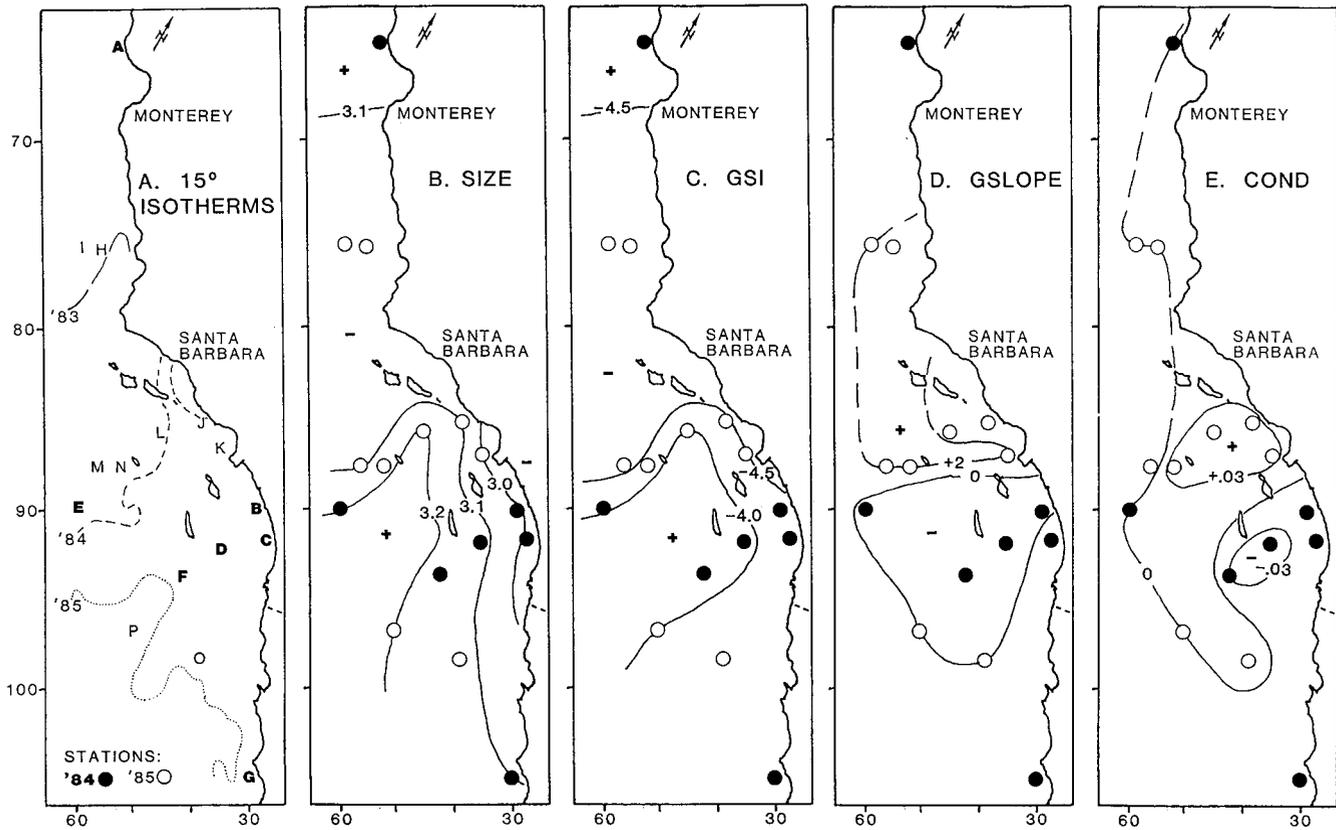


Figure 1. A, 1984 (*bold*) and 1985 CalCOFI winter cruise anchovy sample stations and 15°C sea-surface isotherms for winter 1983–85 (from Fiedler et al. 1986). B–E, contours of equal subsample (age classes within stations) means for life-history variables. Filled circles represent 1984 stations. In B, contours of mean size (table 1) are at approximately 10% intervals for unlogged morphometric variables; 3.1 corresponds roughly to an average fish of grand geometric mean standard length = 105 mm. In C, a difference in mean gonadosomatic index, GSI, of 0.1 again represents a difference of 10% in the unlogged ratio. In D, GSI slope (GSLOPE) = 0.0 corresponds to an allometric coefficient of 1.0. In E, contours of subsample-mean condition are residuals of regression of ln(somatic wet weight) on ln(standard length). Ordinate is CalCOFI coordinate cardinal line; abscissa is CalCOFI station line (for relationship to longitude and latitude see Eber and Hewitt 1979).

variables on standard length and sometimes other variables. Treatment of outliers, except for the variables anal-fin-base length and gonad wet weight, was based on a branching protocol. Very short anal fin bases noted at the time of measurement were remeasured and retained in the data set after incidence of short anal fin base was found to vary geographically. Residuals from regression of female gonad wet weight on gonad dry weight were bimodally distributed; the upper, smaller mode contained females with obviously hydrated oocytes.

For each fish with a complete set of 11 morphometric measurements ($n = 1,912$), residuals for analysis were obtained from predictive multivariate regression of the natural log of each trait on sex and size. Size was defined as the mean of the logs of the 11 morphometric traits (Mosimann 1987). The pooled regression slope rather than the common within-sample slope was used (cf. Reist 1986), because the average difference between the two slopes was small and unbiased. Four other derived variables are used in the analyses: (1) condition—the residual of the predictive regression of ln(somatic wet

weight) upon ln(standard length); (2) gonadosomatic index, $GSI = \ln(\text{gonad dry weight}) - \ln(\text{somatic wet weight})$; (3) a gonad hydration index, $GHI = \ln(\text{gonad wet weight}) - \ln(\text{gonad dry weight})$; and (4) a measure of reproductive allometry—GSI slope, the coefficient from the regression of GSI upon ln(somatic wet weight). This regression was done separately for each age-class within each station. Ponderal measures of reproductive condition were employed because of the impracticality of histological examination on so large a collection of fish. **Throughout the remainder of this paper the names of traits will refer to the logged and otherwise adjusted variables described in this paragraph, not to the raw measurements themselves.**

Principal components analysis (PCA) of the 11 morphometric residuals was followed by both orthogonal and oblique (direct quartimin) rotations, with parameters suggested by Frane et al. (1988). Orthogonal and oblique rotation yielded similar sets of factors; only the results of orthogonal rotation are reported herein.

Mixed-model maximum-likelihood analyses of vari-

ance (ANOVAs; Jennrich and Sampson 1988) were performed to analyze effects of year, age, temperature, station, and interactions upon the dependent variables, size, condition, GSI, and morphometric factors obtained from PCA.

Bivariate plots of pairs of factor scores, etc., segregated by sex where appropriate, were made for 64 subsamples consisting of each age-class within each station. The distribution of numbers of individuals (n) among subsamples was multimodal, with one gap between $n = 11$ and 14, separating peaks at $n = 9$ and 17. There were 37 subsamples with $n > 13$; means and other statistics from subsamples with smaller n were much more variable. Throughout this paper, subsample means are for those subsamples with $n > 13$. The question of within-subsample heterogeneity was addressed by Levene's test for heterogeneity of variance within year class and by intercorrelations of variances of factor scores and size.

A new data set was constructed of subsample means of factor scores and size, condition, GSI, GSI slope, as well as other variables. These included year, sea-surface temperature, year class, age, depth of the bottom under station, distance from nearest mainland, and the long-shore CalCOFI line coordinate (figure 1A). ANCOVA of subsample means among stations after correction, where appropriate, for year, age, size, and the five morphometric PCA factors tested equality of differences among subsamples within and among stations.

Spatial distributions of GSI slope and mean size, GSI, condition, and morphometric PCA factors for subsamples were examined with the aid of contours fitted by eye (figures 1 and 4). A contour passing through a station indicates that at least one subsample mean at that station lay on either side of that contour. Dashed lines indicate conjectural contour positions. As a control on this contouring procedure, subsample means were randomized over stations, and the resultant random contour maps were compared with the original contour maps. Spatial autocorrelation (Rossi et al. 1992) of paired 1985 subsample means, classified into distance categories, was also employed to estimate the spatial scale of geographic variation for each dependent variable.

RESULTS

Sex, Age, Year, and Station Information

Among individuals, sex and age were uncorrelated. Age and year (of sampling) were uncorrelated as well, but a significantly higher proportion of females was found in 1985. Sex ratios and age statistics by station are given in table 1. Among the 1984 stations were those with both highest and lowest sex ratios; conversely, those with both lowest and highest mean age were from 1985. Sea-surface temperature among stations was significantly lower in 1985 than in 1984 (13.7 vs 15.2°C; $t = 3.27$, d.f. 14;

$p < 0.005$). As expected, temperature was correlated with CalCOFI line ($r = +0.701$), and distance offshore with depth ($r = +0.749$).

Size and Condition

Initially we used raw standard length as a measure of size, for detecting outliers and comparison with earlier studies. Subsample-mean standard length varied from 83 mm (station C, age 0, figure 1A) to 123 mm (station P, age 2). Within stations, different subsamples often had distributions with one or more similar modes of standard length. Within a subsample, standard length was unimodally distributed with a minimum coefficient of variation of 4%–5%, but occasionally the distribution was obviously bimodal with a correspondingly larger coefficient of variation, suggesting heterogeneity of such subsamples (see below).

For subsequent analyses we used the consensus measure of size defined in Materials and Methods, as suggested by Mosimann (1987). Sex differences accounted for 1.8% of the total variance among individuals in size, attributable to a higher proportion of females in some of the samples of larger anchovies. Within a subsample there was little difference in size between the sexes, and they were combined for analysis. Somatic wet weight was nearly isometric with the cube of standard length. Condition was weakly correlated with sex (1.9% of variance). Interannual and geographic variation in these and other dependent variables is described below.

Reproductive State

In mature females, the gonad-hydration index GHI can double during the day prior to ovulation (figure 2A; Hunter et al. 1985). For this reason we used dry gonad weight for the gonadosomatic index (GSI). Oocyte hydration was only seen among females with $GSI > -4.6$, which was close to the grand mean GSI in the population (corresponding to a [gonad dry weight]/[somatic wet weight] ratio of 0.01). Despite the difference in behavior of GHI between females and males (figure 2A), there was little difference between sexes in GSI (sex accounting for 0.7% of total variance) or GSI slope, and the sexes were combined for further analysis of reproductive state. Subsample GSI slope showed great heterogeneity. GSI slope, the measure of dry gonad allometry, was negatively correlated with subsample-mean size and especially with mean GSI, even becoming negative at high GSI (figure 2B); correlations with temperature are discussed below.

Principal Components Analysis (PCA) of Morphometrics

PCA of morphometric measures adjusted for sex and size yielded five components with eigenvalues greater

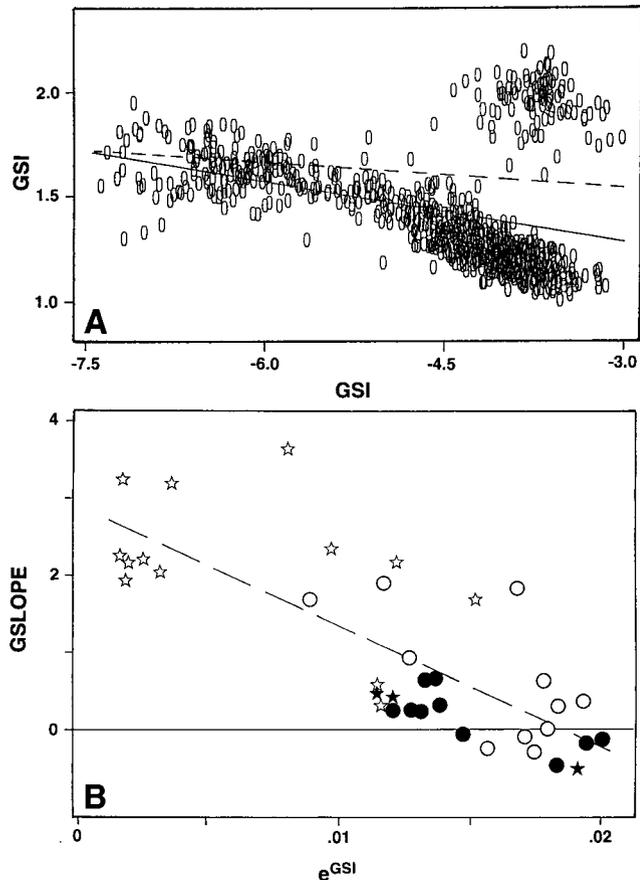


Figure 2. A, gonad hydration index, GHI, as a function of dry gonadosomatic index, GSI, for individual female anchovies. *Solid lines* are regressions for all females; *broken lines* are regressions for all males. Relative water content of gonad decreases more rapidly with maturation among females; cluster of points at upper right represents females with obviously hydrated oocytes. B, GSLOPE, slope of regression of GSI upon $\ln(\text{somatic wet weight})$, as a function of subsample mean GSI, given here on the abscissa as its antilog to linearize the relationship. 1984 subsample points are filled; *circles* and *stars* differentiate subsamples with and without females with hydrated oocytes, respectively. An ordinate of 0 corresponds to GSI isometry.

than 1.0, which together accounted for 72% of total variance. Orthogonal rotation yielded five easily interpretable factors (table 2):

1. *Body length* (MI), with high positive loadings by standard length and lengths from snout to dorsal fin origin and from snout to vent
2. *Jaw length* (MII), with positive loadings primarily by lengths from snout to maxillary tip and from snout to operculum border
3. *Anal-fin-base length* (MIII), with a negative contribution from length from snout to supraoccipital border
4. *Body depth* (MIV), with positive loading by that trait alone
5. *Orbit/preorbit length* (MV), expressing positive correlation with orbit diameter and a complementary negative loading by length from snout to the front of the orbit

Analyses of Variance (ANOVAs)

Maximum-likelihood ANOVAs with age as fixed effect, and year and the interaction age \times year as random effects indicated a significant age effect for GSI; year effects for condition, GSI, body length, and anal-fin-base length; and age \times year effects for size, jaw length, and body depth. Figure 3 illustrates these differences between age classes by year of collection. However, when station (nested in year) is added to the model as a random effect, station alone remains as a highly significant effect; only for size are age and age \times year accorded any significance. The large differences in figure 3 may represent station sampling effects. Table 3 summarizes likelihood-ratio tests of maximum-likelihood ANOVAs with age and temperature as fixed effects, and station within

TABLE 2
 Loadings on Five Factors from Principal Components Analysis of Adjusted Measurements of Morphometric Traits, after Orthogonal Rotation

Trait	Morphometric PCA factors					Comm. ^a
	Body length (MI)	Jaw length (MII)	Anal-fin-base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	
Vent	0.809*	-0.011	-0.047	0.014	-0.014	0.657
Dorsal fin origin	0.737*	-0.007	0.001	-0.120	-0.061	0.561
Standard length	0.761*	-0.210	0.264	0.148	-0.059	0.718
Operculum	0.039	0.828*	-0.100	0.015	0.063	0.701
Maxillary	-0.215	0.786*	-0.094	-0.041	0.009	0.674
Anal-fin base	-0.164	-0.349	0.862*	-0.067	-0.002	0.897
Supraoccipital	-0.318	-0.043	-0.607	-0.164	0.005	0.498
Body depth	-0.075	-0.005	0.038	0.865*	-0.182	0.789
Orbit diameter	-0.269	0.067	-0.124	-0.267	0.837*	0.864
Preorbit	-0.386	0.027	-0.257	-0.537	-0.611	0.877
Head width	-0.021	-0.463	-0.448	0.442	0.164	0.637
v_p^b	0.199	0.150	0.136	0.126	0.105	

*Loadings greater than 0.7.

^aThe communality or squared multiple correlation of a trait with the factors.

^bThe proportion of total variance explained by each factor.

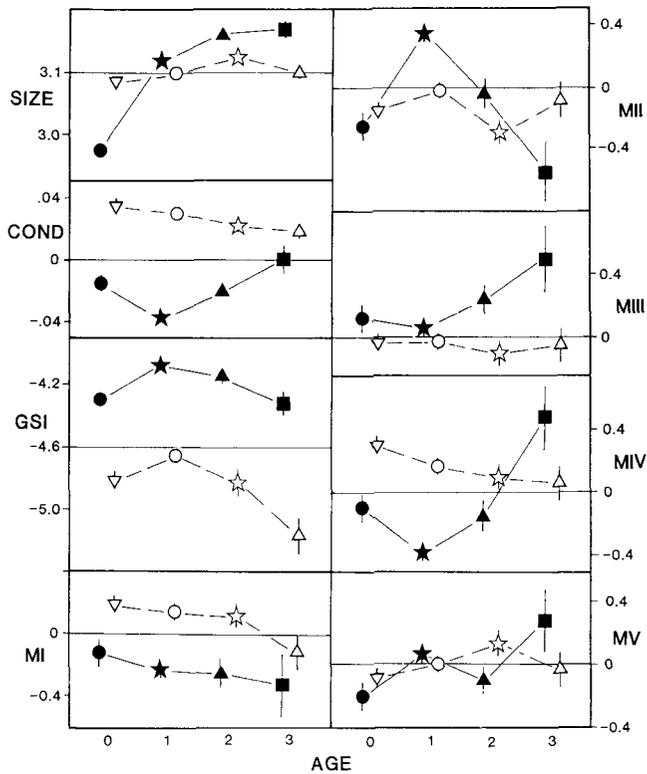


Figure 3. Dependent variable means for year classes within years. Year classes are as follows: 1980, squares; 1981, triangles; 1982, stars; 1983, circles; 1984, inverted triangles. Solid line connects those from 1985. SIZE = consensus size measure; COND = condition factor; GSI = gonadosomatic index. PCA factors, MI-MV, are body length, jaw length, anal-fin-base length, body depth, and orbit/preorbital length. Dimensions are described in text and figures 1 and 4. Standard error bars are misleadingly small; differences between years may be station sampling effects (see Results, ANOVAs).

temperature as a random effect. The overwhelming effects of station can be seen, yet temperature retains some effect on GSI, body length, and body depth.

Correlation Analysis

Correlations of subsample means of dependent variables, among themselves and with independent variables,

are presented in table 4. Two general patterns are seen: (1) condition is positively correlated with body length and body depth, and negatively correlated with jaw length and orbit/preorbit length; and (2) GSI slope is negatively correlated with size and GSI, which are themselves positively correlated. Body length, body depth, GSI slope, and condition subsample means are similarly correlated positively with year and negatively with temperature; mean GSI shows the opposite pattern. Jaw length and orbit/preorbit length are uncorrelated with the independent variables, but jaw length is highly significantly negatively correlated with body depth as well as with condition. Anal-fin-base length is negatively correlated with CalCOFI line, depth, and perhaps temperature; size is positively correlated with distance offshore, depth, and age. Notwithstanding their mutual (but opposite) correlation patterns with year and temperature, GSI and condition were negligibly correlated. Nevertheless, figure 3 suggests a high degree of negative correlation between reproductive and somatic condition among age-classes within years, which is so ($r = -0.847$; d.f. 6, $p < 0.01$).

Spatial patterns

The spatial distribution of subsample-mean size is shown in figure 1B; the contours, at approximately 10% increments in linear dimensions, reflect highly significant differences among subsample means. As noted by earlier workers (references in Parrish et al. 1985), anchovies are generally somewhat larger offshore and over deeper water (table 4), but in contrast to earlier findings, our samples showed no gradient of increasing size from southeast to northwest.

Spatial pattern for GSI subsample-means was similar to that of size (compare figures 1B,C). Notwithstanding the correlations of GSI slope with GSI and size, its spatial pattern was somewhat different (figure 1D). GSI slope >2 (figure 2B) was seen only in a northern group

TABLE 3
 Maximum-Likelihood Analyses of Variance for Traits and Factor Scores of 1,836 Northern Anchovies

Trait or factor	Age (d.f. 3)		Temperature (d.f. 3)		Station (temp) (d.f. 1)	
	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Size	159.75	0.000	1.68	0.642	1432.46	0.000
Condition	1.16	0.762	6.13	0.106	742.75	0.000
GSI	9.96	0.019	8.58	0.035	922.80	0.000
Body length	5.17	0.160	18.14	0.000	11.57	0.001
Jaw length	11.99	0.007	2.25	0.522	245.19	0.000
Anal-fin-base length	1.54	0.673	4.65	0.200	64.15	0.000
Body depth	2.45	0.485	8.41	0.038	171.69	0.000
Orbit/preorbit length	2.24	0.525	1.22	0.749	56.34	0.000

Age (otolith score) and temperature (rounded to nearest degree) are fixed effects, and station within temperature is a random effect in mixed-model ANOVAs. χ^2 is the difference between log-likelihood estimates ($-2 \cdot \ln[\text{maximum likelihood}]$) for the full model and for the model with that effect set to zero; *p* is the associated probability, given the assumptions of the ANOVA. Variables are size, condition, GSI, and five PCA orthogonally rotated morphometric factors (table 2).

TABLE 4
 Correlations among Mean Traits or PCA Factor Scores and Independent Variables for Subsamples of Northern Anchovy

	Body length (MI)	Jaw length (MII)	Anal-fin- base length (MIII)	Body depth (MIV)	Orbit/preorbit length (MV)	Size	Condition	GSI	GSI slope
MII	-0.099								
MIII	0.070	0.027							
MIV	0.228	-0.470*	0.200						
MV	0.002	0.169	-0.275	-0.187					
Size	-0.014	-0.037	-0.124	0.268	0.139				
Cond	0.401*	-0.512*	-0.143	0.524*	-0.354*	0.019			
GSI	-0.163	-0.050	-0.149	0.286	-0.129	0.556*	0.008		
Gslope	0.399*	-0.010	0.047	0.021	-0.130	-0.495*	0.209	-0.726*	
Year	0.566*	-0.093	-0.222	0.374*	0.091	0.005	0.504*	-0.371*	0.554*
Dist	0.410*	0.071	-0.191	-0.074	0.314	0.570*	-0.174	0.227	-0.059
Line	-0.149	0.091	-0.522*	-0.300	-0.167	0.043	-0.031	0.464*	-0.277
Depth	0.254	-0.048	-0.387*	0.021	0.321	0.492*	-0.115	0.284	-0.100
Temp	-0.435*	0.129	-0.346*	-0.483*	0.209	0.031	-0.472*	0.465*	-0.598*
Age	-0.202	-0.015	0.131	-0.057	0.271	0.362*	-0.089	-0.025	-0.273
YC	0.436*	-0.030	-0.215	0.222	-0.191	-0.309	0.311	-0.151	0.491*

Means are for 37 subsamples with more than 13 fish. Variables are: five orthogonally rotated morphometric PCA factors, size, condition, GSI, GSI slope, year (of sampling), distance offshore, CalCOFI line, depth of bottom, sea-surface temperature, age, year class (YC). With 35 d.f., r outside the range $-0.325 < r < 0.325$ (asterisks) is associated with $p < 0.05$ when the distribution is bivariate normal.

TABLE 5
 Analysis of Covariance of Subsample Means for Traits or Factor Scores

Trait or factor	V%	F	p
Size	91.7	30.75	0.000
Condition	94.2	38.84	0.000
GSI	92.0	22.11	0.000
Body length	73.7	3.54	0.014
Jaw length	70.7	2.22	0.078
Anal-fin-base length	61.4	1.36	0.287
Body depth	79.3	6.11	0.001
Orbit/preorbit length	77.7	3.61	0.013

Variables corrected for year, age, size, and PCA factors, where appropriate. V% is percent of total variance among subsample means attributable to station differences; F is ratio of station mean square to subsample-within-station mean square; p is probability that differences among stations are similar to differences among ages within stations. Numerator degrees of freedom are 12; denominator d.f. are 19 (size), 18 (condition, GSI), and 14 (PCA factors).

of 1985 subsamples of maturing anchovies lacking females with hydrated oocytes. All but one of the negative GSI slopes were observed in subsamples containing females with hydrated oocytes, and these GSI slopes did not appear to be random deviations from zero; they formed a compact cluster (figure 1D).

Geographic patterns in subsample means for the five morphometric factors are shown in figure 4. The contours are in standard deviations (SD) from the grand mean (=0) of the standardized factor; 0.5 SD is equivalent to $p < 0.05$ for a t test of subsample mean with $n > 17$. The pattern for body depth (MIV, figure 4D) is strikingly similar to that for condition (cf. figure 1E).

Autocorrelation of subsample means for 1985 declined with distance, from a within-station r of +0.6 to +0.95 to an r near zero at 100–200 km for size, condition, GSI, GSI slope, body depth, and orbit/preorbit length. For

morphometric factors body length, jaw length, and anal-fin-base length, within-station correlation was lower (cf. table 5), and r declined to zero within the first 100 km. For all variables, randomization of subsample means over stations resulted in more complex contour maps, usually with several equally likely alternative configurations; spatial autocorrelation was negligible, as expected.

Heterogeneity within Stations

The null hypothesis of the ANCOVAs of subsample means (table 5) is that even though differences between stations may be large, they are no greater than differences between subsamples within stations. F-statistics were highly significant for size, GSI, and especially condition; they were less so for body length, body depth, and orbit/preorbit length; and they were not significant for jaw length and anal-fin-base length. Since significant differences between stations do exist (table 3), these results indicate that some heterogeneity among subsamples within stations also exists for jaw length and anal-fin-base length.

For the 1982 year class, Levene's tests for heterogeneity of variance among subsamples were significant for size ($p < 0.001$) and the principal components body length, jaw length, body depth, and orbit-preorbital length ($p < 0.05$). For the 1983 year class, Levene's tests were significant for size ($p < 0.001$) and anal-fin-base length ($p < 0.01$). For the 1984 year class, Levene's tests were significant for size and jaw length ($p < 0.001$) and body length ($p < 0.05$). Thus, of 18 such tests (excluding year classes before 1982 for which sample sizes were small), 10 were associated with $p < 0.05$. Heterogeneity within certain subsamples was further suggested by positive cor-

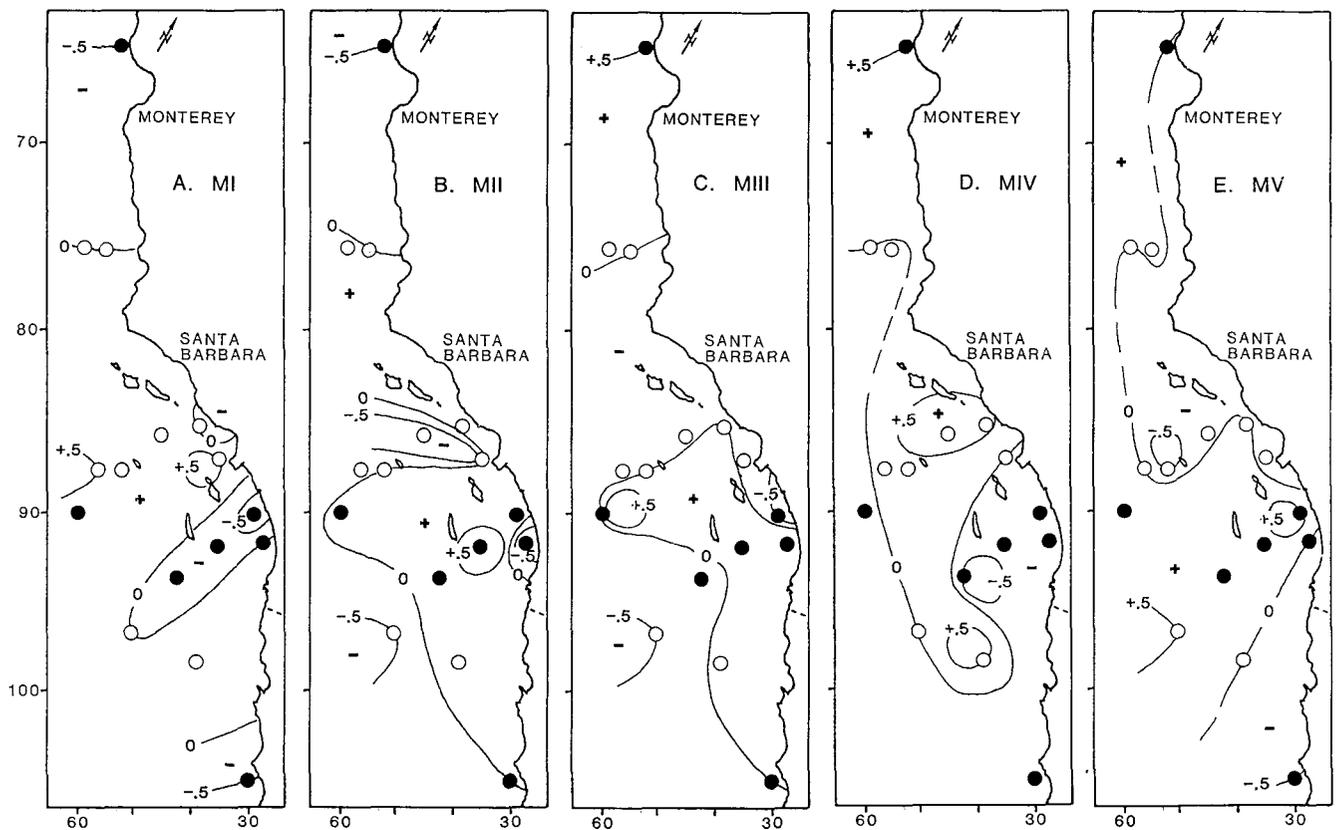


Figure 4. Contours of equal subsample means for orthogonally rotated morphometric factors MI-MV (body length, jaw length, anal-fin-base length, body depth, and orbit/preorbital length), in standard deviations of the standardized factor. Coordinates are CalCOFI coordinate cardinal and station lines as in figure 1. Filled circles are 1984 stations; open circles are 1985 stations.

relation of subsample variances between factors and between factors and size. Of 15 such intercorrelations of subsample variances, 12 were positive ($\chi^2 = 5.40$, $p < 0.025$; the mean of z -transformed intercorrelations was significantly greater than zero by t test, $p < 0.01$). Correlation was hardly reduced when subsample variances were adjusted for sex differences, nor did it appear to result from differences in subsample size.

DISCUSSION

Morphometrics and Condition

We chose the mean of the logs of the 11 morphometric measures as a general size variable, as suggested by Mosimann (1970, 1987). Because we were interested in variation in different parts of a continuously distributed population (rather than among isolated populations; Strauss and Bond 1990), we removed by regression as much as possible of the variance due to size before extracting principal components. To reduce variance introduced by the radical changes in shape accompanying sexual ripening, particularly the hydration of oocytes, we measured body depth at the pectoral girdle, rather than at a more representative pelvic location. We hoped

thereby to recover from each anchovy measures of "shape" independent of size. We were indeed successful in avoiding substantial correlation of morphometric factors with size and with gonadal condition as measured by GSI.

However, subsample means of at least three of the five factors were each significantly correlated with somatic condition (table 4). That body depth was so correlated is reasonable; variation in the body-length factor, comprising, in part, measures of both length and depth, may be similarly explained. Negative correlation of condition with jaw length (table 4) has no such easy interpretation; jaw length was also negatively correlated with body depth, and these correlations of jaw length were in no case weakened after regression upon age, distance offshore, CalCOFI line, depth, temperature, and/or year (unpublished results).

The engraulids' elongate maxillae and opercula are associated with their unique filter-feeding method, in which the buccal and pharyngeal chambers are greatly expanded. Northern anchovies either attack prey individually or filter feed, depending upon prey size and abundance (Leong and O'Connell 1969); one might speculate that the temperature-independent association between

jaw length and condition and body depth is somehow trophic in origin. Part of the covariance discussed in the preceding paragraph arises from similarities among the three neighboring Southern California Bight subsamples, which together constitute most of the 1984, age 1 group (figure 1A, stations B, D, and F; figure 3, filled stars). These fish share a combination of low mean condition, short and slender body, long jaw, and large orbits (figures 1 and 4), which we call the "lean and hungry look" (cf. Blaber et al. 1981 for a similar case in a clupeid).

Size and Shape

Much theoretical and practical effort has been expended in pursuit of precise differentiation of variables of size and shape (cf. Sampson and Siegel 1985; Bookstein et al. 1985; Reist 1986; Mosimann 1987; Strauss and Bond 1990). In light of the findings discussed above, we perceive a certain futility in this, at least in the study of individual variation in continuously distributed populations, growing and reproducing in spatially and temporally variable environments. However they are defined, size and shape of anchovies, both of which include aspects of somatic and reproductive condition, fluctuate greatly during the course of the year and from place to place and year to year. Size and shape are dynamic and all of a piece, and cannot be rigorously separated.

Therefore, we have no illusions that size and our morphometric factors measure absolutely distinct attributes of anchovies. Nevertheless, particularly in correlations with condition and GSI, they reflect different patterns of individual, temporal, and spatial variation. Condition was independent of size but was associated with body length, jaw length, body depth, and orbit/preorbit length (table 4). GSI was highly correlated with size (as was GSI slope, negatively), but was independent of condition and the morphometric factors. Inclusion of pelvic points among the morphometric measures probably would have reunited GSI with morphometrics and helped to provide a better picture of the complex exchanges between somatic and reproductive condition.

Somatic and Reproductive Condition

There is currently both theoretical and practical concern over the nature of trade-offs between reproductive investment and somatic condition and growth, particularly with respect to individual variation (Dygert 1986; Rijnsdorp 1990; Nelson 1993). Although significant *negative* covariance of GSI and condition among age classes within years (figure 3) seemingly supports a trade-off hypothesis, there is little correlation of the two either among individuals (unpublished analyses) or among subsample means.

It is remarkable that—notwithstanding the positive slopes of GSI on somatic wet weight in subsamples with

lower mean GSI—negative GSI slopes are found when GSI is high (figure 2B). The negative correlation of GSI slope with GSI may be caused by temperature (table 4). It appears that with colder temperatures, maturation, especially of the smaller anchovies in a year class, is delayed and perhaps prevented entirely. When temperatures are such that all may mature, relative gonad size may be larger in smaller fish. Our analysis of data collected in the Los Angeles Bight in the winters of 1978 and 1979 (Hunter and Macewicz 1980, table 4) suggests that batch fecundity obeys a similar rule. The slope of the regression of $\log(\text{number of hydrated eggs divided by somatic weight})$ upon $\log(\text{somatic weight})$ in 1978 is -0.176 , significantly different ($p < 0.002$) from the slope of $+0.401$ in the distinctly cooler winter of 1979 (12° – 13° vs 14° – 15° C; Hewitt and Methot 1982). Such size-dependent responses are examples of individual variation in reproductive reaction-norm allometry (Nelson, in press), with consequences for demographic response to temperature and trophic change. Puzzling and misleading patterns of response may result from lumping samples from different years or places (e.g., Parrish et al. 1986, figures 4B, 4C, 10).

Heterogeneity within and among Stations

In this paper, age classes within stations (subsamples with $n > 13$) have been treated as independent samples. For a sedentary species this would often be untenable. But the northern anchovy is a pelagic species capable of moving great distances (Haugen et al. 1969) and not known to return to localized spawning grounds as herring do. Common natal locality or even similar later experiences among different year classes spawning in the same area remain hypotheses to be tested. A priori, one might expect less similarity among anchovies of different ages from the same station than among members of the same year class from nearby stations.

For size, condition, GSI, and body depth, anchovies of different ages are more homogeneous within than among stations (table 4). This might result from assortative grouping, such as by swimming speed, or it might reflect common experience among year classes found at the same locality. There is evidence for both processes. On the one hand, at several stations, different ages displayed similar bimodal distributions of size. Also, heterogeneity of variance among subsamples within a year class was coupled with covariation of subsample variances for morphometric factors and size. These findings all imply that certain midwater-trawl hauls sampled several homogeneous groups with disparate size and morphometric characteristics. Such contiguous but dissimilar groups may have formed by assortative clustering, and may represent the "elementary populations" hypothesized by Lebedev (1969). On the other hand is the ev-

idence of mesoscale spatial autocorrelation (100–200 km for size, condition, GSI, GSI slope, body depth, and orbit/preorbit length). Such similarities among neighboring stations are more difficult to explain by assortative grouping, and therefore imply common experience.

Contours on maps of subsample means randomly reassigned to stations were more complex than those in figures 1 and 4 and often not topologically uniquely determined. Usually such randomized maps had several stations with more than one contour passing through them, signalling heterogeneity among the subsample means reassigned there. Such stations are seen only twice in the observed contour maps: for jaw length at station K and for anal-fin-base length at station E (figures 4B,C). For these factors, variance in subsample means was little different within and among stations (table 5), and within-station means were not highly autocorrelated. If differences in jaw length or anal-fin-base length are established early in life, they 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. Thus, within-station heterogeneity for these factors could imply low spawning-site fidelity, and heterogeneity of origin of the different year classes at a station. These disparate year classes, through common environment and assortative grouping, later come to resemble one another in other ways (size, condition, GSI, body depth).

Spatial and Temporal Variation in the California Current System

Spatiotemporal patterns in anchovy life-history and morphometric characters must be related somehow to variation in the oceanographic regime along California and northern Baja California. This regime (Hickey 1979) is dominated by the southward-flowing California Current, which moves offshore at Point Conception (CalCOFI line 80) and returns onshore near line 100–110 (figure 1A). Inshore of this in the Southern California Bight is a semipermanent counterclockwise gyre. A northward-flowing countercurrent over the continental slope reaches the surface inshore north of Point Conception in fall and winter, as the Davidson Current (McLain and Thomas 1983). In spring and summer north of Point Conception, and most of the year south of line 100, northwest winds cause cold and nutrient-rich upwelled water to spread out locally offshore. Recent evidence suggests incursion of nutrient-poor warm water from the southwest into the bight during the second half of the year (Pelaez and McGowan 1986). Interannual variation of concern is the California El Niño that began in late 1982 and abated somewhat during the 1984 spawning season, but which may have had the largest positive temperature anomalies in

summer 1984 (Fiedler et al. 1986; figure 1A shows 15°C winter isotherms for 1983–85). These changes may have been associated with northward advection, even at several hundred meters' depth (Norton et al. 1985), although there are certain problems with this hypothesis (McGowan 1985).

Variation in production may be related to these annual and interannual patterns of water movement. Fiedler (1983) and Pelaez and McGowan (1986) find correspondences between episodic zones of high surface phytoplankton-pigment concentration seen in satellite images and infrared images of areas of cold (upwelled) water. The latter include an inappropriately named "hot spot" over the submarine peninsula extending south-southeast from Point Conception along CalCOFI offshore coordinate 50 to the latitude of San Diego. Although El Niño events are associated with reduced nutrients, the biological response is likely to be complex and nonuniform and to involve delays at each point (McGowan 1985). Certain subtropical plankton and nekton appear far to the north (Percy et al. 1985). Again, there is room for interpretation about how much of this reflects northward advection vs *in situ* response by plankton (cf. Roesler and Chelton 1987) and active "following of isotherms" by certain nektonic species.

For each dependent variable in our analysis, spatial variation accounted for a much greater proportion of the variance than did interannual variation. Within a station, ages tended to have similar means (although occasional large differences were found with jaw length and anal-fin-base length in particular), and this was often true of neighboring stations as well (e.g., those sharing the "lean and hungry look"). Some or all of the effects of year of sampling may be artifacts of discrete sampling from a geographically variable population, but some of them may be real, reflecting interannual differences in temperature in particular.

We discern two seemingly independent temperature-correlated patterns, one shared by size, GSI, and GSI slope, and another related to condition, body depth, and body length (figures 1 and 4; cf. table 4). Neither consists of a simple cline such as that of temperature with CalCOFI line. Association with temperature accounts for less than 40% of the variance in any of these dependent variables, but sea-surface temperature at capture may be a poor proxy for the physiologically relevant thermal history of an anchovy. The temperatures likely to have significant impact on winter somatic condition and gonadal maturation are those in the previous growing season, which may not be related to temperatures at capture time. And if anal-fin-base length reflects temperature-dependent meristic differences established early in life (McHugh 1951), the connection with station sea-surface temperature is even more remote.

One might argue, then, that the significant correlations we see between morphological and reproductive traits and temperature are a minimum estimate of temperature-associated direct and indirect influences upon those variables. Signs of these influences may be found in the spatiotemporal distributions of subsample means (figures 1 and 4). The similar patterns of condition and body depth in particular resemble Pelaez and McGowan's (1986; cf. also Fiedler 1983) patterns of phytoplankton-pigment concentration and sea-surface temperature, differing mainly in offshore extent. One notices a similar "hot spot" of positive values trending southeastward of Point Conception, and inshore of this a northward "incursion" of negative values, including those subsamples characterized by the "lean and hungry look." We surmise that the correlation pattern here is with temperature as an indicator of prior trophic conditions, whereas the influence of temperature upon gonadal maturation, GSI, and GSI slope is more direct. However, the "incursion" also coincides well with sampling in 1984, and the "hot spot" with sampling in 1985. We cannot completely resolve the correlates of interannual and geographic variation in temperature, although we suspect the geographic differences are more important. Thus we conclude that although an "El Niño signature" may be discoverable in adult anchovies, it may be buried amid the disparate causes of geographic variation.

Fidelity to Locality and Water Mass

Fiedler et al. (1986) find "obvious discontinuities" in Department of Fish and Game (DFG) growth data, a sharp drop in size between October 1982 and February 1983, and a corresponding increase between September and November 1984. They suggest that the smaller anchovies caught during this period may have grown more slowly or have been of southern provenance, moving north with El Niño as certain other nekton is known to do (Percy et al. 1985). Our data agree in suggesting a small size for the 1983 year class, age-0 fish caught in 1984 (cf. Butler 1989). Otherwise, we detect no interannual differences in size, although 1984 and 1985 year-class means differed for the size-adjusted principal component MI, a measure of relative body length (figure 3).

Whether anchovies change their location during an El Niño or other warming event depends upon the degree to which they move independently of the water mass, as opposed to either active migration with it or passive advection. The outcome of a warming event will depend upon two sets of alternative conditions: (1) whether there is indeed mass water transport from the south or west or both during a warming event, or rather an *in situ* increase in water temperature; and (2) whether movements are oriented by geographically fixed features, or alternatively by prey density or some correlated en-

vironmental variable. The relative importance of these alternative but not necessarily exclusive possibilities will determine whether winter-cruise samples from the same location are of different provenance in different years, or whether their origins may be the same.

The available evidence suggests both that anchovies can move quite independently of the water mass, and that they possess a degree of spawning-site fidelity. The Sea of Azov population of the European anchovy *Engraulis encrasicolus* spawns in the Sea of Azov, then migrates through Kerch' Strait to winter in the Black Sea; its distribution within the Black Sea evidently varies with winter temperature (Chashchin 1985, and references therein). Thus their movements appear to reflect both environmental tracking and site fidelity, depending upon season. Adults of the northern race of *Engraulis mordax* may winter inshore with the juveniles, then segregate and move offshore for their summer spawning season (Laroche and Richardson 1980). A similar pattern but of opposite phase—southward and offshore movement for winter spawning—has been described for the central subpopulation in the Southern California Bight (Mais 1974). Haugen et al. (1969) interpret northern California recaptures of southern California anchovies and vice versa as implying movement northward in summer and southward in winter, which if true would be counter to seasonal flows of the California and Davidson Currents, respectively.

We do not know to what extent northern anchovies "follow the isotherms," nor to what extent they might combine summertime foraging flexibility with fidelity to winter spawning locality (but see MacCall 1990). But if anchovies captured in 1984 and 1985 had been of greatly different provenance, we would anticipate more pronounced temperature-influenced differences between them, on the order of the geographic variation we have described. Aside from the slower growth of age-0 fish in 1984, we found no appreciable differences in size. The morphometric differences observed between years would certainly have been exaggerated had El Niño presented us in the winter of 1984 with a different kind of anchovy from the south.

ACKNOWLEDGMENTS

The authors thank R. D. Methot for obtaining the samples of anchovies used in this study, Mary Simmons for her help with data entry, and Lynne Stenzel for her roles in data organization and analysis. This research was funded in part by a grant (R/F 98) from the California Sea Grant College Program.

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