

Abstract.—We describe a simple biostatistical model of reproductive success (logarithm of recruits/spawner) applied to three coastal pelagic fish stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus*. We used the model to detect possible influences of gross climatic conditions and contaminant loadings (particularly of metals and organochlorines) on reproduction in these three stocks. Data included several decades of annual estimates of recruitment and stock size, monthly measures of climate, and annual estimates of contaminant loadings; the model included a compensatory stock-size component before adding environmental effects. The study was meant to generate, rather than test, hypotheses. For the chub mackerel stock, we detected climate influences, but no contaminant influences, on reproductive success, which was usually high during conditions typical of El Niño–Southern Oscillation events. For the northern anchovy stock, we detected no climate or contaminant influences on spawning success; however, the negative results may reflect low statistical power, rather than absence of contaminant influences. For spawning success in the Pacific sardine stock, we detected no consistent climate influences, but we found a strong negative correlation with contaminant loadings. This result is consistent with the hypothesis that contaminant loadings accelerated the collapse of the Pacific sardine stock while it was under stress from severe overfishing. Although many scientific questions about validation of models, mechanisms of action, and identity of specific deleterious contaminants remain to be answered, the observed data are well described by the hypothesis of contaminant-mediated decline.

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Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus**

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In recent years, there has been increasing concern about possible effects of contaminants on the nation's living resources, particularly exploited fish and shellfish populations. Although contaminants such as heavy metals and synthetic organochlorines are commonly detectable in coastal sediments, waters, and organisms (Mearns et al. 1991), it has been difficult, if not impossible, to determine whether sublethal levels of contaminants have influenced the productivity of coastal fish stocks. Mass mortalities and deformities of fish and shellfish have occurred after exposure to high levels of contaminants, but mortality and morbidity in natural populations attributed to chronic low-level exposures is difficult to prove conclusively, even though it may be strongly supported by circumstantial evidence (Sindermann 1978).

In addition, the question of population-level effects has been largely unexplored. For individuals of most species, the physiological effects (if any) of chronic sublethal exposure to contaminants are poorly understood. For populations, the effects of such exposure are not known. Nonetheless,

evidence from many studies of individuals suggests that populations should be affected also.

This paper describes exploratory models of the effects of contaminants, climate, and spawning-stock size on three exploited fish populations off southern California. With a rich body of data, this area is unusually well suited to such a study. The waters off southern California contain elevated levels of numerous contaminants, including PCBs, DDT, and several toxic metals (McCain et al. 1988). Estimates of historical contaminant loadings have been made by Summers et al. (1988), and data on climatic conditions are available from public records. Major coastal pelagic fisheries have been monitored by the California Department of Fish and Game since about 1930.

Two main conceptual approaches might be used to model the effects of contaminant exposure on populations. The first approach is a "bottom-up" one: constructing a

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mechanistic population model that somehow extrapolates known effects on individual organisms to effects at the population level. The second approach is entirely at the population level: construction of statistical models that correlate historical changes in population properties (especially properties thought to be sensitive to environmental fluctuation) to changes in contaminant loadings.

Neither of these approaches is completely satisfactory. Weighing against the first approach is the fact that the existing theory of population biology does not allow extrapolation from physiology and behavior of individuals to the net productivity of the population. Indeed, biological populations seem to have emergent properties unknowable from the observable properties of individuals (Mayr 1982). A similar problem is that combinations of contaminants may work in unforeseen ways; one might say that such combinations have their own emergent properties. Thus the biological activity and availability of mixtures of contaminants in the coastal environment are difficult, if not impossible, to extrapolate from laboratory studies of exposure to individual contaminants. Given the seemingly insurmountable barriers to constructing mechanistic bottom-up models of populations chronically exposed to low levels of contaminants, we used the alternative approach: we constructed empirical statistical models of contaminant effects on populations. The empirical approach, of course, also has many limitations; these are discussed at length in later sections.

Model structure

Evidence suggests that the youngest stages of fishes should be most sensitive to the effects of contaminants (Weis & Weis 1989). For that reason, our model of contaminant effects addresses survival from the egg stage to age of recruitment (roughly the first year of life). The model is based on the widely-used Ricker (1954) model of fish recruitment:

$$R = \alpha P e^{-\beta P} \zeta, \quad (1)$$

where R = recruitment in number of fish or biomass,
 P = parent spawning-stock size (usually spawning biomass),
 α, β = estimated parameters of the Ricker model,
 e = base of natural logarithms, and
 ζ = a lognormally-distributed stochastic component with zero mean.

A common interpretation of Eq. 1 is that α represents the net fecundity of a unit of spawning biomass and β reflects the degree of density-dependence in the stock's recruitment.

The Ricker model is often expressed in terms of the natural logarithm of recruits per spawner:

$$\log(R/P) = a + bP + \varepsilon, \quad (2)$$

where $a = \log(\alpha)$, $b = -\beta$, and $\varepsilon = \log(\zeta)$. (The sign change in b is made merely to simplify the notation; b is negative in a compensatory stock.) Assuming that the total number of eggs spawned is proportional to the spawning biomass P , the quantity R/P is an index of an egg's probability of survival to recruitment. This seems to be a more appropriate quantity to use for detecting exogenous effects than recruitment itself, which is usually held to depend in the first order upon stock size. We refer to the quantity R/P as "spawning success" and to its natural logarithm as "log spawning success." The model of log spawning success (Eq. 2) is linear in the parameters and contains an additive error structure, and thus can be fit by ordinary least-squares (OLS) regression.

Eq. 2 can easily be modified to incorporate external variables, such as climate or contaminant effects, that might affect spawning success. Suppose we have m such variables, $\{x_1, x_2, \dots, x_m\}$, for which we wish to estimate parameters $\{\theta_1, \theta_2, \dots, \theta_m\}$. Then a model including these variables is

$$\log(R/P) = a + bP + \sum_{i=1}^m \theta_i x_i + \varepsilon. \quad (3)$$

In this expanded model, m explanatory variables and population size affect log spawning success in an additive manner. The application of this linearized model is described in a later section. Other adaptations of the Ricker model to represent contaminant effects were made by Goodyear (1983) and Vaughan et al. (1984).

Data sources and processing

Two main categories of data were used in this study: data on fish abundances, and explanatory data on the environment. Data on fish populations comprised time-series of age-structured abundance estimates from virtual population analyses (VPA). We examined three coastal pelagic stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus* (known locally as Pacific mackerel).

These stocks were chosen because they have each supported major fisheries and have been studied sufficiently well so that long time-series of stock and recruitment data are available. These coastal pelagic species also form a conspicuous part of the California Current ecosystem.

Explanatory data (data on the environment) included time-series of two types: variables related to climate, and variables reflecting contaminant loadings or other potential human impacts. These data were subjected to a number of stages of preliminary processing, in-

cluding two principal component analyses, to compute two sets of derived variables (principal components) from a larger number of potential explanatory variables.

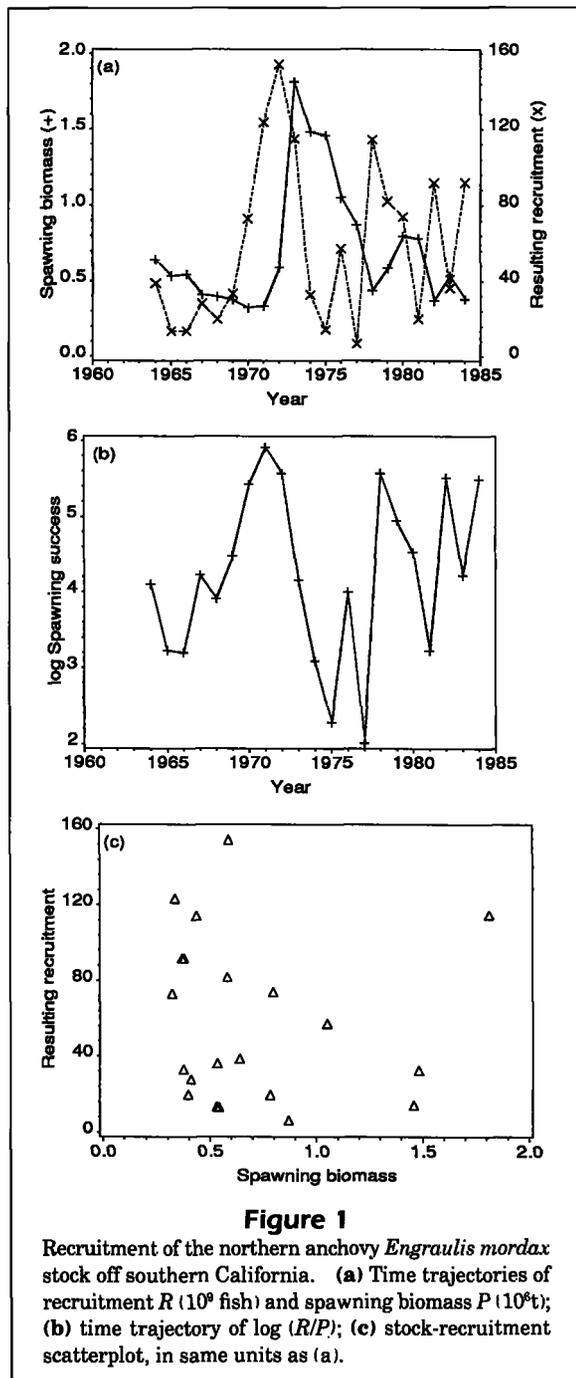
Data on fish abundances

Stock and recruitment data on northern anchovy (Table 1, Fig. 1) were obtained from Table 8 of Methot (1989), who derived his estimates from fishery statistics and research survey data. For spawning-stock size, we used

Table 1

Stock and recruitment data used for modeling effects of contaminants and climate on spawning success of three pelagic fish stocks off southern California. Data on chub mackerel have traditionally been reported, maintained, and analyzed in the English system, and are so reported here.

Year	Northern anchovy <i>Engraulis mordax</i>		Pacific sardine <i>Sardinax sagax</i>		Chub mackerel <i>Scomber japonicus</i>	
	Spawning biomass 10 ³ t	Recruitment 10 ⁹ fish	Spawning biomass 10 ³ t	Recruitment 10 ⁸ fish	Spawning biomass 10 ⁶ lbs	Recruitment 10 ⁶ lbs
1946	—	—	566	3875	97.87	20.11
1947	—	—	405	4261	57.91	139.20
1948	—	—	740	3690	28.90	70.92
1949	—	—	793	290	72.43	11.21
1950	—	—	780	397	89.46	3.59
1951	—	—	277	972	72.05	3.80
1952	—	—	136	1197	32.89	55.35
1953	—	—	202	382	10.62	106.48
1954	—	—	239	264	38.58	45.90
1955	—	—	170	588	80.69	91.41
1956	—	—	108	1586	95.00	20.05
1957	—	—	90	905	77.30	28.00
1958	—	—	177	288	36.98	91.81
1959	—	—	122	111	33.59	70.18
1960	—	—	88	74	63.02	128.67
1961	—	—	54	56	81.32	85.60
1962	—	—	27	11	133.10	18.18
1963	—	—	—	—	168.65	9.58
1964	639,210	38.6	—	—	112.05	2.67
1965	531,520	13.4	—	—	44.27	4.21
1966	541,880	13.3	—	—	17.63	5.75
1967	409,170	27.9	—	—	4.11	1.14
1968	396,260	19.8	—	—	2.57	4.08
1969	374,300	33.1	—	—	—	—
1970	321,880	73.1	—	—	—	—
1971	333,600	123.3	—	—	—	—
1972	588,460	154.2	—	—	—	—
1973	1,812,900	114.9	—	—	—	—
1974	1,481,160	32.6	—	—	—	10.15
1975	1,458,430	14.3	—	—	0.63	2.53
1976	1,050,180	57.2	—	—	5.00	138.43
1977	868,890	6.5	—	—	22.68	89.87
1978	435,370	114.3	—	—	95.06	252.20
1979	582,890	82.0	—	—	166.36	35.40
1980	798,280	74.0	—	—	255.27	185.41
1981	782,770	19.7	—	—	332.28	158.58



Methot's estimates of spawning biomass on 15 February of each year. For recruitment, we used Methot's estimates of the number of recruits on 1 July of the same year. Methot stated that his estimates of recruitments before 1964 are much less precise; we used his estimates of 1964 through 81 (the end of the contaminant data series).

Stock and recruitment data on Pacific sardine (Table 1, Fig. 2) are the estimates of MacCall (1979, Table 3), and were derived from fishery

statistics. Although the estimates extend through 1964, MacCall (1979) discounted the 1963 and 1964 estimates of recruitment as not sufficiently precise. We used the estimates from 1946 (the beginning of the contaminant series) through 1962.

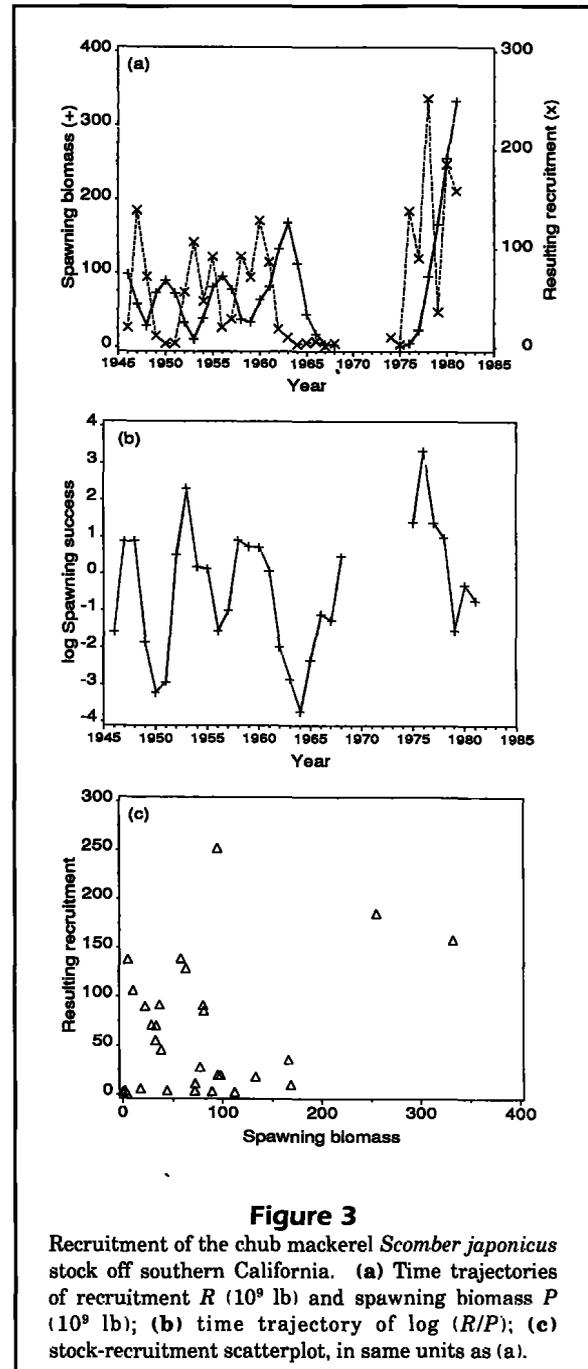
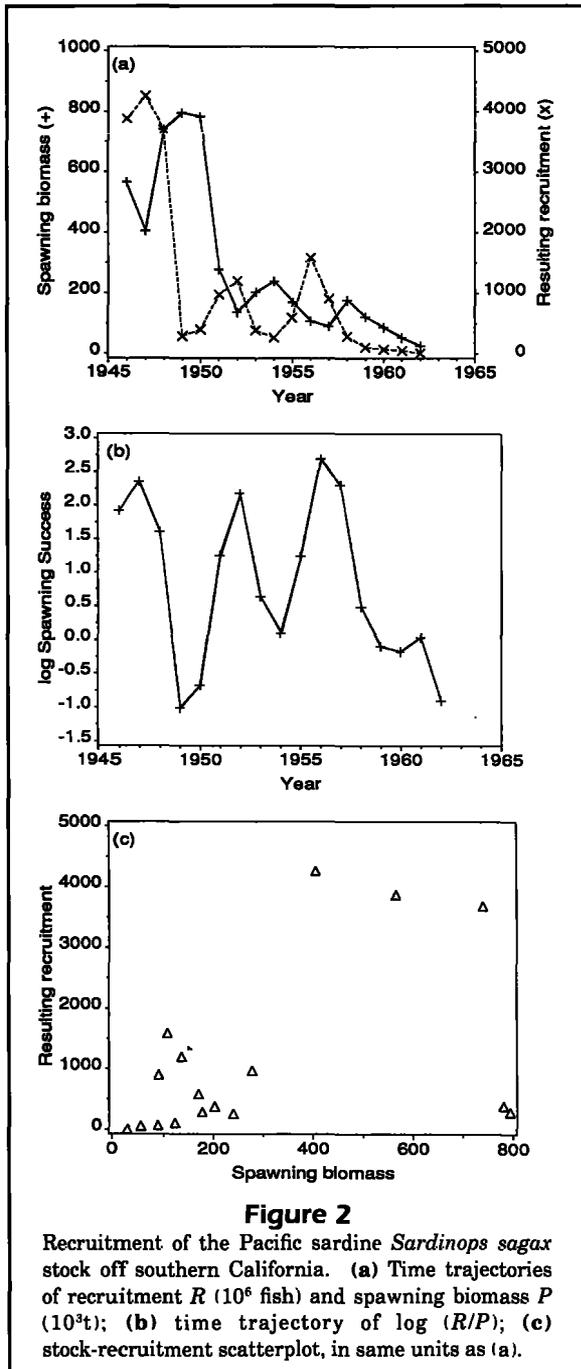
Stock and recruitment data on chub mackerel (Table 1, Fig. 3) are from Table 1 of Prager & Hoenig (1989), who compiled data from MacCall et al. (1985), Parrish & MacCall (1978), and Prager & MacCall (1988a). The estimates, all derived from fishery statistics, were adjusted by Prager & Hoenig (1989) to a common reporting date. The temporal limits of our analysis, 1946–81, were determined by the limits of the contaminant series. The chub mackerel data span a stock collapse and subsequent closure of the fishery and thus have 6 yr (1969–74) of data missing. Nonetheless, the chub mackerel series ($n=30$) is the longest of the three stocks. The data encompass at least two distinct epochs in the existence of the population: the pre-collapse epoch of steadily increasing exploitation rate, and the post-collapse epoch of more strictly regulated fishing and the associated population increase.

Explanatory data: Contaminants

Historical contaminant-loadings data were compiled and reconstructed by Summers et al. (1988) according to a mass-balance approach based on manufacturing volume, land use practices, and mobility of particular contaminants. Summers et al. (1988) also compiled more general measures (e.g., wastewater flow) from governmental records. The resulting annual time-series include five major categories: gross indicators, physical-biological factors, nutrient loadings, organochlorine loadings, and metal loadings (Table 2). Prager & MacCall (1990) discussed the loading patterns of individual contaminants and provided time-series plots of each; here, we review major characteristics abstracted from Summers et al. (1988) and Prager & MacCall (1990).

The human population of southern California has increased sharply over the last 50 yr, and this is reflected in many contaminant-loading patterns, particularly in the first three categories (Table 2). For example, loadings of nitrogen, phosphorus, and total organic carbon arise principally from wastewater (sewage) flow, which has increased with population size; power-plant cooling flows, for the most part, also reflect the growing population's use of electricity. While size of the annual kelp harvest is strongly correlated with human population size, the relationship may be noncausal; this is impossible to ascertain statistically. Nonetheless, size of the kelp harvest was included among other potential indicators of environmental stress, as many species are present in kelp-forest habitat during early stages of life history.

With the exception of PCBs, the organochlorines listed in Table 2 were all introduced in the late 1940s. Most fluctuations in individual loadings have followed legal restrictions on use (e.g., of DDT) and subsequent increased use of



other pesticides. The sharp rise in pesticide use in the 1950s and the subsequent decline in the 1960s and 1970s are similar for many of these compounds, which leads to difficulty in distinguishing their effects statistically. The PCBs, a group of non-pesticide toxic organochlorine compounds, have been used increasingly throughout most of this century, but little is known about the volume of their use and discharge before 1960.

Loadings of metals have varied with growth of the human population and also with fluctuations in patterns of industrial use. Loadings of some particularly toxic metals, such as lead and cadmium, have declined recently because of environmental regulations.

Most of the historical reconstructions of Summers et al. (1988) included values for all years from 1946 through 1981, but some contaminant variables lacked values for 1981. We extrapolated from immediately-

Table 2

Data available on contaminant loadings and other human impacts to the coastal waters of southern California, used for modeling spawning success of three coastal pelagic fish species. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-components analyses, used to reduce the number of variables before modeling. Asterisks (*) indicate variable not used for modeling.

Type of data	Years available
Gross indicators (Indicators group)	
Human population	1890–1980 ^a
Municipal wastewater flow*	1890–1985
Physical-biological factors (Indicators group)	
Kelp harvest	1916–1985
Dredging volume	1900–1983
Power-plant cooling flow	1928–1985
Nutrient loadings (Indicators group)	
Nitrogen	1910–1986
Phosphorus	1910–1986
Total organic carbon	1910–1986
Organochlorine loadings (Organochlorines group)	
Aldrin	1945–1982
BHC or Lindane	1945–1982
Chlordane	1945–1982
DDT	1945–1982
Dieldrin	1945–1982
Endrin	1945–1982
Heptachlor	1945–1982
Polychlorinated biphenyls	1929–1986
Toxaphene	1945–1982
Metal loadings (Metals group)	
Cadmium	1920–1980 ^b
Chromium	1929–1980 ^a
Copper	1929–1980 ^b
Mercury	1929–1980 ^a
Nickel ^c	1945–1980 ^c
Lead	1929–1980 ^b
Zinc	1929–1980 ^b

^a Value for 1981 extrapolated from 1979 and 1980 values.

^b Value for 1981 set equal to 1980 value.

^c Time-series contains missing values within this period.

preceding values as necessary (Table 2). The extrapolated 1981 values, although necessary for the principal-component analyses, had very little influence on later calculations.

The reconstructions of Summers et al. (1988) comprise the best available dataset, and the only one on this scale, describing contaminant loadings off southern California in recent decades. Because of this, verification is difficult. Prager & MacCall (1990) found

that the reconstructions agreed fairly well with some recent estimates of metals loadings made by the Southern California Coastal Water Resources Project (SCCWRP), which has monitored fluxes of metals from southern California sewage outfalls since 1971 (Konrad 1989). However, only a small portion of total metals loadings are in sewage; this may have caused the discrepancies noted for some metals by Prager & MacCall (1990). We also compared reconstructions with a study of metals deposition in anaerobic sediments in the Santa Barbara basin (H. Schmidt & C. Reimers, Scripps Inst. Oceanogr., La Jolla CA, pers. commun.). However, the sedimentary record, much less precise than the reconstructions, was unable to discern any clear trends or patterns in metals since 1932.

Explanatory data: Climate

A large suite of climate data (Table 3) for the years 1920–84 was compiled by Prager & MacCall (1987a,b,c), who described the data sources and processing in detail. Most of the raw data were provided by Dr. Andrew Bakun (Pac. Fish. Environ. Group, NMFS Southwest Fish. Sci. Cent., Monterey CA).

We detrended most of the sea level (SL) and sea-surface temperature (SST) series to remove rising trends with time. Values for 1983 were not used in computing trend lines, to prevent this extreme El Niño year near the end of the series from distorting the results. Only the series of SST in San Diego did not exhibit a significant trend, and accordingly that series was not detrended.

Seasonal effects were removed by standardizing each variable to zero mean and unit standard deviation (SD) by month of year. For example, the January values (1920–84) of Los Angeles rainfall were standardized as a group to mean 0.0 and SD 1.0. Standardization was performed separately for each month and time-series.

The climate dataset had a few missing values that we replaced with estimates. We used the BMDP procedure AM (Dixon et al. 1983) to estimate these values by stepwise regression on the available data. Reasonableness of the estimates was verified by simulation and by comparison with the nonmissing data (Prager & MacCall 1990).

Principal-component analyses

Many of the explanatory variables contained redundant information. For example, sea-surface temperature and sea level exhibit very similar patterns over time, as both are related to El Niño conditions and the flow of the California Current. Another example, noted above, is that many contaminant time-series are tightly

Table 3

Summary of climate data used for modeling spawning success of three coastal pelagic fish stocks off southern California. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-component analyses used to reduce the number of variables before modeling.

Type of data and station location(s)	Years of monthly data available
Rainfall (Rainfall group) San Francisco, Oakland Los Angeles, Long Beach San Diego	1920–1984
Seawater salinity (Rainfall group) Scripps Pier: surface Scripps Pier: bottom	1920–1984
Sea-surface temperature (El Niño group) Farralon Islands Pacific Grove San Luis Wharf San Diego	1920–1984
Sea level (El Niño group) San Francisco Los Angeles San Diego	1920–1984
Bakun's upwelling index (Upwelling group) 30°N, 119°W 33°N, 119°W 36°N, 122°W 39°N, 122°W	1946–1984

coupled to human population size, which generates them. This multicollinearity causes problems in fitting and interpreting statistical models such as ours. In extreme cases of multicollinearity, numerical algorithms used for fitting can fail. A more likely problem is that interpretation is not straightforward, because parameter values depend upon the other variables in the model. When sea-surface temperature is included in a model, for example, it may explain a large amount of the variance associated with sea level, so there is little to be gained from including sea level itself in the model. Yet an effect may truly be due to sea level (or to the strength of the California Current), and this relationship may thus be overlooked. Because of this difficulty, any biostatistical study of this nature is inherently unable to isolate the effects of individual causes. An important related practical problem is that a large number of potential explanatory variables makes any fitting procedure unwieldy.

We addressed some of these statistical problems by combining the explanatory data into new composite variables that did not contain duplicate information. These new variables, constructed by principal-

component analysis, are linear combinations of the original variables. To reduce the number of variables (initially ~216) to a number more easily analyzed by standard statistical software, data on sea level, sea-surface temperature, and salinity were converted to bimonthly means; also, surface and bottom salinities at Scripps Pier were averaged. Monthly rainfall values were transformed into an annual value of total rainfall (preceding 1 July to current 30 June) and a value representing the median date of the season's rainfall. The explanatory dataset with these changes contained 94 variables before reduction by principal-component analysis.

We constructed two separate sets of principal components. The first set was constructed from physical and climate data (Table 3) but not data on contaminants or general stressors (Table 2). A recruitment model based on this analysis would show how much of the variability in spawning success could be attributed to stock size and climatic variation alone. The second principal-component analysis included all explanatory variables, and was used to reveal how much more variability could be explained by adding contaminant information to the analysis.

Weighting was used in the principal-component analyses to avoid giving undue emphasis to variables (e.g., SST) measured at many locations. To determine weights, each variable was assigned to one of six groups, as shown in Tables 2 and 3. Each group received 1/6 of the total weighting, which was divided equally among the variables within the group.

The results of principal-component analyses are frequently difficult to interpret, as the components are formed on purely statistical grounds. Extensive graphical analysis (presented in Prager & MacCall 1987c, 1990) allowed attaching an interpretation to some, but not all, of the components used in these analyses (Table 4). In interpreting results of the recruitment models, we used a different approach, that of measuring the correlation of the model's explanatory effect with the individual variables, as explained below.

Application of model to three fish stocks

Overview

For each stock, we developed two alternative models: one using the principal components of climate data only, and the second using the principal components of climate and contaminant data. We then examined correlations of each model's estimated explanatory time-series (i.e., the summation on the right side of Eq. 3) to the original climate and contaminant variables. Be-

Table 4

Interpretation of principal components (PCs) used as explanatory variables in models of spawning success in three coastal pelagic fish stocks off southern California. Variables W_1 - W_{10} are PCs of data on climate; variables C_1 - C_{10} are PCs of data on climate and on contaminant (e.g., metals, organochlorines) loadings. Because interpretation of PCs is difficult, other methods were used to interpret model results (Fig. 4-6; text). SST = sea-surface temperature, SL = sea level.

Variable	Interpretation
W_1	Heavy rainfall; elevated SL and SST; W_1 has peaks in 1958 and 1983 corresponding to El Niño events.
W_2	Very low rainfall, high SST and SL in second half of year.
W_3	Increased upwelling, especially in mid-year.
W_4	Late rainy season with lower-than-average rainfall, decreased SST at northern stations.
W_5	Reduced upwelling at 30°N station, late rainy season.
W_6	Late rainy season in San Francisco.
W_7	Heavy rainfall in San Francisco, high early-year salinity in La Jolla.
W_8	No clear interpretation.
W_9	No clear interpretation.
W_{10}	No clear interpretation.
C_1	Increased upwelling midyear; high loadings of metals, nutrients, and most organochlorines; C_1 is in part a trend component, increasing from 1945 to 1978 and declining slightly thereafter;
C_2	High loadings of organochlorines, Cd, Cr, and Pb; reduced rainfall.
C_3	Elevated SL and SST, heavy rainfall; highest in years of El Niño events.
C_4	Elevated upwelling, especially at 30°N station; high loadings of Cr and BHC; C_4 is high around 1970, lower in other years.
C_5	Early, wet, rainy season, especially in San Francisco.
C_6	High loadings of Hg, early rainy season in southern California.
C_7	No clear interpretation.
C_8	No clear interpretation.
C_9	No clear interpretation.
C_{10}	No clear interpretation.

cause one of the models contained no contaminant data, agreement between the two models on the importance of contaminant variates was considered an indication of severe and troublesome collinearity between relevant climate and contaminant variables. Alternatively, it might simply indicate no contaminant effects. In the presence of strong contaminant effects, and lacking such severe collinearity, one would expect the explanatory effect from the model including contaminants to be more highly correlated with the contaminant variables.

Selection of explanatory variables

It is widely recognized by modelers and statisticians (e.g., Gilchrist 1984:11) that a profound source of uncertainty in statistical modeling is the possibility of error in specifying the model's structure. Such specification error biases parameter estimates and renders most confidence intervals and hypothesis tests invalid (Kennedy 1979, Gilchrist 1984). Unfortunately, the possibilities of specification error and its ramifications are often overlooked when statistical models are used in ecology. The models chosen and presented here were undoubtedly misspecified; they may have included unimportant effects or omitted important ones, and they were limited to a linear functional relationship, which is unlikely to be the true one.

After specifying the linear structure of Eq. 3, choice of variables was the main concern. When no theoretical basis exists to guide it, choice of variables in a regression model must be regarded as heuristic. Neither the theory of the underlying discipline—ecology—nor that of statistics can answer this question unequivocally, so we were forced to use an empirical approach. We started by retaining only the first 10 components from each of the principal-component analyses. (In each case, this retained ~80% of the weighted variance.) To arrive at a parsimonious model, we fit regression models to all combinations of 10 or fewer variables and ranked the many models by C_p , a goodness-of-fit statistic from Mallows (1973). For each combination of stock and data type (climate or combined), we accepted the model with the lowest C_p . However, alternative models of similar fit were similar in structure.

Any method of variable selection in which many candidate explanatory variables and combinations of variables are examined may lead the investigator to accept models which fit well solely through chance. This point has recently been emphasized by Flack & Chang (1987). Although the use of C_p is a relatively conservative approach, the true statistical significance of our results is unknown. Thus we view the modeling exercise as one of hypothesis generation, rather than hypothesis testing. The limitations of inference that come from an empirical choice of model structure are not unique to this study; they pertain to all modeling exercises except those in which

the final model structure and set of explanatory variables are correctly chosen before fitting. Here, we use elements of hypothesis testing, but acknowledge the impossibility of testing the hypotheses rigorously.

Detecting the influence of contaminants

We started with the following null hypothesis: "any apparent influence of contaminants can be explained by random variability alone, including chance correlations of contaminant loadings with climate variability." We imposed three statistical criteria to be met before we would consider rejecting this null hypothesis on the basis of a model including contaminant-loadings data. The first criterion was qualitative: the correlations of the model's explanatory effect with most contaminant variables had to be negative. The other criteria were quantitative: the regression coefficients of the model had to be statistically significant at $\alpha=0.05$, and the inclusion of contaminant information had to provide more explanatory power than use of climate data alone. If all three criteria were met, we would admit the possibility of contaminant influence on spawning success. The three criteria are described in more detail immediately below.

Sign test Of the variables in Table 3, the metals and organochlorines have been found by bioassay to have deleterious effects on fish (Weis & Weis 1989). (We omitted nickel because of an incomplete time-series and, more importantly, its relatively low toxicity.) Power-plant cooling flow also is generally considered deleterious, but the remaining variables in the indicators group could be favorable as well as unfavorable. The signs of the correlations with the 16 "deleterious" variables were subjected to a (one-tailed) statistical test of the following null hypothesis: "The observed number of negative correlations could arise by chance alone." Under this null hypothesis, the probability of a negative correlation between a contaminant variable and the model's estimated explanatory time-series is 0.5. Assuming independence among the 16 contaminant variables (an assumption that may be violated; see below), the probability of obtaining x negative correlations by chance is given by the binomial probability $f(x; n=16, p=0.5)$. The probability of observing 11 or more negative correlations is 0.105, and of observing ≥ 12 is 0.038. Thus, the conventional error rate of $\alpha \leq 0.05$ requires ≥ 12 negative correlations between the 16 deleterious contaminant variables and the explanatory time-series from a model that uses the combined explanatory data.

Such a test concludes that apparent contaminant effects are qualitatively significant if 12 or more negative correlations are found. However, the true prob-

ability of Type-I error is >0.038 , because many of the contaminant variables are positively correlated with one another, violating the assumption of independence in the binomial probability model and increasing the tail probabilities. While we cannot calculate an exact critical value of x in view of lack of independence, the value would be larger than the nominal value of 12 required for a model to pass this test.

Test of coefficients This test was used to assess whether the coefficients of the chosen model were significantly different from zero. Although we always chose the model with lowest C_p , that criterion does not depend directly on how precisely the regression coefficients are estimated. To test the significance of regression coefficients, we used the standard t -tests (at $\alpha=0.05$) provided by the statistical software, and required all coefficients to be significant for the model to pass the test.

Improvement-in-fit test Our third criterion required that the model that incorporated contaminant information (i.e., which used the combined explanatory data) had to provide a substantially better fit to the spawning success data than the model using the climate data alone. To judge this, we used the Schwarz criterion (Smith 1988), a statistic for comparing non-nested models. The Schwarz criterion requires an estimate of σ , the true model variance; we used the MSE of the better-fitting model. To pass the test, the model with combined data was required to have a higher value of this statistic than the model with climate data.

Results

Northern anchovy

Not unexpectedly for a short-lived species, the spawning biomass of this northern anchovy stock appears to depend strongly upon the preceding few years' recruitments. A peak in spawning biomass generally follows a corresponding peak in recruitment by 1 or 2yr (Fig. 1a). The stock-recruitment relationship, although noisy, appears density-dependent, in that spawning success improves at lower stock sizes (Fig. 1c), and each model includes a significant compensatory term (the negative stock-size parameter; Table 5). Ricker (1954) and MacCall (1980) have pointed out that cannibalism of eggs or larvae by the adults could cause such compensation.

Neither the climate model nor the combined model explained even half of the variability in log spawning success of northern anchovy (Table 5). Although the model incorporating contaminants had somewhat

Table 5

Summary results of regression models of logarithm of recruits per spawner for three coastal pelagic fish stocks off southern California. Predictor variables were parent stock size (P) and either principal components (W_i , $i=1, \dots, 10$) of climate data (models denoted \circ) or principal components (C_i , $i=1, \dots, 10$) of climate data and data on contaminant loadings (models denoted \bullet). Each model also included an intercept. Variable selection used an all-subsets algorithm with the C_p statistic; thus models may include variables not significant at $P < 0.05$, and all P values are considered nominal.

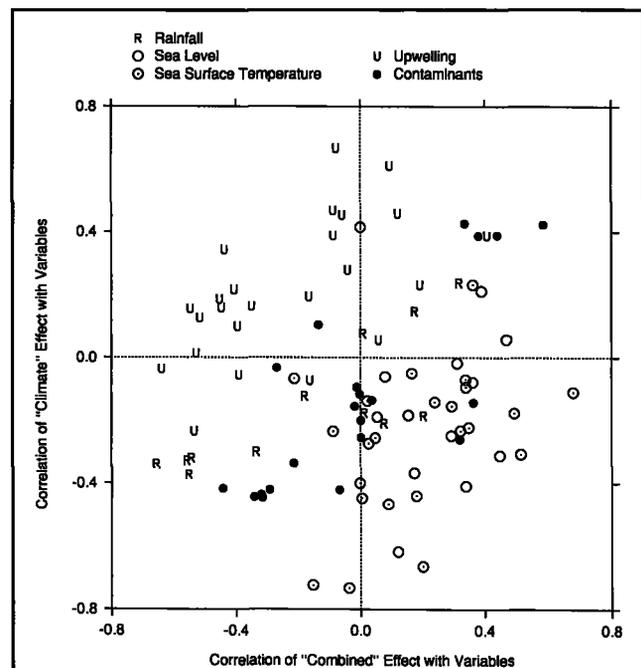
Variables included in model (with sign of coefficient) and nominal probabilities of t -statistics for H_0 : coefficient = 0.	df of model, error	F statistic	Nominal Prob > F	R^2
Northern anchovy <i>Engraulis mordax</i>				
\circ $-P$, 0.025; $-W_5$, 0.13	2, 15	4.20	0.036	0.36
\bullet $-P$, 0.17; $-C_3$, 0.087; $-C_7$, 0.13	3, 14	4.14	0.027	0.47
Pacific sardine <i>Sardinops sagax</i>				
\circ $-W_5$, 0.030	1, 15	5.77	0.030	0.28
\bullet $-P$, 0.0004; $-C_1$, 0.0001; $-C_5$, 0.002; $+C_{10}$, 0.002	4, 12	14.4	0.0002	0.47
Chub mackerel <i>Scomber japonicus</i>				
\circ $-P$, 0.0001; $-W_2$, 0.015; $+W_3$, 0.021; $+W_8$, 0.008; $-W_7$, 0.023; $-W_{10}$, 0.09	6, 23	6.74	0.0003	0.64
\bullet $-P$, 0.0003; $+C_3$, 0.094; $-C_4$, 0.004	3, 26	8.11	0.0006	0.48

higher R^2 and nominal significance level* than the model including only climate effects, it is impossible to attribute this difference to the effects of contaminants on recruitment. Given the small sample size and relatively small difference in fit, it seems more logical to attribute it to chance.

The two models of anchovy spawning success can be compared by plotting the correlations of the two corresponding explanatory effects with the original explanatory variables (Fig. 4). For some variables (e.g., those related to rainfall), correlations are similar between models; however, many other variables fall into the second and fourth quadrants of the plane, meaning that they are positively associated with spawning success in one model and negatively associated in the other. For example, the two models assign opposite signs to the influence of most upwelling variables. Based on this inconsistent pattern of correlations (Fig. 4) and the lack of nominally significant parameters (except for the stock-size parameters) in Table 5, we conclude that these models identify neither climate- nor contaminant-related variability in the spawning success of this stock.

Indeed, the major determinants of anchovy recruitment strength remain to be discovered. Smith (1985) speculated that recruitment might be controlled in late-larval stages through "plasticity of the interaction between growth rate and survival." Peterman & Bradford (1987) detected a decrease in larval survival associated with episodes of high wind speed; however, Peterman et al. (1988) did not detect significant corre-

*To emphasize the impossibility of determining true significance levels, reported significance levels are denoted "nominal."

**Figure 4**

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of northern anchovy *Engraulis mordax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Plot suggests that neither model offers a clear explanation of anchovy spawning success.

lation between abundance of larvae and of later early stages or between larval abundance and subsequent recruitment. Because our explanatory data do not include wind speed, we were unable to address this specific question. Cury & Roy (1989) demonstrated that spawning success in coastal pelagic fishes responds nonlinearly to upwelling, but our linearized model could not include this possible relationship.

Methot (1989) has shown that the age of maturity in northern anchovy increases from 1 to 2 when temperatures are below average. Our data already account for this effect, because the spawning-stock estimates of Methot (1989) incorporate this effect of temperature.

The only other likely determinant of anchovy recruitment is spawner abundance itself. This is a straightforward phenomenon in which very low abundance produces very low recruitment. Our stock-recruitment plot (Fig. 1c) does not illustrate this phenomenon; however, the plot begins after the lower abundances of the 1950s, when the effect would have been most pronounced.

Pacific sardine

As in the northern anchovy, the spawning biomass of Pacific sardine depends strongly upon immediately-preceding recruitments, with peaks in recruitment preceding peaks in spawning biomass by about 2 yr (Fig. 2a). Interpretation of the stock-recruitment plot (Fig. 2c) is problematic: If the 2 yr of highest spawning biomass (1949 and 1950) are disregarded, the plot appears biphasic, with small spawning biomasses producing small recruitments and large biomasses producing large recruitments. But if all years are included, recruitment appears to be density-dependent (or strongly influenced by external factors). The stock-size effect estimated by the model with climate effects was not significant ($P=0.66$); we refit the model without a stock-size effect (Table 5), reducing the R^2 by only 1%. The model with combined climate and contaminant effects identified a statistically significant stock-size effect with the correct sign for compensation (Table 5). This model also fit the data much better.

The two models give quite different pictures of the climatic effects associated with good spawning success in this Pacific sardine stock (Fig. 5). Correlations with rainfall-related signals were mostly negative for both models. Sea level and sea-surface temperatures were estimated to have mostly negative effects in the climate model, but many of these were estimated as positive in the combined model. Correlations with upwelling variables were all positive in the climate model, but were mixed in the combined model.

Most correlations with contaminant variables were negative in both models. In the climate model, correla-

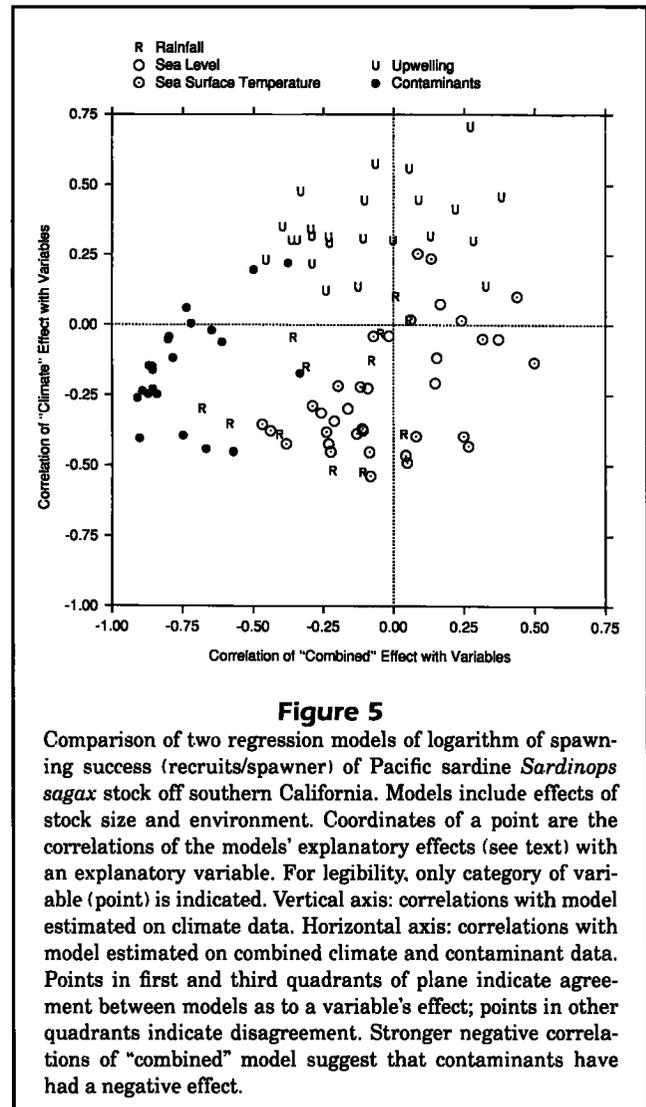


Figure 5

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Stronger negative correlations of "combined" model suggest that contaminants have had a negative effect.

tions ranged from ~ -0.25 to -0.50 . In the model with combined effects, the correlations ranged from ~ -0.25 to ~ -0.95 . These strong and consistently negative correlations are consistent with the hypothesis that contaminants affected the dynamics of the Pacific sardine stock, perhaps contributing to its collapse.

Chub mackerel

The models of chub mackerel spawning success included statistically-significant, compensatory stock-size parameters of similar magnitude (Table 5). Compensation has been demonstrated in previous analyses of this stock (Parrish & MacCall 1978, MacCall et al. 1985), and is apparent in Fig. 3b.

Including contaminant variables added little to the model. The climate model had lower MSE than the combined model, and its nominal significance level was more extreme (Table 5). One is left with the impres-

sion that adding the contaminant variables merely muddied the picture.

The two models give similar pictures of the forces that appear to be associated with variability in spawning success of chub mackerel (Fig. 6). We consider the climate variables first. Both models showed moderate-to-strong positive correlations of spawning success with sea-surface temperature early in the year, moderate-to-positive correlations with sea level early in the year, and weak-to-moderate correlations with upwelling later in the year. Correlations with rainfall-related variables were weak.

The models were also similar in correlations with contaminant variables. Correlations with metal loadings were weak-to-moderate, but of different signs for different metals; this suggests chance (noncausal) correlations. Much of the signal in the metal loadings

occurred in the late 1960s and beyond, when the chub mackerel stock was declining from overfishing and then recovering (MacCall et al. 1985); this coincidence could have induced noncausal statistical correlations. Correlations with organochlorines were negative. In interpreting this, it is relevant that spawning success in chub mackerel is highly autocorrelated and appears periodic (Fig. 3b). The organochlorine abundances are also very highly autocorrelated, usually consisting of a single peak. This could easily lead to correlations like those observed, even if the observed contaminant levels did not affect spawning success.

Although several contaminants correlate very highly with spawning success, the correlation patterns are nearly identical for the two models, one of which contains no information on contaminants. We interpret this to indicate that any contaminant effects are indistinguishable from effects of climate variables that fluctuate similarly over time. The strong agreement between the two models also suggests that recruitment-based contaminant analyses of this stock may be exceptionally prone to Type-II error, i.e., failure to detect any contaminant effects that might actually be present.

Parrish & MacCall (1978) also explored the effects of climate on chub mackerel spawning success, but comparison of this work and theirs is difficult for two reasons. Parrish & MacCall (1978) examined many explanatory variables not included in this study. In addition, changes in the estimated maturity schedule and the VPA-based stock and recruitment information (Prager & MacCall 1988) have resulted in a markedly different, as well as considerably extended, stock and recruitment series. Nonetheless, many of our estimated correlations agree with those of Parrish & MacCall (e.g., the positive effects of sea-surface temperature in the south, and the upwelling index at 30°N). Whereas Parrish & MacCall found that spawning success had a negative correlation to sea level at La Jolla, we estimated positive correlations with sea level at La Jolla and Los Angeles from January to June and independence in the later months.

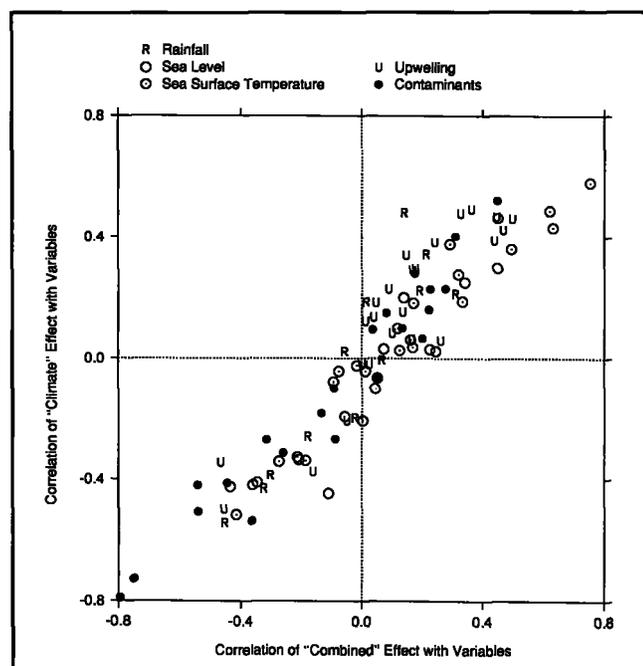


Figure 6

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of chub mackerel *Scomber japonicus* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Strong agreement between models suggests that addition of contaminant data adds little to this model.

Statistical evaluation of contaminant effects

In a preceding section we developed three statistical criteria for admission of possible contaminant effects. The sign test required 12 negative correlations between 16 "deleterious" contaminant variables and the explanatory effect of a model using the combined explanatory data. Correlations for models of all three stocks were mostly negative. Models of northern anchovy (Fig. 5) and chub mackerel (Fig. 6) each contained 11 negative correlations, but neither result was sufficient to reject

the null hypothesis. However, all 16 correlations were negative for the Pacific sardine (Table 6).

Regression coefficients were significant in models of Pacific sardine and chub mackerel. The model of northern anchovy spawning success fit relatively poorly (Table 5), and although the overall model was statistically significant, the individual regression coefficients were not.

According to the Schwarz criterion *S*, the models using combined data were marginally preferable to the models using climate data for chub mackerel and northern anchovy (*S* increased in the third significant figure). For sardine, the combined model was strongly preferable (*S* in ratio 2:1). Even allowing that the chub mackerel and northern anchovy models passed this test, the only stock to pass all three tests for suspicion of contaminant effects was the Pacific sardine.

Discussion

A somewhat similar biostatistical study was conducted by Martin Marietta Environmental Systems to examine possible effects of contaminants on fishes in five estuaries of the U.S. Atlantic coast, with emphasis on the Hudson-Raritan basin (Summers et al. 1985, 1987). The study used a categorical regression model of historical landings (Rose et al. 1986); the autoregressive model did not attempt biological or demographic realism. After accounting for the effects of hydrographic conditions and previous stock sizes, Summers et al. (1987) detected correlations related to contaminant variables including dissolved oxygen, dredging, and biochemical oxygen demand. The study concluded that there were consistent patterns of anthropogenic influ-

ences among similar stocks across different estuaries. In a second categorical regression study, Summers et al. (1990), while expressing some reservations about ultimate causes, concluded that sewage loadings have had a negative effect on white bass *Morone americana* production in the Choptank River, Maryland.

The present study was not undertaken with the expectation of finding clear evidence that contaminants affected fish stocks, nor clear evidence to the contrary. We knew of many reasons that contaminant effects might be difficult to detect, including major theoretical and practical difficulties in the data, shortcomings in biological knowledge, and the limitations of available statistical methodology (for details, see Appendix). As expected, we failed to detect contaminant effects on anchovy or chub mackerel, although we are unable to state whether this reflects a lack of such effects or merely low statistical power. In contrast, the results for Pacific sardine suggest that contaminant stress, at a time of severe overfishing, contributed to the decline and collapse of this stock. Partly because we searched for the best among many possible models, we cannot attach any level of statistical certainty to this suggestion. Our search selected a model of high explanatory power ($R^2=83\%$) in which contaminants were strongly represented, and that, we believe, makes a strong case for further research into the question. Important areas of research would include investigating how such a model of historical events, not formulated a priori, can be statistically validated (or invalidated); which individual contaminants may have contributed to the stock collapse; and by what mechanisms contaminants may have played a role in the decline of Pacific sardine.

An alternative hypothesis about Pacific sardine is that the true spawning-success relationship is depensatory rather than linear, and thus depensation, rather than exogenous influences, mediated the decline of the stock. Consistent with this hypothesis, the stock-size component of our model (Fig. 7a) fits the observed spawning-success data quite well until the mid-1950s (years of very low population size) when the stock-size component predicts higher spawning success than was observed. To examine this alternative hypothesis in more detail, we fit spawning-success models using the following variant of the gamma function:

Table 6

Statistical criteria used to screen models of spawning success of three coastal pelagic fish stocks off southern California. As predictors, models used parent stock-size and principal components derived from measures of climate and of contaminant loadings. Models were required to meet all three criteria in this table before being considered suggestive of contaminant influences on spawning success.

Statistical criterion	Fish stock		
	Northern anchovy	Pacific sardine	Chub mackerel
Number of significant negative correlations with contaminants thought to be deleterious (12 required).	11	16	11
Significance of coefficients in model that included contaminants.	no	yes	yes
Improved fit of model including contaminants, compared with model including only climate. (Improvement judged by Schwarz criterion.)	yes	yes	yes

$$\log(R/P) = a + \gamma \ln P + bP + \sum_{i=1}^m \theta_i x_i + \epsilon. \quad (4)$$

This differs from our original model, Eq. 3, only in including the term containing the estimated parameter γ . When $\gamma = 0$, this term drops out and the model is equivalent to Eq. 3. When $\gamma < 0$, the model is more strongly compensatory than Eq. 3; when $\gamma > 0$, the model is depensatory. In results of fitting this model, the depensatory effect was estimated as significant only in the absence of climate or combined variables ($\hat{\gamma} = 1.57, P < 0.025$ for a one-sided t -test). With the introduction of climate variables, the depensatory effect became smaller and not statistically significant ($\hat{\gamma} = 1.02, P < 0.19$); with the introduction of the combined variables, the depensatory effect disappeared ($\hat{\gamma} = -0.53$, the wrong sign for depensation). In the model with a depensatory parameter, correlations of the explanatory effect (summation term in Eq. 4) with contaminants were within 2% of those obtained from the model without the depensatory parameter. Of course, the correct specification of spawning-success relationships may be more complex than even Eq. 4. Nonetheless, these results indicate that a simple model including depensation cannot account for the observed decline in spawning success residual to stock-size effects. When this decline, as modeled by our combined variables (Fig. 7b), is combined with Ricker stock-size effects, the resulting model fits well the observed data on Pacific sardine (Fig. 7c).

Are there plausible mechanisms by which contaminants may have contributed to the decline of the sardine population? The high fat content of sardines, anchovy, and mackerel makes them likely to accumulate fat-soluble compounds such as the organochlorines listed in Table 2. It is known that DDT has caused widespread reproductive failures in birds, including those in this geographical area (Anderson et al. 1975). Also, fish have been observed to depurate PCBs by transferring them into eggs (Binder et al. 1984). Since the early stages of many fish species have exhibited reduced survival rates after exposure to toxic compounds (Weis & Weis 1989), plausible mechanisms do exist. The Pacific sardine stock was under severe overfishing pressure at the time of its collapse, and such pressure would increase its susceptibility to environmental stress. The possibility that contaminants may be implicated in the collapse of a major marine fishery is a novel and startling one.

Acknowledgments

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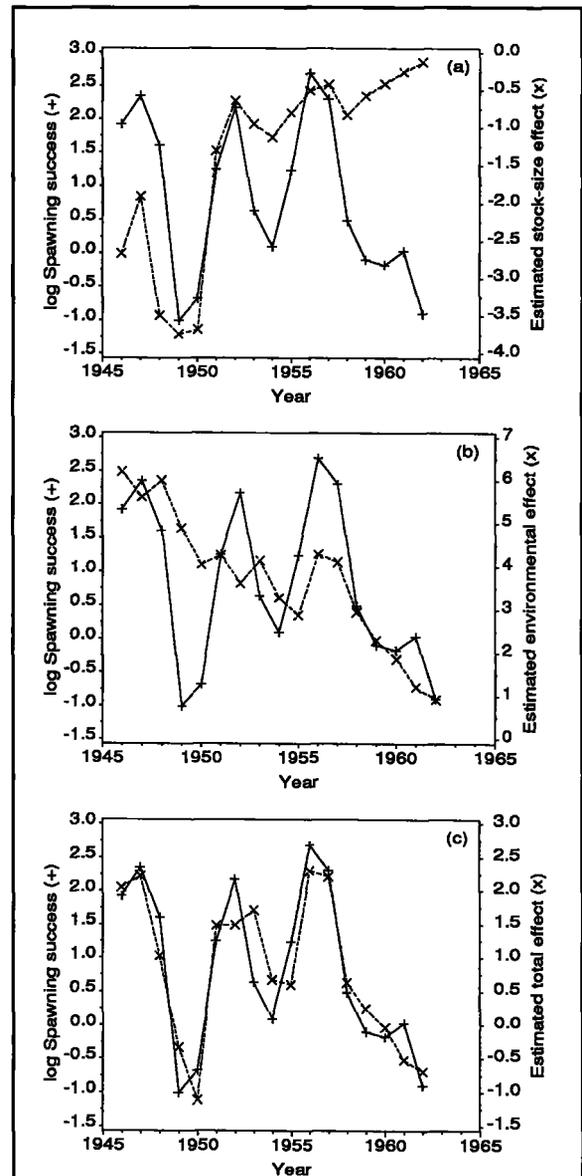


Figure 7

Components (dashed lines) of a model of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Each panel also shows the observed spawning-success data (solid line) after logarithmic transform. (a) Model component associated with estimated stock-size (depensatory) parameter; (b) model component associated with estimated parameters corresponding to climate variability and contaminant loadings; (c) predicted values from full model (intercept plus stock-size and environmental effects). The environmental component is more influential in the mid-1950s and later, when contaminant loadings generally increased.

tional data to fill several gaps. J. Browder, V. Restrepo, and W. Richards reviewed the manuscript in draft; the work was improved by their suggestions. Two anonymous reviewers also

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Appendix

We encountered many statistical difficulties and uncertainties in our biostatistical approach to detecting contaminant influences. Anyone attempting to interpret our results or to conduct a similar analysis should be cognizant of the following issues concerning data, biological understanding, and statistical methodology.

Difficulties relating to the data

- imprecision in data on stock and recruitment;
- imprecision in measurements of physical (climatic) conditions;
- imprecision in measurements and reconstructions of contaminant loadings;
- lack of residence-time models for contaminants in the water column and sediments, necessitating the use of loading (influx) values, rather than estimated *in situ* concentrations;
- substantial environmental variability that cannot be modeled effectively, and that would thus become "noise";
- strong trends in some resource and contaminant histories that can produce ambiguous correlations between these quantities;
- time-series that are short by statistical standards, although long by comparison with others available;
- multicollinearity: similar patterns over time in different explanatory variables.

Shortcomings in biological understanding

- only rudimentary knowledge of biological response to environmental variability and contaminants;
- poor models of environmental influences on larval production and recruitment;
- poor knowledge of spawning-at-age schedules, especially in light of increased evidence of multiple spawnings within seasons;
- little knowledge of natural mortality rates for most species;
- little or no knowledge of the true form of stock-recruitment relationships for most species.

Problems with statistical methodology

- lack of methods to address the problem of errors-in-variables, except in the simplest cases;
- lack of methods to determine the statistical power of hypothesis tests; and
- lack of methods to identify conclusively a model with the optimum number of parameters, or, for that matter, the correct non-zero parameters;

- possible presence of nonlinear effects, but insufficient data to identify and estimate a nonlinear model.

Similar problems arise in diverse areas of biostatistical analysis of populations and ecosystems, including most studies conducted for fishery management.

We attempted to reduce the effects of collinearity among the explanatory variables by using principal-components analysis. Unfortunately, stock size was at times correlated to other variables. The inability to identify effects of individual climate or contaminant variates is an unavoidable result of collinearity. This problem was accentuated by autocorrelation in the explanatory data and in the stock and recruitment series. Time trends in several explanatory variables, including stock size, compounded the problem of multi-collinearity, as they can lead to spurious (noncausal) correlations.

Even after the principal-component analysis, the suite of possible explanatory variables was large. For parsimony, we chose subset models for each stock. As stated, it is nonetheless probable that our models contain specification error. There are three main forms of specification error: (1) omission of relevant variables or inclusion of irrelevant ones, (2) a wrong functional form for the model (e.g., quadratic response when linear is specified), and (3) changes in the true parameters over time. Consequences of specification error can include biased parameter estimates and biased estimates of variance (Kennedy 1979), which in turn can lead to reduced statistical power. Using principal components, which are biologically arbitrary combinations of variables, may conceivably contribute to specification error (including errors in variables, as defined below).

Most of the recruitment time-series derived from VPA were short and did not coincide exactly with the contaminant data series, themselves not exceptionally long. A major consequence of modeling with a small sample size is low statistical power.

Observation error in explanatory variables causes difficulties in OLS parameter estimates, including inconsistency and, in the bivariate linear case, bias towards zero (Theil 1971, Kennedy 1979). This is known in the field of econometrics as the "errors-in-variables" or "errors-in-predictors" problem, and is sometimes considered a special case of specification error (e.g., Theil 1971). It has been demonstrated that recruitment models used in fisheries are subject to this problem (Walters & Ludwig 1981, Goodyear & Christensen 1984). If one is interested only in a predictive model, the bias is not important. If the parameter estimates are the object, however—as in the present case—the bias is especially problematic because its direction and magnitude are

known only in a few simple cases. By analogy to the results in bivariate linear regression, we suspect that coefficients of our regression models are biased towards zero. The estimated correlations with individual explanatory variates, including contaminants, may also be biased towards zero because of the smearing of the relationship by errors in the predictors.

Further complication is caused by the strong correlations between potential explanatory variables reflect-

ing climate and those reflecting contaminant loadings (Prager & MacCall 1990, Table 6.1). A few examples are the correlations between annual dredging removals and total rainfall in San Diego ($r=-0.32$), PCBs loadings and July–August SST at San Luis Wharf ($r=0.63$), and lead loadings and May–June upwelling at 39°N, 122°W ($r=0.79$). This collinearity makes it nearly impossible to distinguish, by statistical means, the effects of climate from those of contaminants.