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Variation in the condition factors of California pelagic fishes and associated environmental factors

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ABSTRACT

Time series of condition factors for mackerel, *Scomber japonicus*, jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax*, stocks in the Southern California region were compared with time series of oceanographic indices to develop hypotheses concerning physical environmental forcing of the population dynamics and energetics of small pelagic fishes. Mackerel and jack mackerel condition factor time series showed decade-scale variation, whereas those of anchovy showed coherent fluctuations for 1 to 2 years. Mackerel, and to a lesser extent jack mackerel, condition factors were correlated with proxy indices of alongshore advection (sea level), offshore advection (Ekman transport), ambient temperature (shore station temperature), and ambient salinity (shore station salinity). The condition factor of anchovy was much less correlated with environmental variables. Multiple regression analyses which included sea level, upwelling and salinity proxies explained 80% (33%) of the variance in the annual (monthly) condition factor of mackerel. The first-order variation in condition factors of mackerel and jack mackerel suggests that they are responding to very large-scale perturbations of the California Current system which are at least partially described by variations in sea level. The population size of mackerel is apparently also responding to these large-scale perturbations, making it difficult to isolate environmental dependence of condition factors from density dependence. The second-order variation is more regional in nature and unexpectedly it appears to be associated with upwelling in the Baja California region.

Key words: mackerel, jack mackerel, anchovy, condition factors, California current system, climate and fisheries

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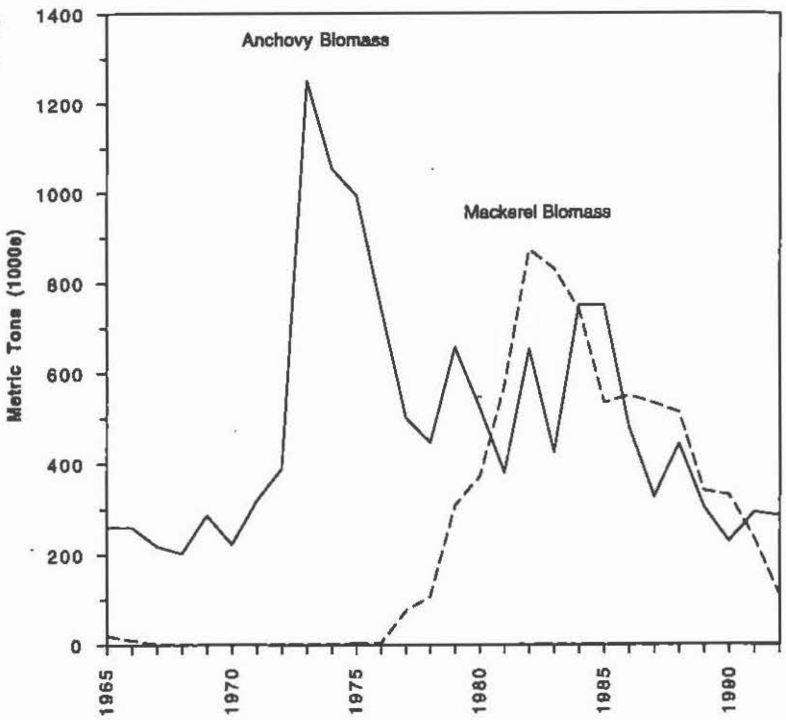
INTRODUCTION

Interannual variation in population biomass of small pelagic fishes is the preoccupation of many fishery biologists and managers; however, variation on longer time scales may have the most significant impact on regional fisheries (Kawasaki, 1983, 1992). Although variability in population size commonly is attributed to conditions affecting the early life history stages (i.e. the recruitment process; Beyer, 1981; Bakun, 1985), it is worth noting that processes affecting rates of the exploited component of the population (particularly those associated with fecundity and natural mortality) have not been excluded as candidates for causality of interannual, and especially interdecadal, variability.

Potential causes of natural variation in the population biomass of small pelagic fishes that act on older fish include environmental forcing, interspecies interactions and density-dependent factors. It is likely that the causative factors act by altering one or more population rates (i.e. growth, mortality, age at maturity, fecundity and recruitment). Although there are numerous studies on growth of adult fishes, variability in adult growth rates of the magnitude necessary to cause large interannual population fluctuations or of the duration necessary to cause decade-scale population fluctuations have not been reported. In fact the present paradigm suggests that growth rates of fishes vary in response to population size rather than the reverse. The lack of studies describing interannual variability of adult natural mortality rates suggests that this research area is relatively intractable. Measurement of interannual variation in the fecundity of indeterminate spawners has not yet been attempted.

Thus, biological time series that can be used to assess biotic and abiotic mechanisms which alter the population rates of post-recruit fishes are limited. One type of data that is available for many fish populations is condition factor (the observed weight of a fish divided by the expected, or average weight, of a fish of the same length). A fish's condition factor is a measure of conditions during some previous period, probably a minimum of several months, and is affected by interactions

Figure 1. Biomass estimates (age 1+) of mackerel (Jacobson *et al.*, 1994) and anchovy (Jacobson and Lo, 1993).



among food availability, physical factors and the physiology of the fish. Food available is further dependent upon environmental conditions, population density, migration, and the geographical location and depth of the habitat. The physiology of fishes is influenced by age, sex, and reproductive state, as well as by abiotic factors (e.g. temperature). Thus it is likely that condition factor of fishes varies in association with growth rate, natural mortality rate, age at maturity, and fecundity. In the small pelagics addressed in the present paper (northern anchovy, *Engraulis mordax*, mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*), seasonal growth in weight varies considerably more than growth in length (Mallicoate and Parrish, 1981), implying that condition factor also will have considerable seasonal variability.

The purposes of this study are: (1) to develop time series of condition factors for mackerel, jack mackerel and northern anchovy, (2) to compare these time series with time series of oceanographic indices in order to (3) develop hypotheses concerning how physical environmental factors affect the condition factors and by implication, the energetics of pelagic fishes in the California Current.

Background

The fisheries for the three pelagic species included in this analysis have had wide decade-scale variability in landings over the period for which condition factor can be determined. The anchovy fishery in California was regulated by a quota for the entire period of the study; however, this did not markedly limit the catch as the quota was reached in only four seasons during the early 1970s, and in each case the quota was increased to prevent stopping the fishery. The Mexican anchovy fishery in Ensenada, which is based on the same stock as the California fishery, developed during the 1970s, reaching a peak of 258 745 t (metric tonnes) in 1981. This fishery was not regulated by catch limitations and recently collapsed. The mackerel fishery in California was in the final stages of collapse at the beginning of the study period (1966). A moratorium was finally established in 1970 by the State of California and it continued until 1977; from 1977 until 1985 the fishery had regulations that lowered the catch rate after a quota had been exceeded. Since 1985 the regulations did not limit the catch unless the estimated population biomass fell below 150 000 t, which it did not do during the period covered in this study. Jack mackerel catches have never been regulated by a quota, and as the catch is minor in relation to estimates of stock size it is not considered to be an indicator of the population biomass (MacCall and Stauffer, 1983; Mason, 1991).

Estimates of population biomass are available for anchovy and mackerel (Fig. 1). Recent anchovy estimates are from a stock synthesis model (Jacobson and Lo, 1993). Cohort analyses are available for part of the 1966–1988 period for mackerel (MacCall *et al.*, 1985; Prager and MacCall, 1988; Jacobson *et al.*, 1994). Firm estimates are not available for mackerel during, and just prior to, the moratorium (1968–1976), due to the very low numbers of fish caught and sampled during this period; however, evidence from egg and larval surveys (MacCall and Prager, 1988), as well as the very minor tonnage of mackerel taken in the jack mackerel landings (i.e. less than 100 tons year^{-1} from 1971 to 1974) clearly show that the biomass of mackerel off California remained at an extremely low level from the late 1960s until the minor year class of 1974. For the purposes of this study, the biomass levels that occurred during the 1969–1974 period are assumed to be 2000 tons, which is the level predicted by the cohort analyses in the late 1960s.

A very rapid increase in stock size occurred due to the very high recruitment rates which occurred in 1976 and 1978 and biomass reached a historical maximum in 1982 following three years with exceptional year classes (Jacobson *et al.*, 1994).

METHODS

Biological data

Data sources Biological data were collected by the California Department of Fish and Game through their programmes for sampling and ageing mackerel, jack mackerel and northern anchovy from the commercial catches. Sampling procedures for northern anchovy have been described by Collins (1969); however, the sampling procedures for mackerel and jack mackerel have not been published. Samples for all three species were taken exclusively from landings at the port of San Pedro, California. Information on the three species include date of capture, length, weight, sex, maturity stage, physical condition, age (from otoliths) and year class. Jack mackerel and mackerel sizes were recorded as fork length. Jack mackerel were measured in 0.25 cm increments from 1966 to 15 June 1972 and in mm thereafter. Mackerel were measured in 0.25 cm increments from 1966 to 1973 and in mm thereafter. All measurements were converted to mm for these analyses. Northern anchovy size was recorded as standard length (mm). Mackerel and jack mackerel were weighed in g and anchovy were measured to 0.1 g. Physical condition (i.e. good, damaged or rotten) and handling (i.e. fresh or frozen) of the fish also was recorded.

The mackerel ($N = 44\,021$) and jack mackerel ($N = 57\,242$) data include samples from 1966 to 1988. During the period of very low mackerel biomass (1967–1975), mackerel samples often were taken from boatloads dominated by jack mackerel; mackerel and jack mackerel commonly school together. Conversely, during periods of high mackerel landings, jack mackerel samples often were taken from boatloads dominated by mackerel. The anchovy samples ($N = 68\,304$) are limited to the 1966–1982 period as there has not been a directed anchovy-reduction fishery in San Pedro since 1982. In addition there are no data during July and August as the reduction fishery was closed during the summer and after 1978, the fishery was closed in February and March during the peak of spawning.

Sample treatment Clark (1928) clearly showed that condition factor of eviscerated sardine, *Sardinops sagax*, was essentially the same as that of whole fish, and that changes in fat content (rather than the presence of undigested material in the stomach or the development of gonads) dominated monthly condition factors. However, our preliminary analyses showed that frozen/thawed fish were heavier (for a given length) than fresh fish in all three species. Similar patterns have been observed in frozen/thawed Pacific herring (Reilly and Moore, 1982) and capelin (Bailey *et al.*, 1977). Only fresh fish were used for the calculation of the length–weight equations, and all frozen fish were corrected for the bias caused by freezing and thawing in fresh water; this inclusion of frozen samples was necessary because large numbers of samples from later years were frozen prior to laboratory workup. All fish classified as rotten or unsuitable for length–weight analyses were excluded from the analyses. After the sample classification system for freezing was adopted, many samples unfortunately were not recorded as either fresh or frozen. We excluded these data from the condition factor analyses.

Environmental data

We assessed the associations of condition factors with local and larger-scale environmental variables, including upwelling indices (six locations), sea level (three locations), salinity (two locations), sea surface temperature (two locations), and Trenberth's (1984) Southern Oscillation index (Table 1, Fig. 2). Unfortunately, temperature, salinity and sea level data were not available for the entire 1965–1988 period at any location on the Pacific coast of Baja California.

RESULTS

Length–weight equations

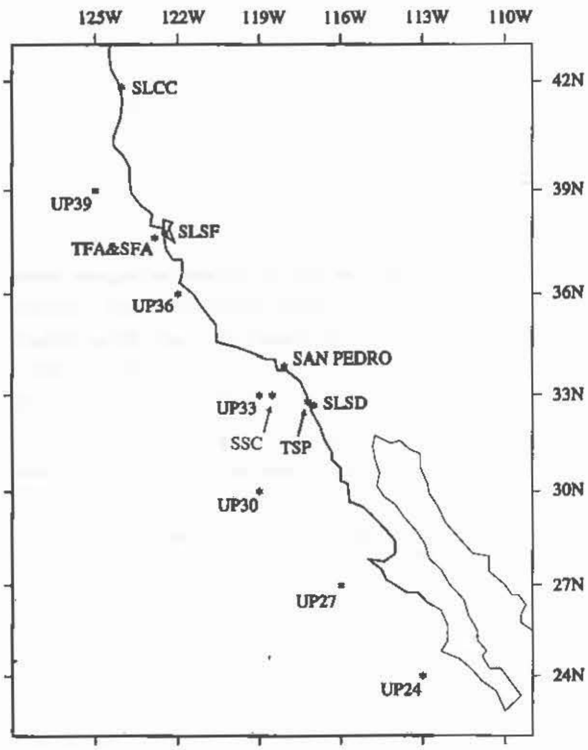
Separate length–weight equations were calculated (Table 2) for each species by sex category (i.e. imma-

Table 1. Environmental variables and sources of data used to evaluate relationships with condition factors (monthly means, 1965–1988).

Environmental variable	Abbr.	Source
Sea level		Cayan *et al.* (1988);
Crescent City	SLCC	updates provided by
San Franciso	SLSF	G. T. Mitchum,
San Diego	SLSD	University of Hawaii.
Sea surface temperature		M. Orpilla, NOS
Farallon Islands	TFA	Ocean Application Group,
Scripps Pier	TSP	Monterey, California
Upwelling indices		D. M. Husby, NMFS Pacific
24°N, 27°N,	UP24	Fisheries Environmental Group,
30°N, 33°N,	to	Monterey, California
36°N, 39°N	UP39	
Surface salinity		M. Orpilla, NOS
Farallon Islands	SFA	Ocean Application Group,
San Clemente Island	SSC	Monterey, California
Southern Oscillation index[a]	SOI	C. F. Ropelewski
		NOAA Climate Analysis Center,
		Camp Springs, Maryland

[a]Calculated as in Trenberth (1984) from Darwin and Tahiti pressures.

Figure 2. Study area.



ture, male, female); immature fish were those for which sex could not be determined due to the small size of their gonads. Parameters were estimated with linear regressions of log-transformed data and include a correction for the bias introduced by the log transformation (Beauchamp and Olson, 1973). The data used to determine the equations were limited to the period of 1966–1984 because the 1985–1988 data were not then available.

These length–weight equations were used to develop the condition factor time series. Condition factors (CF) were calculated as:

$$CF = (\text{weight observed})/(\text{weight expected}) \quad (1)$$

where: (weight expected) = a^* (observed length)^b, and a^* and b are the calculated length–weight coefficients from Table 2.

Analyses of variance

The intention was to achieve time series that best represent changes in the condition factor of each species. Therefore analyses of variance were undertaken to account for the variance caused by handling (i.e. fresh vs. frozen), seasonality, age and sex. The analysis of variance due to handling differs from the others because the treatment (freezing) only applied to a

Table 2. Length–weight relationships† ($W = a^{*}L^{b}$) calculated using data from fresh fish sampled at San Pedro, California during 1966–1984.

Species	Sex‡	a	a*	b	N	s^2	$e(s^2/2)$
M¶		0.000 001 133 7	0.000 001 139 1	3.416	25106	0.009 48	1.004 751
JM		0.000 004 809 1	0.000 004 826 4	3.150	45242	0.007 17	1.003 591
AN		0.000 011 971 2	0.000 012 034 9	2.964	39123	0.010 61	1.005 319
By sex							
M	0	0.000 000 854 3	0.000 000 858 9	3.472	6489	0.010 69	1.005 359
M	1	0.000 001 003 5	0.000 001 007 8	3.437	8735	0.008 57	1.004 294
M	2	0.000 000 771 0	0.000 000 783 4	3.480	9882	0.008 85	1.004 435
JM¶	0	0.000 006 530 7	0.000 006 555 6	3.090	14491	0.007 61	1.003 812
JM¶	1	0.000 005 091 2	0.000 005 109 2	3.140	14884	0.007 08	1.003 546
JM¶	2	0.000 004 794 7	0.000 004 810 9	3.150	15867	0.006 76	1.003 386
AN¶	0	0.000 005 256 7	0.000 005 290 2	3.131	949	0.012 69	1.006 365
AN¶	1	0.000 012 981 3	0.000 013 047 6	2.947	15474	0.010 19	1.005 108
AN¶	2	0.000 013 578 8	0.000 013 651 7	2.939	22700	0.010 71	1.005 369

†Observed size ranges: mackerel (M), 120–450 mm FL, 50–1100 g; jack mackerel (JM), 120–350mm FL, 40–500 g; anchovy (AN), 80–160 mm SL, 5–45 g.

‡0, sex not determined (immature); 1, male; 2, female.

$a^{*} = a[e(s^2/2)]$. The 'a' parameter corrected for the bias introduced by linear regress of log-transformed data as in Beauchamp and Olson (1973).

¶Length-weight relationships used for calculation of condition factor time series.

portion of the fish in the data bases; age, sex, and month classifications occur for all fish in the three data bases.

Fresh vs. frozen fish In the three species the mean condition factor of frozen fish was 3% to 5% higher than that of fresh fish sampled over the same time period. Calculations of the condition factor of each species by length strata were made to assess potential differences in freezing due to size; no within-species trends were found. Frozen samples were spread over the year so seasonal variation in handling was not expected to bias results and within-year comparisons were made to exclude the possibility of temporal changes. Each species' mean condition factors of frozen fish was used as a correction factor in later analyses (i.e. the observed weight of individual frozen fish was divided by the correction factor). Anchovy required two correction factors as different physical-condition classification systems were used in the sampling procedures during 1967–1975 and 1976–1982. The correction factors were 1.0313 for mackerel, 1.0330 for jack mackerel, 1.0493 for anchovy during the period of 1967–1975 and 1.0454 for anchovy during the period of 1976–1982.

Analyses of variance were made using the above correction factors and only the fish that had been frozen. The total sum of squares was obtained from the differences between the observed condition factor and the expected condition factor; the expected condition factor was obtained from the length–weight relationships for fresh fish (Table 2). The 'treatment' sum of squares was the reduction in the total sum of squares obtained by applying the correction factors for frozen fish. All four analyses of variance (two for anchovy) were extremely significant (F values between 741 and 5380 with critical F (1%) ≤ 6.8).

All of the following analyses of variance were made by using a 'base' sum of squares in which corrections, as described above, were applied to all frozen fish.

Seasonality, age and sex The three factors analysed were sex, age and month of capture (hereafter called month). Separate length–weight equations were used for males, females and undetermined sex (Table 2). Condition factors were adjusted for the effects of month and age by dividing individual condition factors by mean monthly or age-specific condition factor (Table 3).

The analyses of variance were carried out in a stepwise process with the 'treatment' that accounted for the most variance in the previous step being included in the calculation of the next step. For example, if month accounted for the greatest reduction in variance in the

Table 3. Month and age correction factors for mackerel (M), jack mackerel (JM) and anchovy (AN).

	Correction factor			Number of fish		
	M	JM	AN*	M	JM	AN*
Month						
1	0.944	0.951	0.985	3 234	3 933	8 112
2	0.946	0.953	1.016	2 464	3 449	3 443
3	0.935	0.960	1.003	2 197	4 349	4 396
4	0.953	0.962	1.033	2 762	4 192	8 736
5	0.998	1.012	1.024	2 800	4 375	8 585
6	1.044	1.041	1.005	1 790	4 442	2 366
7	1.050	1.056	–	3 042	5 564	–
8	1.050	1.033	–	2 777	4 283	–
9	1.031	1.011	1.029	2 172	3 991	3 379
10	1.034	0.994	1.006	2 942	3 679	8 139
11	0.999	0.979	0.978	3 204	5 152	9 157
12	0.985	0.965	0.974	2 305	3 967	9 648
Age						
0	1.007	0.973	0.933	6 425	7 891	1 894
1	1.000	0.989	0.997	9 705	23 167	17 836
2	0.987	1.009	1.004	6 671	13 636	22 816
3	0.992	1.018	1.011	5 059	5 074	15 597
4	0.986	1.017	1.008	1 995	1 229	5 856
5	1.000	1.000	1.007	1 273	295	1 613
6	1.012	1.008	0.988	477	65	323
7	1.030	0.988	1.000	67	16	24
8	1.086	0.941	1.024	17	3	2

*No data for anchovy in July or August.

first step then the corrections for month were included in the calculations of condition factors used to determine the second step of the analysis. There is some confounding between the age and sex classification because the 'indeterminate' sex category is composed primarily of immature, young fish of age group 0 or 1.

Month was the most significant factor in reducing the variance of condition factor in mackerel, jack mackerel and anchovy; respective F values for month were 624.3, 744.7 and 387.9 (critical F (1%) ≤ 2.3). F values for sex and age categories also were highly significant. With month included in the calculations, age was the most significant factor in reducing variance in mackerel (F = 86.7) and sex was the most significant factor in jack mackerel (F = 76.7) and anchovy (F = 185.0). Anchovy was the only species in which the third factor (age) resulted in significantly reduced variance (F = 69.8: critical F (1%) ≤ 2.8); inclusion of the sex category in mackerel and the age category in jack mackerel resulted in increases rather than decreases in variance. The corrections applied reduced the variance of the mackerel, jack mackerel, and anchovy 1966–1984 data by 19.3%, 15.0% and 18.1%.

Condition factor time series

The model used to calculate the expected weights of mackerel was the combined sexes length–weight relationship (Table 2) corrected for age and month of capture by dividing with the individual's respective age and month correction factors (Table 3). The expected weights of individuals that have been frozen were also divided by the correction for freezing (1.01313). Separate length–weight equations for sex classification were used to calculate the expected weights of jack mackerel (Table 2). These expected weights were corrected for the month of capture by dividing by the month correction factors (Table 3) and for freezing by dividing by 1.0330. The expected weights of anchovy were also calculated with separate length–weight equations for sex classification (Table 2). Expected weights were corrected for age and month of capture (Table 3) and fish that were frozen were corrected by dividing the

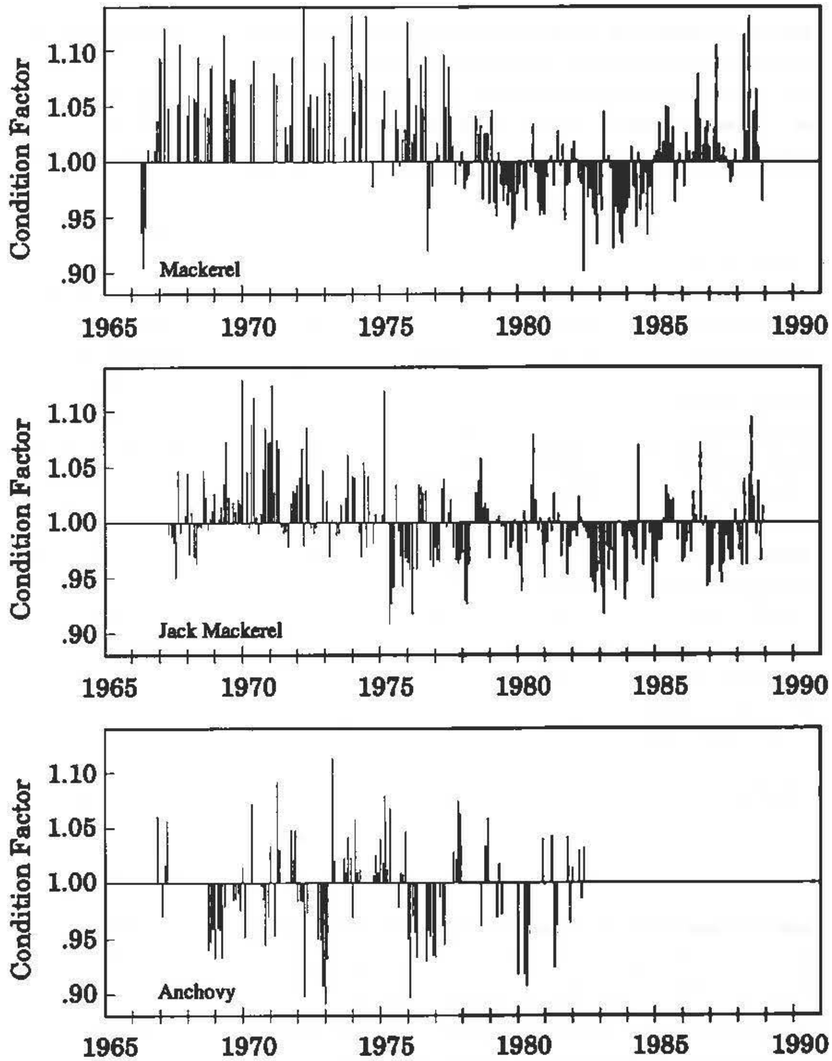


Figure 3. Monthly variation in the condition factor of mackerel, jack mackerel and anchovy sampled in the southern California fishery.

expected weight by the corrections for freezing (1.0493 for 1967–1975 and 1.0454 for 1976–1982).

For the condition factor time series the mackerel and jack mackerel time series were updated to 1988; the anchovy time series ended with the 1982 halt in the reduction fishery. The final time series included 43 435 mackerel, 56 943 jack mackerel and 65 961 anchovy. Monthly time series were the mean condition factor of fish captured during the individual month. Quarterly and annual time series were calculated as the means of the monthly means.

The time series of monthly condition factors for each species exhibit low-frequency patterns. Mackerel and jack mackerel condition factors fluctuate on a decadal time scale and the anchovy time series has periods of high and low condition factors extending over 1 to 2 years (Fig. 3). As expected, annual condition factors were at a minimum for mackerel and jack mackerel during the 1983–1984 El Niño; the anchovy data set ended in 1982. Condition factors for mackerel and jack mackerel are significantly correlated ($P \le 0.001$) using monthly, quarterly and annual time series (Table 4). There is also a clear trend of increasing correlation coefficients from the monthly to quarterly to annual time series (i.e. $r = 0.47; 0.56; 0.68$). None of anchovy time series was significantly correlated ($P \le 0.05$) with the mackerel or jack mackerel time series.

Correlation analyses with environmental factors

Correlation analyses were made with monthly, quarterly and annual mean condition factor time series and 14 environmental time series. The monthly environmental time series were corrected for seasonality by subtracting the respective monthly means of the 1966–

Table 4. Correlation coefficients among condition factors of mackerel, jack mackerel and anchovy; and between condition factors and population biomass of anchovy and mackerel. Whole numbers above diagonals are number of observations.

	Mackerel	Jack mackerel	Anchovy
Monthly means			
Mackerel CF	–	193	67
Jack mackerel CF	0.469***	–	84
Anchovy CF	−0.107	0.107	–
Quarterly means			
Mackerel CF	–	82	43
Jack mackerel CF	0.564***	–	46
Anchovy CF	−0.001	−0.065	–
Annual means			
Mackerel CF	–	22	17
Jack mackerel CF	0.683**	–	16
Anchovy CF	−0.156	−0.042	–
Biomass			
Anchovy biomass	0.194	−0.075	0.056
Mackerel biomass	−0.700**	−0.581**	−0.015
No. of observations	23	22	17

**Significant at $P \leq 0.01$. ***Significant at $P \leq 0.0001$.

1989 data sets to make them comparable to the seasonally corrected condition factor time series. It should be noted that the seasonally corrected time series have lower correlations than would occur using seasonally uncorrected time series at the lag which would place the seasonal cycles in, or out, of phase. Quarterly and annual condition factors and environmental factors were calculated from the corrected monthly means.

There is no a priori reason to assume any 'best' temporal interval to describe relationships between condition factors and environmental factors. Therefore, a number of environmental time series were used to assess temporal and lag differences in the relationships with condition factors (i.e. means of the current month, the means of the previous 1, 3, 6 and 12 months, and the means of the previous 4–6 and 7–12 months). Correlations also were run to assess seasonal differences in the relationships between condition and environmental factors.

As previously mentioned, one of the purposes of this work was to develop hypotheses concerning the environmental forcing of the condition of the three species. We note that the large number of correlation analyses carried out invalidates the use of the observed significance levels of individual correlation coefficients for hypothesis testing. A second factor that invalidates their use in statistical tests is that the environmental data series are themselves intercorrelated; there were 72 (out of 91) significant correlation coefficients ($P \leq 0.05$) using the seasonally standardized monthly time series and 38 (out of 91) significant coefficients using the annual time series (Table 5). In addition, the monthly and quarterly condition factor time series, the annual mackerel and jack mackerel condition factor time series, most of the monthly and quarterly environmental time series, the annual temperature time series at Scripps Pier and the annual sea level time series at San Diego all exhibit considerable autocorrelation, which reduces the effective number of degrees of freedom for hypothesis testing.

The authors caution that the significance levels in the following analyses are solely presented for their value in pattern recognition of potential relationships between condition factors and environmental factors; it is not intended that they represent statistical tests. The statistical analyses are intended to be used as hypothesis generators, not hypothesis tests.

Mackerel Condition factor in mackerel was moderately correlated with a broad range of environmental factors; 84 of 126 correlations had $P \leq 0.05$, 61 had $P \leq 0.01$ and 30 had $P \leq 0.0001$ (Table 6). The highest correlation coefficients ($A = -0.64$, $Q = -0.48$, $M = -0.43$) were with sea level at San Diego (SLSD). In the lagged environmental series the highest coefficient was with the previous 1–3 months (−0.45) and all of the lagged series, which included the previous month, had a higher coefficient than the current month (i.e. lag 0). Similar patterns occurred with sea level at San Francisco (SLSF) and Crescent City (SLCC) but coefficients were lower to the north; all correlation coefficients with the three sea level locations were negative and nearly all had $P \leq 0.05$. Negative coefficients occurred at all time intervals and lags with sea surface temperature at Scripps Pier (TSP) and all had $P \leq 0.05$. This pattern also occurred at the shorter-interval time series with sea surface temperature at the Farallon Islands (TFA).

The largest coefficients with the upwelling indices were at 27°N (and to a lesser extent at 24°N) off central Baja California ($A = 0.52$, $Q = 0.42$, $M = 0.26$). The monthly condition factor was most highly correlated with upwelling in the previous month and previous 3 months at 27°N ($r = 0.38$ and 0.35). There was a marked lack of correlation at the shorter time lags with condition factors in mackerel and upwelling indices off southern, central and northern California although there was a pattern of positive correlation with the

Table 5. Correlations among annual and monthly environmental factors. Bold figures are significant at $P \leq 0.05$.

Years: Pearson correlation matrix (N = 23).

	SLCC[a]	SLSF	SLSD	TFA	TSP	UP39	UP36	UP33	UP30	UP27	UP24	SFA	SSC
SLSF	**0.845**												
SLSD	**0.592**	**0.828**											
TFA	**0.710**	**0.593**	**0.425**										
TSP	0.385	**0.578**	**0.783**	0.400									
UP39	**−0.493**	**−0.549**	−0.404	**−0.722**	−0.297								
UP36	**−0.431**	**−0.590**	**−0.602**	**−0.485**	**0.480**	**0.493**							
UP33	−0.259	−0.342	**−0.456**	−0.161	**−0.499**	0.034	**0.761**						
UP30	−0.115	0.012	0.122	−0.133	−0.139	0.199	0.240	0.340					
UP27	−0.306	−0.317	−0.287	−0.053	**−0.419**	0.174	0.003	0.199	**0.454**				
UP24	−0.125	−0.190	−0.088	−0.218	−0.270	0.379	−0.024	−0.078	**0.462**	**0.760**			
SFA	**−0.753**	**−0.824**	**−0.505**	**−0.541**	−0.373	**−0.473**	0.355	0.064	−0.049	0.197	0.169		
SSC	−0.288	**−0.432**	**−0.446**	−0.261	−0.301	0.242	0.256	0.154	0.003	0.076	0.047	**0.456**	
SOI	**−0.617**	**−0.593**	**−0.698**	**−0.575**	**−0.587**	0.401	**0.584**	0.402	0.190	0.218	0.199	0.328	0.407

Months: Pearson correlation matrix (N = 288, 1966–1989). Corrected for seasonality by subtracting the respective monthly mean from each month.

	SLCC	SLSF	SLSD	TFA	TSP	UP39	UP36	UP33	UP30	UP27	UP24	SFA	SSC
SLSF	**0.746**												
SLSD	**0.407**	**0.717**											
TFA	**0.496**	**0.470**	**0.295**										
TSP	**0.295**	**0.477**	**0.650**	**0.295**									
UP39	**−0.519**	**−0.303**	−0.077	**−0.376**	−0.097								
UP36	**−0.481**	**−0.423**	**−0.192**	**−0.334**	**−0.118**	**0.618**							
UP33	**−0.188**	**−0.284**	**−0.266**	**−0.167**	**−0.286**	0.096	**0.625**						
UP30	**−0.237**	**−0.266**	−0.078	**−0.255**	**−0.242**	**0.138**	**0.371**	**0.551**					
UP27	−0.092	**−0.281**	**−0.339**	**−0.149**	**−0.411**	−0.012	0.059	**0.419**	**0.625**				
UP24	−0.029	**−0.203**	**−0.213**	**−0.209**	**−0.271**	0.080	0.052	**0.205**	**0.406**	**0.756**			
SFA	**−0.418**	**−0.522**	**−0.144**	**−0.317**	**−0.155**	**0.180**	**0.239**	**0.117**	0.079	0.023	−0.003		
SSC	**−0.220**	**−0.334**	**−0.271**	**−0.173**	−0.108	0.066	**0.134**	**0.137**	0.112	0.059	−0.024	**0.276**	
SOI	**−0.393**	**−0.457**	**−0.512**	**−0.304**	**−0.289**	**0.170**	**0.215**	**0.177**	**0.153**	**0.132**	0.090	**0.132**	**0.175**

[a]Abbreviations as in Table 1.

upwelling indices at 33°N and 36°N at the longer time lags. Oddly, there were several significant negative correlations at the longer time lags with the upwelling index at 30°N.

Condition factor was positively correlated at $P \leq 0.01$ with salinity at San Clemente Island (SSC) at all time intervals and lags. There was a similar pattern with the Southern Oscillation index (SOI), although the quarterly and one-month lags were only significant at the $P \leq 0.05$ level. The same general pattern occurred also for salinity at the Farallon Islands, except that the correlation was not significant at $P \leq 0.05$ for the annual time series.

Environmental factors, which are clearly associated with condition factor in mackerel (i.e. sea level at San Diego, temperature at Scripps Pier, upwelling at 27°N, salinity at San Clemente Island, and the SOI), show a consistent pattern of increasing correlation coefficients from the monthly to quarterly to annual time series.

Jack mackerel Correlations with the condition factor time series in jack mackerel have a similar pattern to that of mackerel but the correlation coefficients are generally smaller; 54 of 126 correlation coefficients had $P \leq 0.05$, 43 had $P \leq 0.01$ and 17 had $P \leq 0.0001$ (Table 7). The largest correlation coefficients were

Table 6. Pearson correlation coefficients; San Pedro mackerel condition factors vs. environmental variables (EV, abbreviated as in Table 1).

	Time series								
			Month[a]						
EV	Annual	Quarter	0	1	1–3	4–6	1–6	7–12	1–12
SLCC	−0.211	−0.185	−0.162*	−0.214**	−0.252**	−0.162*	−0.243**	−0.132	−0.233**
SLSF	−0.410	−0.376**	−0.322***	−0.374***	−0.374***	−0.227**	−0.331***	−0.262***	−0.330***
SLSD	−0.640**	−0.481***	−0.428***	−0.440***	−0.450***	−0.364***	−0.438***	−0.377***	−0.441***
TFA	−0.067	−0.258*	−0.252**	−0.220**	−0.205**	0.029	−0.112	0.033	−0.056
TSP	−0.502*	−0.385**	−0.272***	−0.298***	−0.258**	−0.163*	−0.247***	−0.229**	−0.267***
UP39	0.182	0.163	0.094	0.050	0.082	0.011	0.060	0.032	0.069
UP36	0.159	0.087	0.001	0.061	0.115	0.138*	0.159*	0.100	0.167*
UP33	0.237	0.094	0.004	0.091	0.146*	0.090	0.152*	0.160*	0.214**
UP30	−0.122	−0.001	−0.103	0.092	0.024	−0.246**	−0.137	−0.232**	−0.181*
UP27	0.520*	0.418***	0.258**	0.381***	0.350***	0.054	0.245**	0.151*	0.256**
UP24	0.284	0.313**	0.154*	0.247**	0.194**	−0.009	0.108	−0.031	0.061
SFA	0.201	0.220*	0.139*	0.149*	0.213**	0.176*	0.241**	0.154*	0.246**
SSC	0.540**	0.352**	0.272***	0.288***	0.333***	0.234***	0.333***	0.316***	0.379***
SOI	0.419*	0.273*	0.238**	0.186*	0.231**	0.276***	0.274***	0.206**	0.292***
d.f.	20	84	213	213	213	213	213	213	213
Number of correlations: total 126 84* 61** 30***									

*Significant at $P \leq 0.05$. **Significant at $P \leq 0.01$. ***Significant at $P \leq -0.0001$.
[a]Number of months by which the environmental time series precedes the monthly condition factor time series.

again with sea level at San Diego (A = −0.64, Q = −0.52, M = −0.38) and the highest coefficients with the monthly time series were with the previous month and the previous 3 months. Coefficients were lower to the north. The pattern of positive correlations with sea surface temperature at Scripps Pier was similar to that described for mackerel.

The only consistent pattern of higher correlations between condition factor and the upwelling indices was at 27°N (positive); however, there were positive correlations with the longest lags (7–12 and 1–12 months) at 33°N and 36°N. All correlations with $P \leq 0.05$ with salinity and the SOI were positive; however, the coefficients were lower than in mackerel and the highest coefficients were at the shorter time intervals.

Correlations with the annual and quarterly time series were highest (negative) with sea level at San Diego, sea level at San Francisco and temperature at Scripps Pier. Similar to mackerel, the largest correlations (positive) with the upwelling indices were at 27°N. Also similar to mackerel, there is a consistent pattern of higher correlation coefficients in the longer-period time series and the pattern occurs with the same suite of environmental factors.

Anchovy The condition factor of anchovy had the lowest correlations with environmental variables; 24 of 126 coefficients had $P \leq 0.05$, 8 had $P \leq 0.01$ and only 3 had $P \leq 0.0001$ (Table 8). Again the highest correlations were with sea level at San Diego (A = −0.35, Q = −0.49, M = −0.41) and there was a general pattern of negative coefficients with sea level at the three locations. The only correlations significant at $P \leq 0.01$ with temperature were the zero- and one-month lags at Scripps Pier. There was no pattern in correlation with the upwelling indices and the only correlations with $P \leq 0.05$ were at the longer lags at 39°N. There were no correlation coefficients between condition factor and SOI with $P \leq 0.01$, and only one with salinity (i.e. the salinity for the previous 12 months at San Clemente Island, which also has the highest correlation between salinity and the mackerel condition factor).

None of the correlations with the annual condition

Table 7. Pearson correlation coefficients; San Pedro jack mackerel condition factors vs. environmental variables (EV, abbreviated as in Table 1).

	Time series								
			Month[a]						
EV	Annual	Quarter	0	1	1–3	4–6	1–6	7–12	1–12
SLCC	−0.256	−0.163	−0.085	−0.180**	−0.200**	−0.070	−0.162*	0.001	−0.101
SLSF	−0.457*	−0.347**	−0.242**	−0.306***	−0.288***	−0.110	−0.222**	−0.120	−0.198**
SLSD	−0.640**	−0.517***	−0.384***	−0.430***	−0.411***	−0.262***	−0.362***	−0.202**	−0.314***
TFA	0.087	−0.062	−0.051	−0.029	0.020	0.141*	0.095	0.193**	0.177**
TSP	−0.504*	−0.380**	−0.275**	−0.284***	−0.251***	−0.094	−0.204**	−0.091	−0.179**
UP39	0.009	−0.001	−0.017	0.051	0.050	0.009	0.038	−0.041	−0.002
UP36	0.274	0.067	−0.050	0.080	0.093	0.068	0.103	0.169**	0.179**
UP33	0.324	0.232*	0.067	0.117	0.138*	0.049	0.119	0.226**	0.233**
UP30	0.079	0.125	0.049	0.130*	0.093	−0.057	0.021	−0.024	−0.004
UP27	0.441*	0.376**	0.230**	0.285***	0.264***	0.043	0.190**	0.112	0.195**
UP24	0.004	0.156	0.109	0.101	0.038	−0.084	−0.024	−0.060	−0.052
SFA	0.241	0.132	0.128	0.063	0.089	−0.026	0.041	0.027	0.043
SSC	0.343	0.280**	0.164*	0.224**	0.158*	0.018	0.098	0.075	0.103
SOI	0.378	0.268*	0.202**	0.254***	0.260***	0.207**	0.257***	0.089	0.202**
d.f.	19	85	235	235	235	235	235	235	235

Number of correlations: total 126 54* 43** 17***

*Significant at $P \leq 0.05$. **Significant at $P \leq 0.01$. ***Significant at $P \leq 0.0001$.
[a]Number of months by which the environmental time series precedes the monthly condition factor times series.

factor time series and environmental factors were significant at the $P \leq 0.05$ level and only sea level at San Francisco and San Diego were significant in the quarterly time series. In contrast to the patterns found in the mackerels, in anchovy the highest correlations were generally between the quarterly time series.

Seasonal analysis

There is no reason to assume that the condition factor of a fish stock will have the same relationship with a given environmental factor at all times of the year and it is also possible that condition factor may be related to stock biomass in one season and not in another. To assess possible seasonal effects, correlations among quarterly time series were calculated. The analyses included both within-quarter (e.g. winter vs. winter) and lagged environmental variables for the previous three quarters. The seasonal relationships between the condition factors of mackerel and jack mackerel were significant ($P \leq 0.01$) in the winter (Jan. to Mar., $r = 0.68$) and fall (Oct. to Dec., $r = 0.60$) quarters and significant ($P \leq 0.05$) in the spring ($r = 0.44$) and summer ($r = 0.49$) quarters. None of the seasonal correlations between anchovy and mackerel or anchovy and jack mackerel were significant. Seasonal correlations between environmental indices and anchovy were omitted due to the small number of observations.

Mackerel Similar to the previous analyses, the seasonal analyses exhibit an extensive set of 'significant' correlations between condition factor in mackerel and environmental factors (Table 9). Sea level at San Diego had the most extensive effect (10 out of 16 correlations significant at the 5% level). Sea level at San Diego in the spring appeared to have the greatest effect, being significantly correlated with condition factor in all four quarters. Summer sea levels were significantly correlated with condition factor in the summer, fall and winter. Condition factor reaches a minimum during the winter and in this quarter it was significantly correlated with sea level at all lags.

Salinity at San Clemente Island during the spring and summer quarters was significantly correlated with condition factor in the spring, summer and winter quarters. The highest correlation ($r = 0.78$) was between con-

Table 8. Pearson correlation coefficients; anchovy condition factors vs. environmental variables (EV, abbreviated as in Table 1).

	Time series								
			Month[a]						
EV	Annual	Quarter	0	1	1–3	4–6	1–6	7–12	1–12
SLCC	−0.239	−0.274	−0.223*	−0.116	−0.181	−0.121	−0.194	0.155	−0.011
SLSF	−0.234	−0.337*	−0.303**	−0.200*	−0.206*	−0.003	−0.146	0.186	0.031
SLSD	−0.345	−0.490**	−0.405***	−0.354**	−0.382***	−0.161	−0.305**	0.208*	−0.081
TFA	−0.225	−0.175	−0.174	−0.152	−0.160	−0.132	−0.168	0.143	0.005
TSP	−0.225	−0.442	−0.397***	−0.261**	−0.182	−0.002	−0.109	0.242*	0.090
UP39	0.064	0.124	0.078	0.163	0.151	0.215*	0.249*	0.112	0.239*
UP36	0.007	0.206	0.060	0.127	0.131	0.111	0.154	−0.113	0.036
UP33	−0.045	0.158	0.068	0.121	0.112	0.079	0.115	−0.113	0.005
UP30	−0.080	0.032	0.095	0.106	0.122	0.090	0.123	−0.017	0.057
UP27	−0.237	−0.119	0.029	0.035	0.024	−0.044	−0.012	−0.123	−0.096
UP24	−0.255	−0.149	0.032	0.031	0.004	−0.105	−0.061	−0.135	−0.118
SFA	−0.118	0.009	0.015	−0.025	−0.075	−0.122	−0.112	−0.002	−0.082
SSC	−0.138	0.179	0.051	0.136	0.197*	0.207*	0.242*	0.236*	0.278**
SOI	−0.237	0.236	0.182	0.219*	0.213*	0.075	0.159	−0.154	0.010
d.f.	15	46	100	100	100	100	100	100	100

Number of correlations: total 126 24* 9** 3***

*Significant at $P \leq 0.05$. **Significant at $P \leq 0.01$. ***Significant at $P \leq 0.0001$.
[a]Number of months by which the environmental time series precedes the monthly condition factor time series.

dition factor in the winter and salinity during the preceding summer. Condition factors in the winter and spring are moderately correlated with upwelling in the winter at 27°N and 24°N; spring condition factor is also 'significantly' correlated with winter and spring upwelling at both locations. Winter condition factor is moderately correlated with the SOI in winter (and with the preceding fall and summer) and with the Scripps Pier sea surface temperature in winter (and preceding fall). Condition factor appears to be the most associated with environmental conditions during the winter; however, sea level at San Diego and salinity at San Clemente Island during the spring and summer appear to affect condition factor during much of the year.

Jack mackerel There is a marked seasonal pattern in the relationships between condition factors and environmental factors in jack mackerel. Significant correlations occur essentially in the fall and winter quarters and the relationships are similar in these two quarters (Table 9). Winter condition factors are moderately correlated with sea level at San Diego during the winter and fall; fall condition factors are correlated with sea level during the fall, summer, and spring. The highest correlation was between winter condition factor and winter sea level San Diego ($R = 0.79$). The only pattern in the relationships between upwelling and condition factors is the positive correlation of fall and winter condition factors with fall and winter upwelling at 27°N. Fall and winter condition factors were significantly correlated with the summer salinity at San Clemente Island. The only significant correlation with temperature at Scripps Pier was between the winter condition factor and the winter temperature. The fall SOI was significantly correlated with the fall and winter condition factors. Jack mackerel also had a number of significant correlations at the longer lags with environmental conditions to the north (i.e. salinity and temperature at the Farallon Islands, and sea level at San Diego and Crescent City).

Condition factor in mackerel and jack mackerel appear to be seasonally associated with a similar suite of environmental factors. Both have a broad range of correlations with sea level at San Diego, and in both, the highest correlations are with condition factor in the fall and winter. Both have few significant correlations with the upwelling indices; however, both have significant correlations between winter condition factor and

Table 9. Pearson correlation coefficients between quarterly (seasonal) condition factors and quarterly (including lagged) environmental factors[a]; values not significant at the $P \leq 0.05$ level are omitted. (1:4 indicates the correlations between the 1st quarter (Jan.–Mar.) and the previous 4th quarter (Oct.–Dec.).

	d.f.	UP39	UP36	UP33	UP30	UP27	UP24	SFA	SSC	SOI	SLSD	SLSF	SLCC	TFA	TSP
								Mackerel							
1:1	18					0.686	0.455		0.474	0.562	−0.646	−0.446			−0.638
1:4	18					0.469				0.542	−0.570				−0.554
1:3	18								0.784	0.461	−0.462				
1:2	18								0.563		−0.524				
2:2	20					0.464	0.486		0.527		−0.506				
2:1	18			0.424		0.651	0.467								
2:4	20														
2:3	20								0.619						
3:3	20								0.507		−0.592	−0.490		−0.490	−0.425
3:2	20								0.595		−0.475				
3:1	18									0.445					
3:4	20								0.501						
4:4	20														
4:3	20										−0.494				
4:2	20				−0.486						−0.660			0.491	
4:1	18										−0.492				
								Jack mackerel							
1:1	19					0.497					−0.794				−0.744
1:4	19									0.477	−0.539				
1:3	19								0.710						
1:2	19				0.467									0.459	
2:2	20														
2:1	19														
2:4	20														
2:3	20														
3:3	20										−0.481				
3:2	20														
3:1	19														
3:4	20							0.458				−0.466	−0.449		
4:4	20					0.532				0.480	−0.538				
4:3	20								0.610		−0.551	−0.507			
4:2	20										−0.572			0.588	
4:1	19														

[a]Abbreviated as in Table 1.

upwelling at 27°N (jack mackerel condition factor is also significantly correlated in the fall at 27°N and mackerel is significantly correlated in the spring at both 27°N and 24°N). Both have quite high correlations between winter condition factor and salinity at San Clemente Island the previous summer, and both tend to have some correlation between fall and winter Southern Oscillation indices and fall and winter condition factors.

Population biomass effects

The three annual condition factor time series were not significantly correlated with anchovy biomass; however, annual condition factor time series for both the mackerel ($r = -0.70$) and jack mackerel ($r = -0.58$) were negatively correlated ($P \leq 0.001$) with mackerel biomass (Table 4). It should be noted that the mackerel biomass estimates and the mackerel and jack mackerel annual condition factors are highly autocorrelated (i.e. $r = 0.92$, 0.65, and 0.61 at lag 1).

The relationships between the annual biomass estimates of mackerel and the condition factors of mackerel and jack mackerel was also highly seasonal. Mackerel had the highest coefficients in the winter ($r = -0.70$) and fall ($r = -0.62$) and lesser, but still significant, relationships in the spring ($r = -0.50$) and summer ($r = -0.51$). Jack mackerel condition factors were significantly correlated with annual mackerel biomass estimates in the winter ($r = -0.53$) and fall ($r = -0.58$) but not in the spring ($r = -0.14$) and summer ($r = -0.25$). Mackerel biomass estimates were not significantly correlated with seasonal anchovy condition factors and there were no significant correlations between the annual anchovy biomass estimates and seasonal condition factors.

Multiple regression models

Stepwise multiple regression techniques were used to determine multivariate relationships between condition factors and environmental time series. The models were based on a criteria to enter of *P*-to-enter ≤ 0.05 and separate regressions were made for the annual, quarterly and monthly time series. To reduce the large number of potential environmental variables in the monthly models, which could have included all of the lagged environmental variables, only the means of the previous 3 months of each environmental variable were entered into the stepwise process. Mackerel and anchovy biomass and the condition factors of the other species were also included in a second set of regressions; however, the biomasses of anchovy and mackerel were not included as potential independent variables in the quarterly and monthly models as each has only one value per year.

Mackerel The 'best' model for annual condition factor in mackerel included five environmental variables, sea level at San Diego, upwelling at 27°N, salinity at San Clemente Island, sea level at San Francisco and upwelling at 30°N, and it explained 80% of the variance (Table 10). The models fitted with the quarterly ($r^2 = 0.41$) and monthly ($r^2 = 0.33$) time series included the same set of variables, except sea level at San Francisco, which entered in the same order. When the biological time series were included as independent variables, the first variable to enter the annual model was the biomass of mackerel, followed by salinity at San Clemente Island and upwelling at 27°N ($r^2 = 0.70$). The first variable to enter the quarterly ($r^2 = 0.52$) and monthly ($r^2 = 0.43$) models was the condition factor of jack mackerel and they both contained the same suite of environmental variables (salinity at San Clemente Island and upwelling at 27°N, 30°N and 36°N). It appears that sea level at San Diego, mackerel biomass and mackerel condition factor served as proxies for one another in the several models.

Jack mackerel The 'best' annual jack mackerel model included sea level at San Diego and temperature at the Farallon Islands ($r^2 = 0.58$). The quarterly model included sea level at San Diego and upwelling at 27°N ($r^2 = 0.30$), and the monthly model included sea level at San Diego, temperature at the Farallon Islands and upwelling at 27°N and 24°N ($r^2 = 0.33$). When the biological time series were included as independent variables, the mackerel condition factor was the first variable to enter each model. The annual model included upwelling at 30°N ($r^2 = 0.57$), the quarterly model included sea level at San Diego and upwelling at 30°N ($r^2 = 0.45$) and the monthly model included sea level at San Diego ($r^2 = 0.27$).

With the condition factor of mackerel included as a potential independent variable, the 'best' jack mackerel model consisted of only the mackerel condition factor and sea level at San Diego ($r^2 = 0.27$); without the condition factor of mackerel the 'best' model included sea level at San Diego, temperature at the Farallon Islands and upwelling at 27°N and 24°N ($r^2 = 0.33$).

Anchovy No variables entered the stepwise regression for anchovy using the annual time series. The quarterly model for condition factor of anchovy included sea level at San Diego and upwelling at 24°N ($r^2 = 0.37$) and the monthly model included sea level at San Diego and the mackerel condition factor ($r^2 = 0.20$).

DISCUSSION

Although there are considerable differences in the patterns of variation in the time series of the condition factors of mackerel, jack mackerel and anchovy, there is a remarkable and rational similarity in the patterns of correlation between their condition factors and the environmental time series. One has only to look at the mackerel and jack mackerel condition factor time series to note that the dominant pattern of variation is common to both populations, and that it is regime, or decadal, in scale. The statistical analyses show that this large-scale pattern is best seen in a negative relationship with sea level at San Diego, and to a lesser degree in sea levels at San Francisco and Crescent City. It is also apparent in the negative relationship with sea surface temperature at Scripps Pier and in the positive relationship with the Southern Oscillation index. This suite of environmental variables is highly intercorrelated and

Table 10. Stepwise multiple regression models: A, mackerel; B, jack mackerel; C, anchovy. (*P*-to-enter model ≤ 0.05.)

		Annual r^2		Quarterly r^2		Monthly r^2	
A. Mackerel models							
Environmental data only:	*N*	23		86		215	
Sea level San Diego		0.410	1	0.231	1	0.202	1
Upwelling 27°N		0.533	2	0.305	2	0.255	2
Salinity at San Clemente Is.		0.627	3	0.350	3	0.305	3
Sea level San Francisco		0.725	4				
Upwelling 30°N		0.799	5	0.407	4	0.329	4
Biological data included:	*N*	22		82		193	
Mackerel biomass		0.490	1				
Jack mackerel CF				0.318	1	0.220	1
Salinity at San Clemente Is.		0.593	2	0.364	2	0.344	2
Upwelling 27°N		0.695	3	0.492	4	0.358	3
Upwelling 30°N				0.420	3	0.416	4
Upwelling 36°N				0.522	5	0.434	5
B. Jack mackerel models							
Environmental data only:	*N*	22		87		237	
Sea level San Diego		0.410	1	0.268	1	0.169	1
Temperature Farallon Is.		0.580	2			0.197	2
Upwelling 27°N				0.303	2	0.212	3
Upwelling 24°N						0.325	4
Biological data included:	*N*	22		82		193	
Mackerel CF		0.467	1	0.318	1	0.220	1
Sea level San Diego				0.410	2	0.274	2
Upwelling 30°N		0.569	2	0.448	3		
C. Anchovy models							
Biological data included	*N*	17		48		67	
Sea level San Diego		–	0	0.258	1	0.146	1
Mackerel CF						0.195	2
Upwelling 24°N				0.368	2		

may be an indicator of a common environmental variation. Secondary, more regional patterns of correlation occur as a positive relationship with upwelling off Baja California and a positive relationship with salinity at San Clemente Island. The multiple regression analyses with the mackerel and jack mackerel condition factors consistently show the additive nature of these three environmental patterns.

Correlations between environmental variables and anchovy condition factors were generally quite low; however, as in the mackerels, the highest correlations were with sea level at San Diego; correlations with Scripps Pier were also relatively high. The 'best' anchovy multiple regression model included environmental variables which occurred in the mackerel and jack mackerel models (i.e. sea level at San Diego and upwelling off southern Baja California).

Large-scale pattern The decadal time scale of variation in the condition factors of the mackerels, as well as the environmental variables associated with the large-scale pattern described above, suggest that this dominant pattern is caused by changes in oceanic circulation which are at least the size of the California Current and perhaps larger. It is also apparent from the patterns of correlations observed in this analysis that the signals from this process are more apparent in the winter and less apparent in the summer.

Sea level is most commonly used as an indicator of alongshore transport (Reid and Mantyla, 1976; Chelton *et al.*, 1982); however, it is actually an indicator of several processes. For example, lower sea level at San Diego is also associated with increased upwelling, increased salinity, lower SOI and lower temperatures (Table 5). Highest sea levels are associated with El Niño events that result in a reduced advection of nutrients and forage from the north as well as a warmer, deeper upper mixed layer that reduces the nutrient enrichment normally derived from local wind-driven Ekman transport. Sea level, which is an inverse index of Equatorward flow in the California Current (i.e. lower sea level indicates increased Equatorward advection), has been shown to be an indicator of zooplankton biomass in the CalCOFI region (Bernal and McGowan, 1981; Chelton *et al.*, 1982). Zooplankton in the near-shore Southern California and Baja California region is dominated by species with subtropical affinities; the increased biomass associated with stronger Equatorward advection is therefore not caused simply by advection of zooplankton from central California, as this region has a zooplankton fauna with subarctic affinities (Bernal and McGowan, 1981; Roesler and Chelton, 1987).

There was a general pattern of negative correlation between condition factors and temperature. Negative correlation coefficients with the monthly condition factor time series were highest for the shorter lags at Scripps Pier (i.e. lag 0, lag 1 or lag 1–3 months). The seasonal analyses show that mackerel and jack mackerel condition factor series were strongly negatively correlated with Scripps Pier temperature in the winter. Negative correlations with temperature imply that warmer water is detrimental to condition factor and this is consistent with the pattern of correlation observed with sea level because increased flow of the California Current (i.e. lower sea level) tends to decrease temperature; note the strong positive correlation between temperature and sea level (Table 5). Higher temperatures also result in increased metabolic rates which affect condition factors.

The mackerel and jack mackerel time series of condition factor were positively correlated with the Southern Oscillation index (SOI) at nearly all time intervals and lags; however, only the previous month and previous 1–3 months were correlated with the anchovy time series. The SOI is generally strongly correlated with the sea level and SST time series; however, the local temperature and sea level time series appear to be better predictors of the condition factors than the SOI.

Upwelling off Baja California Correlation coefficients between the condition factor time series and upwelling indices were generally positive and quite low. The exception was that the monthly time series for mackerel and jack mackerel had moderately strong associations with upwelling off central and southern Baja California. In the quarterly and annual time series, upwelling at 27°N was moderately, positively correlated with condition factor in both mackerel and jack mackerel. In addition, upwelling in Baja California was prominent in the multiple regression analyses for both mackerel and jack mackerel and to a lesser extent anchovy. Lack of correlation with the California upwelling locations, except at the longer time lags, suggests that upwelling off Southern California and north of Point Conception has little direct influence on condition factors in the mackerels and anchovy. This is consistent with Bernal's and McGowan's (1981) work that showed changes in zooplankton concentrations in the Southern California Bight were not associated with the local Bakun upwelling indices.

In the seasonal analyses, winter and spring condition factors of mackerel were significantly correlated with winter upwelling off central Baja California (27°N) and winter and fall condition factors of jack mackerel were significantly correlated with fall and winter upwelling at 27°N. In this regard, fall and winter radiolarian distributions suggest that faunas from the south are brought northward in the near-shore region of the California Bight (Casey *et al.*, 1986), and off northern Baja California the northward flow at the shelf break is strongest in the fall and most wide-spread in the winter (Lynn *et al.*, 1982; CalCOFI line 100). This may indicate that during the fall and winter, when zooplankton biomass (Chelton *et al.*, 1982), upwelling at 27°N (Bakun, 1973) and condition factors are lowest, food availability for small pelagic fishes in the inshore regions of the southern California gyre is more influenced by waters from Baja California than by those from central California.

Salinity at San Clemente Island Most correlation coefficients with salinity were positive: however, salinity at San Clemente Island was the one environmental variable that had markedly different patterns in each of the three species. Salinity at San Clemente Island and the condition factors of mackerel were highly correlated at all time intervals and lags. Those of jack mackerel had generally quite low correlations, with only the monthly time series at the shorter lags being significant. Those of anchovy were only significantly correlated at the longer lags. The seasonal analyses suggest a persistent positive association between the summer salinity at San Clemente and mackerel condition factor in the summer and following fall, winter and spring. Summer salinity at San Clemente Island is also correlated with fall and winter condition factors in jack mackerel. In the context of this study, salinity is somewhat of a mixed signal in the Southern California Bight as the relationship between salinity and forage for small pelagics is confounded by the fact that two of the factors that are expected to be associated with increased forage have opposing effects on salinity. Increased Equatorward flow of the California Current decreases salinity and upwelling increases salinity. The core of low-salinity water that extends south of Point Conception indicates that salinity is an inverse indicator of southward advection and increased productivity (Bernal and McGowan, 1981; Chelton *et al.*, 1982). While this appears to be true for the offshore core of the California Current and the time series examined by Bernal and McGowan (1981), we found salinity at San Clemente Island to be negatively correlated with sea level at San Diego in both the monthly and annual time series (Table 5); that is, lower sea level (increased southward transport) was associated with increased salinity. In this regard, the two sources of higher-salinity water are the nearshore tongue of cool upwelled water which extends south of Point Arguello in the spring and summer (Reid, 1965) and the California Undercurrent which, at 30°N, has a core of high salinity at 200–500 m just off the shelf break (Wooster and Jones, 1970).

It is possible that none of the temporal intervals used (month, quarter and year) accurately portrays the relationships between condition factor and environment factors. In fact it is likely that condition factors are influenced by processes operating on several time scales. The monthly condition factor time series contain considerable variation among adjacent months and it is likely that much of this variation is noise resulting from too few samples to obtain good estimates of the actual mean monthly condition factor. Although the number of fish in the monthly means is normally greater than 100, the number of boatloads sampled in many months is quite small. If between-school variance in condition factor is great in relation to within-school variance, the small number of boatloads sampled per month could produce considerable noise in the monthly means. Generally the highest correlation coefficients occurred with the annual time series; however the highest correlations with the monthly time series commonly occurred at the shorter lags (i.e. within the previous month or the previous 3 months). In addition the seasonal analyses suggest that condition factors in jack mackerel, and to a lesser degree mackerel, are most highly correlated with sea level, and other environmental variables, during the fall and winter seasons when their condition factors are falling and at a minimum. The above factors demonstrate the problem of trying to establish the length of time that is associated with the establishment of an individual's condition factor.

To reduce the possibility of spurious correlation of unrelated variables which have common, or lagged seasonal cycles, the mean seasonal cycle was removed from all time series; however, this process may have also artificially lowered the correlation coefficients of valid relationships. If, for example, alongshore flow (as measured by sea level at San Diego) is one of the factors that regulates the condition factor of mackerel, removal of the seasonal cycle will result in an artificially low correlation coefficient.

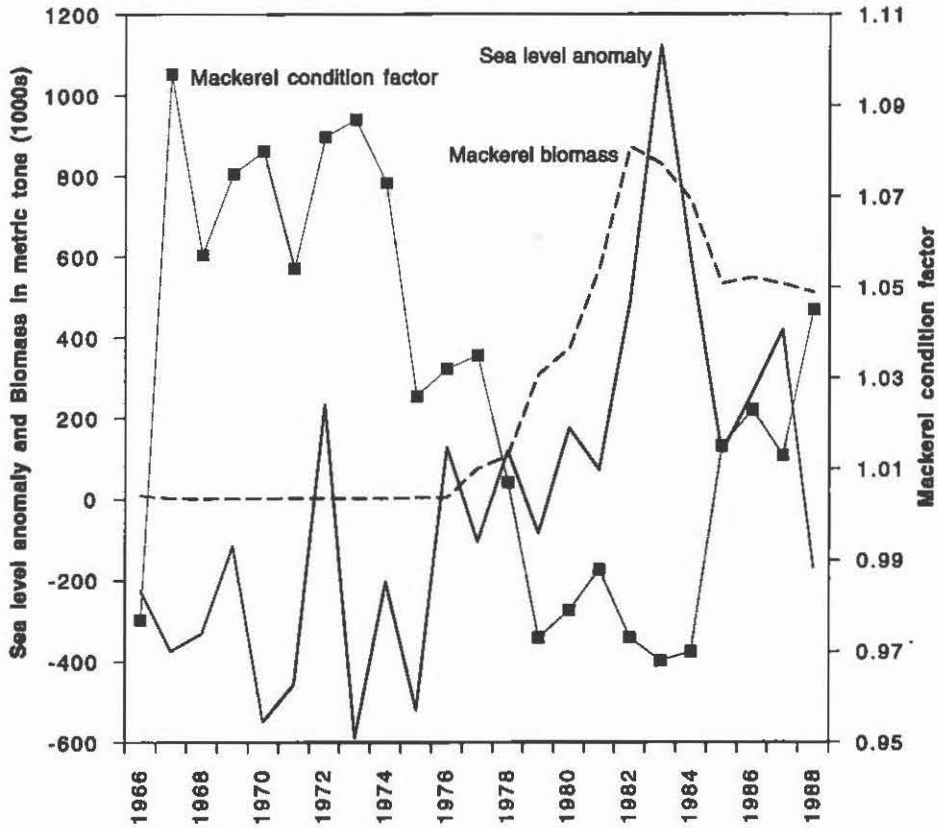
CONCLUSIONS

Correlation patterns and multiple regression models are consistent with the hypothesis that condition factor is regulated by environmental factors that influence food availability. Higher condition factors were associated with lower sea level at the coast, increased upwelling in central Baja California, and lower sea surface temperatures; all of these factors are associated with increased nutrients and productivity.

Condition factors in anchovy, which are lower in the food chain, were much less related to abiotic oceanographic factors than were mackerel and jack mackerel, which are higher in the food chain. This is certainly an unexpected result. In this regard we note that correlations between the mackerels and environmental factors have a consistent pattern of smallest coefficients with the monthly time series and largest coefficients with the annual time series: this pattern does not occur in anchovy. This suggests that lower-trophic-level fishes are responding to processes operating on relatively short time scales, whereas higher-trophic-level fishes are more affected by processes operating on longer time scales. In the case of the mackerels this even appears to include process at the decadal scale.

Condition factors in the mackeral and jack mackerel time series have a number of similarities. They have similar decade-scale trends, nearly identical seasonal cycles and both the annual and monthly time series are strongly positively correlated; this is not unexpected because mackerel and jack mackerel commonly school together and mackerel and jack mackeral samples were commonly taken from the same boatloads. However, it is unexpected that the correlation coefficients between the condition factors of mackerel and jack mackerel are larger (i.e. A, $r = 0.68$; Q, $r = 0.56$; M, $r = 0.47$) than those between the condition factor of either species and any environmental variable (i.e. A, $r = -0.64$; Q, $r = 0.52$; M, $r = -0.45$). This suggests that mackerel and jack mackerel are responding to the same environmental conditions and that each species is a better predictor of the effect of that environment on the other species than are the environmental data series used in this study. The seasonal statistical analyses show that the condition factors of mackerel and jack mackerel are

Figure 4. Relationships between mackerel condition factor, mackerel biomass and the anomaly in sea level at San Diego.



highly positively correlated during the fall and winter seasons when their condition factors are falling ($r = 0.60$ and 0.68). During the spring and summer when condition factors are rising and at a maximum the relationship is much weaker ($r = 0.44$ and 0.49). This suggests that the relationship between the condition factors of mackerel and jack mackerel is primarily the result of factors which affect their condition factor during the fall and winter when food is presumably the most limiting.

It is also noteworthy that the population biomass of mackerel has a higher correlation with the annual condition factor in mackerel ($r = -0.70$) than does any environmental variable. This suggests that the condition factor of mackerel is at least partially regulated by density dependence; the fact that the seasonal analyses show that the correlation is highest in the winter, just before zooplankton abundance begins to increase, strengthens this suggestion. However, it should be noted that sea level at San Diego and the population biomass of mackerel are highly correlated ($r = 0.78$) and it is therefore difficult to determine if condition factor is varying in response to the environment or to population biomass. It is likely that both condition factor and population biomass are affected by environmental conditions associated with variations in sea level (Fig. 4). A further puzzling feature is that the 7 year minima in the mackerel condition factor (1978–1984) preceded the peak in mackerel biomass. In fact condition factor was low during the whole period of maximum population growth (1978–1982) and it returned to high levels when the population was still at a very high level. Current thinking would suggest that a fish population increases during periods of favourable environmental conditions when condition factors would be expected to be high, not when condition factors are at a minimum. In this regard it should be noted that both mackerel and jack mackerel are indeterminate spawners and as yet we have no information on the potentially very large interyear, or interdecadal, variability in their annual fecundity. The patterns seen in the data presented here suggest that the decreased condition factors observed during periods of population growth may be the result of increased reproductive output due to reduced age at maturity and/or increased spawning frequency.

Condition factor in jack mackerel may be affected by interspecific competition with mackerel; however, it is possible that mackerel and jack mackerel populations have similar trends and that variations in the condition factor of jack mackerel are also density dependent. In this regard Mason (1991) showed a positive correlation between reproductive success in mackerel and jack mackerel.

It is clear that no single factor had a dominant effect on the condition factors of the mackerel, jack mackerel or anchovy populations of the California Current. Instead, a number of factors including environmental conditions, density dependence, and possibly interspecific competition act together to regulate condition factors. Multiple regression models incorporating a number of these factors were found to account for a small to large amount (15–80%) of the variance in condition factors.

The values of empirical fishery/environmental relationships have achieved a generally low opinion by the fisheries science community (Bakun, 1985; Drinkwater and Meyers, 1987; Walters and Collie, 1988); in the authors' opinion, the results of the present study provide some insight which may be of use to future researchers. Most importantly, the results of the analyses suggest that the proper, classical approach of hypothesis development, acquisition of data, and statistical analyses to test the hypothesis is not necessarily better than the 'shotgun' approach used in the present study. Our correlation analyses with mackerel condition factors and a wide range of environmental variables resulted in 62 out of 126 correlations being significant at the $P \leq 0.01$ level. This suggests that almost 50% of 'proper' hypothesis tests of environmental conditions and mackerel condition factors would have resulted in acceptance of the hypothesis.

Secondarily, readily available and commonly used environmental indices (such as monthly mean sea level data, derived from a tidal station, and the offshore component of monthly mean Ekman transport, calculated from model-derived atmospheric pressure fields) are not the clean proxies of alongshore advection and upwelling that the researcher would desire. Instead, the available physical environmental variables are highly intercorrelated, and when a 'good' correlation coefficient is found it is very difficult to ascertain which mechanism or process is responsible.

It was stated earlier in this document that one of the purposes of the work was to develop, not test, hypotheses. In this regard the approach appears to have been partially successful; based on the results of the correlation analyses we suggest two hypotheses concerning mackerel and jack mackerel and none for the anchovy.

The first-order variation in condition factors of mackerel and jack mackerel suggests that they are responding to very large-scale perturbations of the system which are at least partially described by variations in sea level. These perturbations are at least decade-scale temporally and California Current-scale spatially. This first-order variation is associated with alongshore advection, as described by the inverse of sea level, which has decade-scale perturbations that are similar to those observed in the condition factors of the mackerels. The California Current spatial scale is apparent in the high degree of correlation between sea level at stations in San Diego, San Francisco and Crescent City and in the similar patterns of correlation with condition factors in the mackerels. This first-order variation is consistent with the results of Bernal and McGowan (1981) who described the relationship between CalCOFI total zooplankton samples and sea level. In this case the relationship, even though on a scale of decades the number of degrees of freedom in the study is only anecdotal, at least confirms the relationship described by Bernal and McGowan (1981) and Chelton *et al.* (1982). It should be noted that density-dependent variation in condition factors of the mackerel is a confounding factor as both mackerel biomass and alongshore advection have similar decade-scale variation. The hypothesis that the largest component of variability in the condition factor of the mackerel and jack mackerel, and by association their fecundity and productivity, is caused by decade-scale oceanographic fluctuations is one which will be difficult to test. Palaeosediment analysis is a possible approach; however, mackerel and jack mackerel scales have not yet been examined. The most direct approach would be to design sampling programmes to determine the basic population rates occurring during regimes of population expansion and collapse. The most significant component lacking in the available database is estimates of annual fecundity.

The second-order variation in condition factors of the mackerels is more regional in nature and it is best seen in the upwelling indices. The more regional nature of the meteorological system can be seen in a comparison of the correlations among the upwelling locations, in contrast to those among the sea-level stations. The correlations between upwelling locations drops off much more quickly with distance than do those between sea-level stations (Table 5). In agreement with Bernal and McGowan (1981), there was no pattern of association with upwelling indices in the Southern California Bight nor was there a marked association with indices from the upwelling maximum zone to the north of Point Conception. Rather, the strongest relationship was with upwelling in Baja California, and the important period is not during the upwelling maximum period, which occurs in the spring and early summer, but during the fall and winter. The hypothesis suggested by this information is that the condition factors of mackerels, at least in the near-shore region where most of the fishery occurs, is affected by forage advected from Baja California and the effect is largest during the fall and winter when mackerel condition factors are declining and at a minimum. One way to approach testing this hypothesis is to determine if the CalCOFI total zooplankton volumes in the near-shore region of the Southern California Bight are correlated with fall and winter upwelling in, or advection from, Baja California.

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