

## THE RECOVERY OF THE CALIFORNIA SARDINE AS RELATED TO GLOBAL CHANGE

DANIEL LLUCH-BELDA, SERGIO HERNANDEZ-VAZQUEZ,  
DANIEL B. LLUCH-COTA, CESAR A. SALINAS-ZAVALA  
Centro de Investigaciones Biológicas de Baja California Sur  
A. C. Apartado Postal 128  
La Paz, B. C. S. México 23000

RICHARD A. SCHWARTZLOSE  
Centro de Investigaciones Biológicas de Baja California Sur  
and Scripps Institution of Oceanography  
University of California, San Diego  
La Jolla, California 92093

### ABSTRACT

California sardine abundance has fluctuated significantly in the past, and the population has remained at either low or high levels for sustained periods longer than a decade. Abundance now appears to be increasing from the low values in the mid 1970s. In a previous paper, evidence that small pelagic fishes from the main fisheries of the world vary synchronously with each other and also with global climatic variations was presented and named the "regime problem." This paper extends that analysis by looking for coherence between interdecadal variations in temperature both at local and global scales, and at variations in California sardine abundance. Possible relationships between this approach and previously presented ones are discussed, including the "recruitment problem" and the "fishery problem." Possible implied mechanisms are also briefly discussed.

### RESUMEN

La abundancia de la sardina California ha variado considerablemente en el pasado; la abundancia ha permanecido bajas o altas por periodos sostenidos mayores de una década. En la actualidad, hay indicios de que la abundancia se ha incrementado respecto de los valores bajos de mediados de los 70. En un trabajo previo, se presentó evidencia de que tanto las fluctuaciones climáticas globales como las variaciones de la abundancia de pelágicos menores de las principales pesquerías del mundo ocurren simultáneamente, lo que se denominó el "problema del régimen." El presente trabajo extiende el análisis mencionado buscando coherencia, tanto entre las variaciones interdecadales de temperatura a nivel local y global, como en las fluctuaciones de la abundancia de la sardina California. Se discute éste enfoque y sus posibles relaciones con otros que se han presentado, entre los que se incluyen el "problema del reclutamiento" y el "problema de la pesquería." Los posibles mecanismos involucrados también son discutidos brevemente.

### INTRODUCTION

In spite of the difficulties of precisely determining the population size, it seems evident that the sardine

population off northern Baja California and California has fluctuated widely, with changes of orders of magnitude. Population abundance changed from supporting the most voluminous fishery in North America (reaching some 800,000 MT during its production peak) to a total biomass estimate of less than 5,000 MT (Wolf 1992).

Changes in abundance have occurred over relatively short periods, but the population has remained at either a high or low mode for sustained periods. Recently, the population has been increasing from the low levels of the mid 1970s. The spawning biomass in 1990 may have been as high as 62,000 to 214,000 MT (Barnes et al. 1992). This recovery may be explored through different approaches.

Historically, the first proposed mechanism affecting the abundance of sardine populations was over-exploitation of the stocks, or the "fishery problem." The idea is that heavy fishing exerts major predation pressure on the population; this is particularly important if nonspawning fish are affected. This intense pressure has been assumed to severely affect the reproductive capabilities of the species.

It is generally accepted that an intense fishery can at least potentiate the collapse of a population, and perhaps delay its recovery if the population has been severely depleted. When fishery pressure is eliminated, the population is expected to increase, particularly after periods of heavy exploitation. The California sardine remained at low abundance levels from the early 1950s to the late 1970s, but subsequently increased; thus there seems to be a relationship between the recovery and the fishing moratorium imposed since 1967.

However, questions regarding the fishery problem remain. Previous papers presented evidence that the magnitude of the changes in abundance of sardine populations is beyond the mere effect of the fishery (Clark and Marr 1955; Radovich 1982). Moreover, it is well known from scales deposited in marine sediments (Soutar and Isaacs 1969) that the high-low abundance patterns may exist even in the absence of a fishery.

A second approach, the "recruitment problem," stems from the early work of Hjort (1914), and has been postulated by a number of authors. It is based

on the assumption that the differential survival of the egg-to-larvae stage determines the amount of recruitment, and thus sardine abundance in following years. Most papers dealing with the subject were reviewed and discussed by Lasker and MacCall (1983), who concluded that despite the specific mechanism proposed by each author, it is the availability of food that determines larval survival.

In a previous paper, Lluch-Belda et al. (1989) presented evidence concerning abundance changes in the main fisheries areas of the world. The data indicate that around Japan and off the west coasts of North and South America the sardine populations are fluctuating in phase, and that the sardine population in a fourth area off South Africa fluctuates out of phase with the Pacific populations. All these fluctuations are also in phase with some large-scale environmental variations. This hypothesis of coherence between sardine abundance and environmental variables has been named the "regime problem" (Alec MacCall, pers. comm.).

The present paper extends the analysis by Lluch-Belda et al. (1989) by relating the temperature regime changes on global and regional scales to the fluctuations of the sardine population off the west coast of North America. Proposed mechanisms relating temperature regimes and California sardine abundance are discussed, as well as possible connections between the regime problem, and the other two approaches—the fishery problem and the recruitment problem.

## DATA AND METHODOLOGY

Local California sea-surface temperature (SST) and surface-air temperature (SAT) series from San Francisco (the northernmost recorded area of spawning; Radovich 1982) and San Diego (in the Southern California Bight, the main spawning area) were used. A number of other SST and SAT series from locations covering most of the coast (figure 1; also see figures 2 and 3) were also used to analyze the spatial and temporal coherence. Only the longest and most complete data series were used. All series are from Cayan et al. 1991, and were standardized by expressing the data as anomalies of the monthly averages.

To eliminate secular trends, series were detrended by expressing the data as departures from the least squares fitted line. Data were also smoothed to eliminate high-frequency variability by using the cubic spline procedure in a commercial statistical software package (Graphtool). We consistently used the same smoothing degree (0.5) in all cases. We calculated combined series by averaging the detrended and

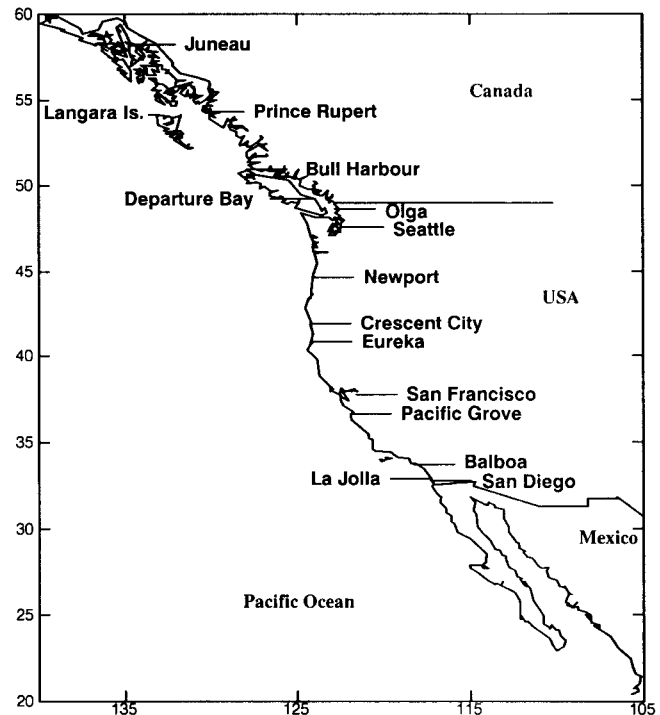


Figure 1. Coastal stations for SST and SAT data.

smoothed local SST (thus obtaining a combined SST series) as well as the SAT (obtaining a combined SAT series).

For a planetary index, we used the global air surface temperature (GSAT) series from Jones and Wigley (1990), as digitized from their figure 1. We used the same criteria for standardizing, detrending, and smoothing the GSAT as for the local SST and SAT series.

A number of indices of sardine abundance have been developed, each with its own limitations. For this paper, we selected three: (1) total landings from the U.S. and Baja California after Radovich 1982; (2) virtual population analysis (VPA) biomass estimates after Murphy 1966 (for the years 1932–44), and MacCall 1979 (for the years 1945–65), complemented with indirect estimates of spawning biomass after Smith 1990 for the years in which VPA estimates are not available; and (3) scales contained in marine sediments after Soutar and Isaacs 1974.

Finally, we used CalCOFI cruise data to obtain the average proportion of positive stations for both sardine eggs and larvae for the area between lines 80 and 100, and from the coast to station 100 of the CalCOFI grid, thus covering the Southern California Bight.

## GLOBAL AND LOCAL TEMPERATURE REGIMES

Climatic variation has long been recognized on larger time scales, such as glacial periods. Nowa-

days, global change on a shorter time scale is a common issue. Recently it has been associated with global warming due to the greenhouse effect, which results from the addition of abnormally high amounts of certain gases to the atmosphere. However, some years ago several climatologists warned about the existence of large interannual changes that had been previously undetected (see, for instance, Gribbin 1986). In fact, many papers were written about the large-scale changes in climate before the global circulation models were forecasting generalized warming (Hansen et al. 1981).

On the other hand, long before the actual recognition of climatic change, some authors pointed to large-scale shifts in the distribution of several species and related them to regional warming or cooling periods. Noticeably, Hubbs (1948) discussed the warm period occurring during the 1880s to 1890s, mostly as related to shifts in the distribution of several marine organisms, including the California sardine.

Periods of interannual thermal variation may be classified in terms of duration: the century-long time trend (secular), the interdecadal variation, and

the high-frequency interannual changes, including the El Niño Southern Oscillation events. Regime changes are associated with the second component.

To identify the existence of such regimes along the west coast of North America, we compared local temperatures indices with a global index of change. As a first approach, we selected San Diego (related to the main spawning area of sardine) and San Francisco (the northernmost spawning center) SST and SAT series, and compared them with the selected global index (GSAT).

In figure 2, we plotted the GSAT series in the upper panel, with original data represented by circles, and the simple linear trend of the series (i.e., least squares fitted line). In the middle panel, we plotted the annual SAT anomalies for San Francisco and San Diego, with the simple linear trends for each data series. Finally, the lower panel shows the annual SST anomalies for both ports, with their linear trends.

Taking the maximum variation (the largest minus the smallest value in each series) as 100%, to standardize the values, the mean annual increase in temperature for the GSAT series is 0.3%, quite the same

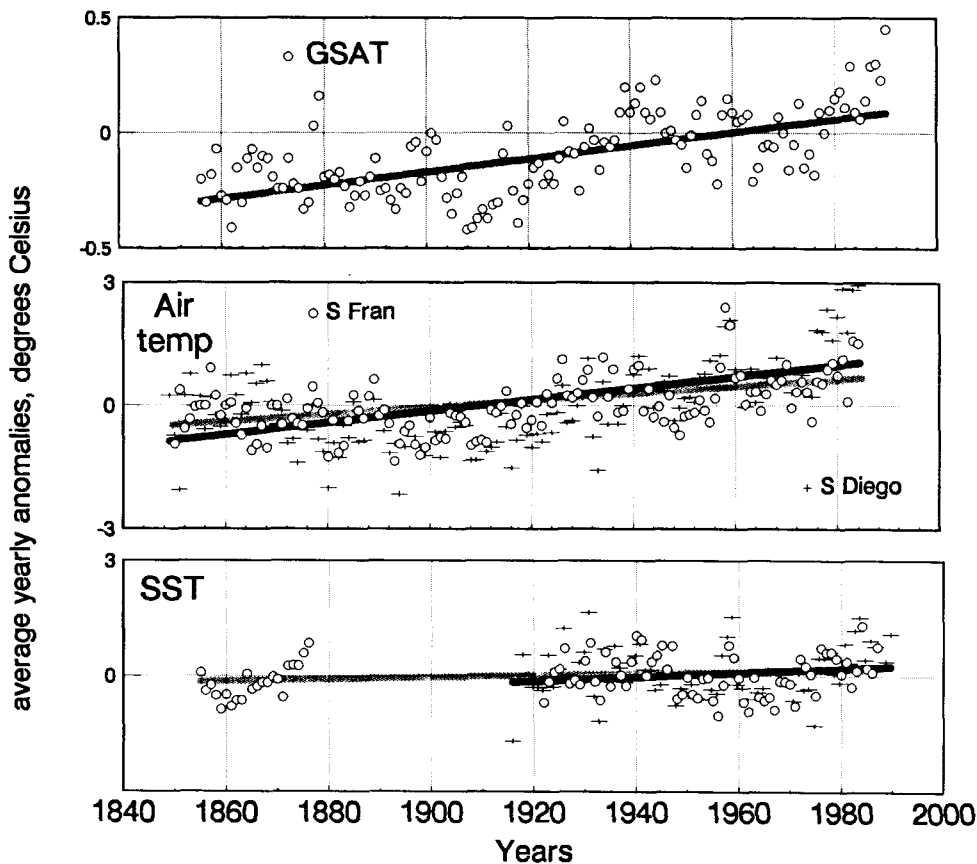


Figure 2. Temperature indices (data and linear trends). *Top panel:* GSAT, after Jones and Wigley (1990). *Middle panel:* San Francisco and San Diego SAT. *Bottom panel:* San Francisco and San Diego SST.

as the average for the two SAT series. However, the mean annual increase is only 0.1% for the SST series, or roughly one-third of the GSAT and SAT series. Leaving aside the fact that the GSAT series trend is as high as that of the air temperatures of fast-growing (and thus fast-warming) cities (which is indeed surprising, since only a tiny amount of the earth's surface is covered by fast-growing cities), it is evident that the ocean is warming at a slower rate.

It is unlikely that sardine abundance would be affected by this secular trend in SST. But it is evident from figure 2 that major changes occur in periods of about a decade; these changes are present both in the sea and in the air, as well as in the global index.

Once the secular trend is eliminated by detrending, and the high-frequency interannual variation is

eliminated by smoothing, the resulting series basically show interdecadal variation. The annual average detrended and smoothed anomalies are shown in figure 3 (SAT) and figure 4 (SST). Besides the already mentioned variability, both figures show spatial coherence between the locations along the North American west coast, in both sea and air temperatures, for most times and most places. For the purposes of this presentation, and since we are interested only in major changes (i.e., persistent spatial and temporal changes), SST and SAT series may be pooled and combined in two series — one for SST and another for SAT.

The combined SST and SAT series from the beginning of the century are shown in figure 5, together with the detrended and smoothed GSAT

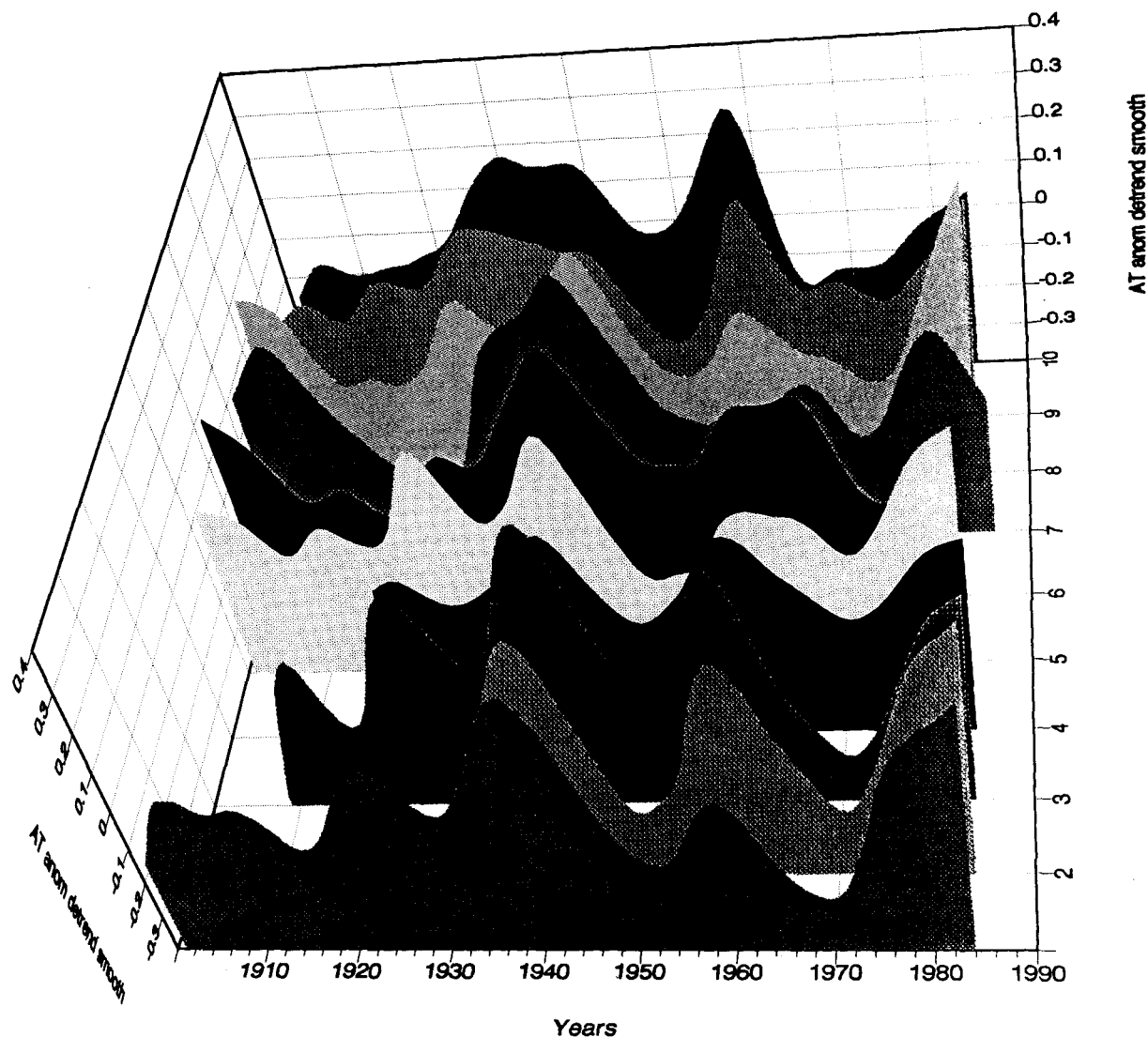


Figure 3. Detrended and smoothed SAT series (expressed as anomalies) of the following stations (from front to back): Juneau AK (1), Langara Island CAN (2), Prince Rupert CAN (3), Bull Harbour CAN (4), Olga WA (5), Seattle WA (6), Newport OR (7), Eureka CA (8), San Francisco CA (9) and San Diego CA (10). Anomalies in degrees Celsius.

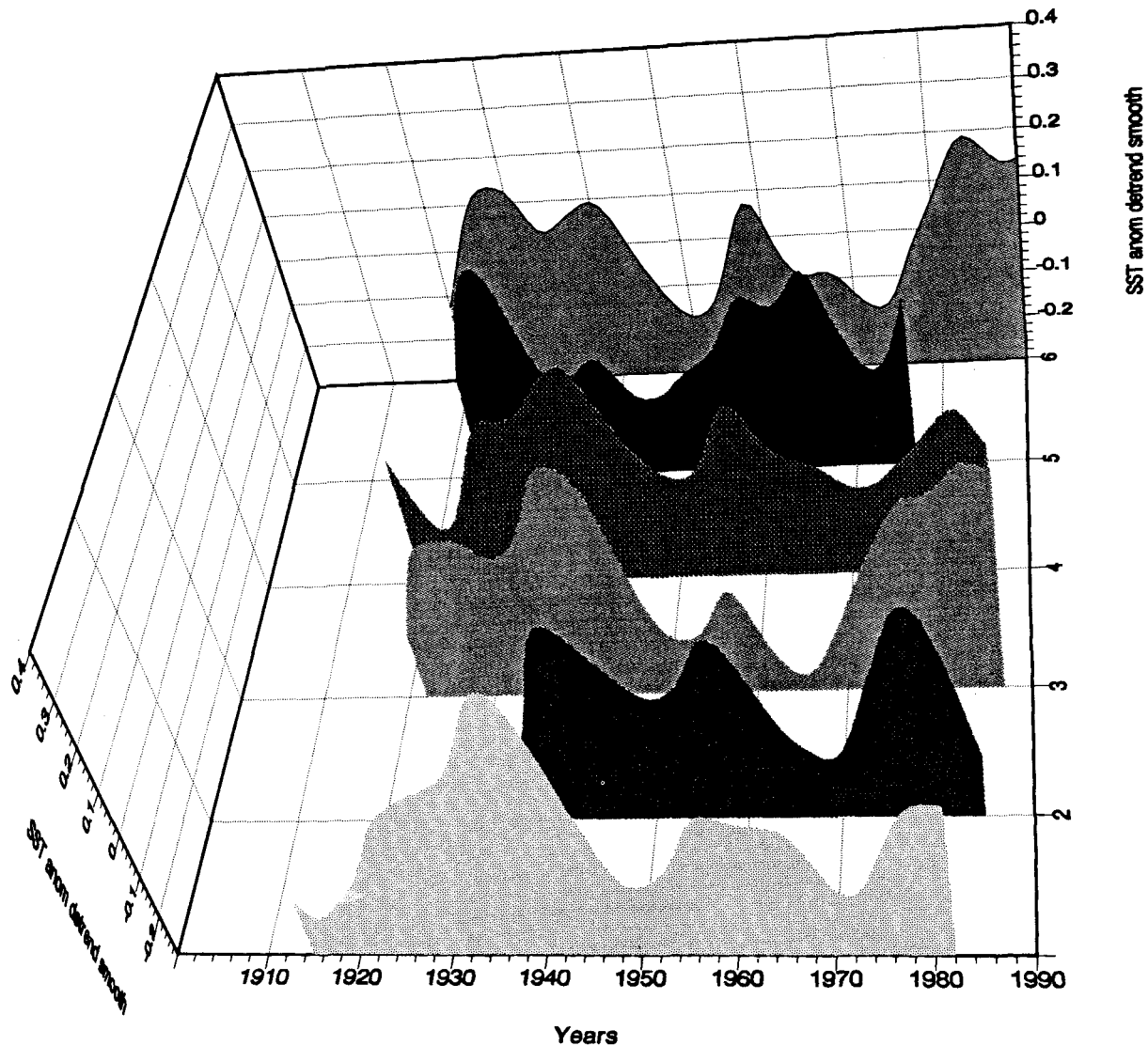


Figure 4. Detrended and smoothed SST series (expressed as anomalies) of the following stations (from front to back): Departure Bay CA (1), Crescent City CA (2), San Francisco CA (3), Pacific Grove CA (4), Balboa CA (5) and La Jolla CA (6). Anomalies in degrees Celsius.

series. Despite minor deviations, there is a coherent pattern between the three series with respect to parallel cooling-warming trends. However, a main difference between series is evident: a cooling trend is clear in the SAT since the early 1980s, while the SST continued to rise, although with a much lower rate than in the previous period. On the other hand, there is no change in the GSAT series, which shows a sustained warming trend since the late 1970s.

We suggest that regimes would be sustained periods (longer than one decade) of warm or cold average temperatures, as compared to the long-term means, which are coherent between time and geographic area. From figure 5, and in very rough terms, we can identify coherence between the global and the local levels. There was a cold regime from

the beginning of the century up to around 1930; a warm regime between 1930 and about 1950, which peaked around 1940; a subsequent cold regime from 1950 until the mid 1970s (although a brief but intense warming was present during the late 1950s and the early 1960s, and was particularly evident at the local level); and a warm regime beginning in the mid 1970s and peaking during the early 1980s. Since then, local and global regimes do not agree: while global warming is persistent, local SAT has undergone a new cooling, and the local SST rate of change has decreased.

#### CALIFORNIA SARDINE ABUNDANCE REGIMES

In order to identify coherence between thermal and abundance regimes, we plotted the three se-

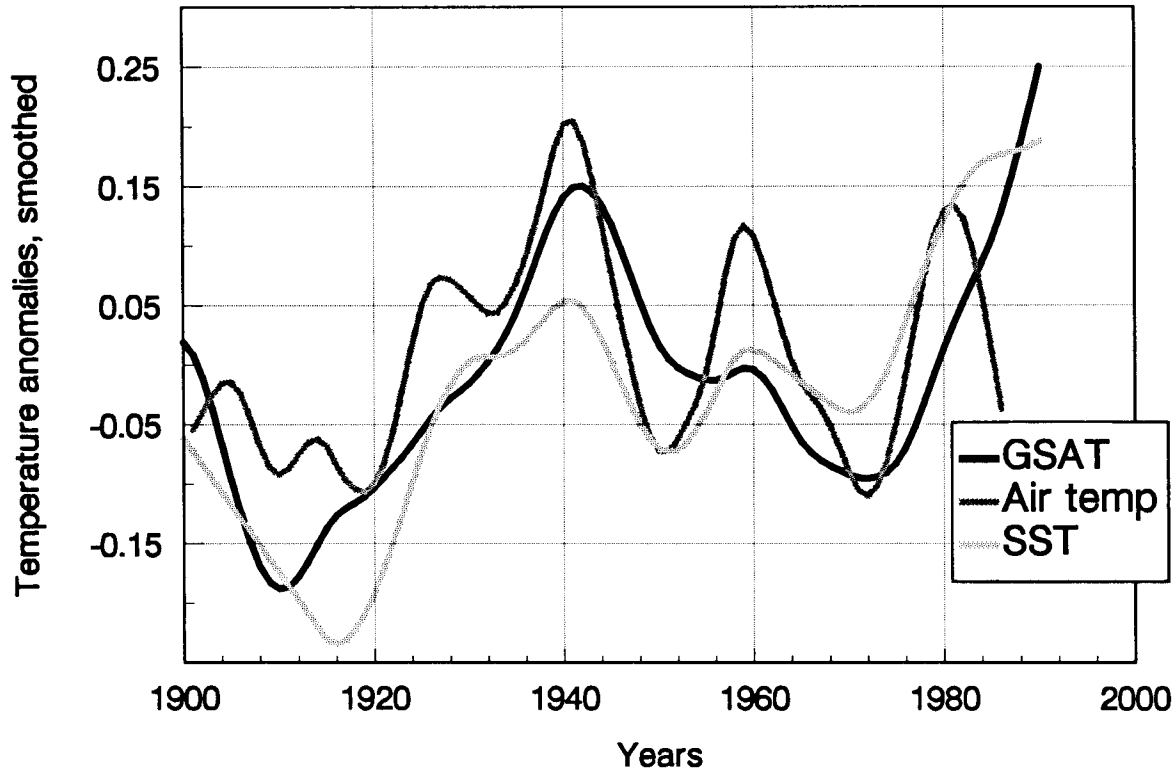


Figure 5. Averaged anomalies of the series presented in figures 3 (SAT) and 4 (SST), corresponding to the North American coastal stations showed in figure 1, together with the GSAT from Jones and Wigley (1990).

lected indices of sardine abundance together with the detrended-smoothed GSAT series (figure 6). Some considerations about these abundance indices may be useful. The first fact that we face when dealing with any abundance index is that, up to now, all of them have some limitations.

The validity of catch data as an index of abundance has been repeatedly questioned, since no variations in effort are taken into account. Radovich (1982) objected to the use of catch-per-effort data. Even though the analysis of minor variations in abundance might be rejected on the basis of these limitations, there should be no doubt that catch data do reflect gross trends in abundance. Except in the case of a regulated fishery (either by moratorium or some sort of effort limitation), landings are indeed roughly proportional to abundance. Thus we used available data from U.S. and Mexico fisheries until 1967, when a moratorium was declared for California.

Scale-abundance data from marine sediments of the Santa Barbara Basin are an independent estimate of population abundance. They have the limitation of being available for only one location; however, this location is near the center of the spawning area for the California sardine. Although the indices of abundance are limited, conclusions based on a si-

multaneous analysis (if the indices are in agreement) can be more reliable than indices that are analyzed individually.

There is a correspondence between the different sardine abundance regimes (figure 6). Sardine populations were abundant before the 1950s, scarce from then until the late 1970s, and growing since then to the mid 1980s. These abundance regimes are parallel to the global thermal regimes indicated by the detrended and smoothed GSAT series in the lower panel of figure 6. Warm global thermal regimes correspond to high abundance regimes of the California sardine, and vice versa. Thus, and from the aforementioned correspondence between local and global temperature regimes, it may be concluded that local temperature, global surface-air temperature, and California sardine abundance regimes are all similar.

#### PROPOSED MECHANISMS OF CHANGE AND POSSIBLE RELATIONS TO OTHER APPROACHES

A number of hypotheses for possible mechanisms have been proposed concerning the effect of environmental change on sardine abundance. Kondo (1980) suggested that the rapid increase in the Japanese sardine stock after 1970 resulted from a very strong year class, which was caused by a gradual

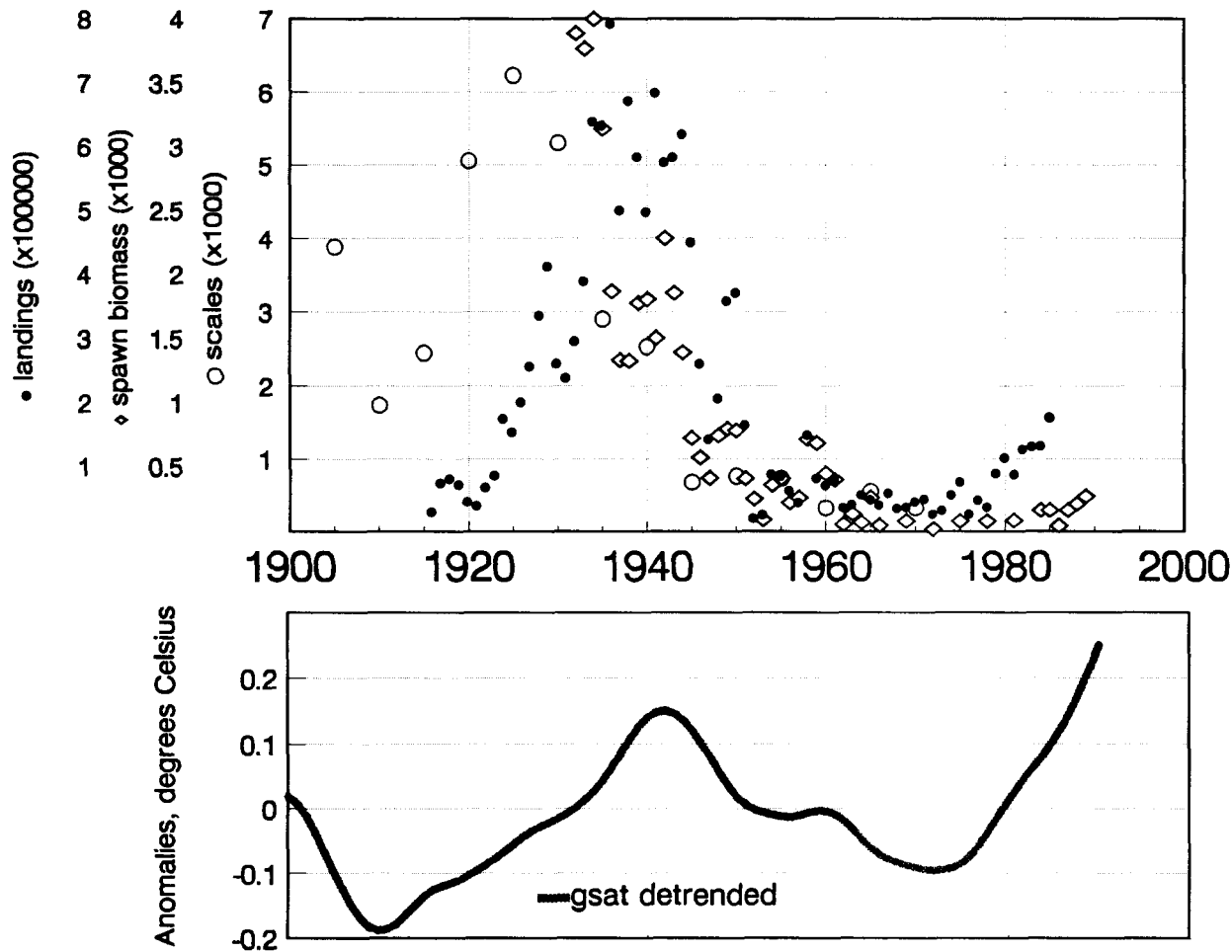


Figure 6. Indices of sardine abundance (landings, spawning biomass, and scales in varved sediments) as compared with the GSAT from Jones and Wigley (1990).

expansion of the spawning area, greater egg abundance, and more favorable conditions for the postlarval stage as a result of a shift of the Kuroshio Current. This current changed from meandering to straight when it was affected by an anomalous southern intrusion of the cold Oyashio Current. This shift in the oceanic circulation created a broad area suitable for copepod nauplii, thus allowing sardine postlarvae to survive the critical period after yolk absorption.

The effect of temperature in this mechanism may be generalized with respect to climatic regimes, since shifts in oceanic circulation are expected from one thermal regime to another. Lange et al. (1990) analyzed SST and sea-surface pressure series for the 1950–86 period, and pointed out that during recent years a weakening of the California Current and a reduction in upwelling activity have occurred.

This shift may lead to increased spawning area and egg abundance. It is not clear, however, if it may also

lead to favorable conditions for the sardine larvae. On one hand, Lange et al. (1990) proposed low levels of productivity as a result of this change; thus a reduction in food supply for the larvae is to be expected. On the other hand, larval survival may be favored through thermal stratification (Lasker 1981) and reduction in turbulence and upwelling-derived offshore advection (Parrish et al. 1981).

Kawasaki and Omori (1988) proposed that increased solar input not only results in higher SST, but encourages expansion of the Japanese sardine population by increasing phytoplankton production. They noted that since this species depends strongly on phytoplankton it is also closely related to solar radiation.

If this mechanism applies to the California sardine, certain relationships must also be true. Abundance, temperature, and productivity must change rather simultaneously with each other if they are directly related to solar radiation. However, a direct

SST-productivity relationship does not seem consistent with the idea that upwelling activity determines productivity.

Regarding the effect of global warming on upwelling, Bakun (1990) suggested a mechanism in which enhancement of daytime heating by solar radiation, combined with nighttime inhibition of cooling, should lead to an increase in wind-stress-derived upwelling activity and thus to relative cooling of the surface coastal waters. He stated that upwelling activity has been decreasing in California since 1975, in agreement with the observed warming trend in SST. With this concept, there would be an inverse relation between SST and productivity, in both the secular and the interdecadal time scales.

Lange et al. (1990) obtained a data series of coastal primary production as indicated by the flux of diatoms to the marine sediments in the Santa Barbara Basin, for the period from 1950 through 1986. Unfortunately, this series covers only a period of low sardine abundance. However, Lange et al. found that during the 1954–72 period (cold SST), productivity was higher than in the period of warm SST during 1973–86, by a factor of five. They suggested that this difference was associated with the reduction in upwelling, and thus were in agreement with Bakun (1990). From these papers, it seems that sardine abundance is not directly governed by primary production in California, but the evidence must be considered inconclusive because no indications of primary productivity during a high-abundance mode are discussed.

We proposed a mechanism based on the spawning temperatures and some upwelling-related factor (Lluch-Belda, Hernández-Vázquez et al. 1991; Lluch-Belda, Lluch-Cota et al. 1991). The idea is that the California sardine population expands its habitat wherever proper SST and moderate upwelling activity exist. High productivity areas such as the Southern California Bight are in the cold limits of the sardine distribution, and can be occupied by resident populations only when SST is relatively high for sustained periods, allowing abundance to increase.

When cooling occurs, sardine spawning is restricted to Punta Eugenia, a less-productive area where spawning occurs year-round because of the higher temperatures and convenient upwelling activity. Besides temperature, there is a level of upwelling that is optimal for sardine spawning; when the levels are too high or too low, spawning decreases. In this mechanism, the association with thermal regimes is based on the direct effect of temperature on spawning activity.

From the above-discussed mechanisms, it is evident that some aspects of the recruitment problem and the regime problem are related. MacCall (1986) stated that sardine population growth and intraspecific competition are the main factors that force the expansion of the sardine population. Indeed, a growing population during a warm period should go through this process. Parrish et al. (1981) proposed that offshore advection during intensified upwelling may result in the loss of eggs and larvae to areas unsuitable for growth. Ahlstrom (1965) noted that high productivity (resulting from intensified upwelling) results in poor sardine year classes. Lasker (1981) proposed that a nonstratified ocean may result in poor survival. Indeed, many of these mechanisms may also operate within the regime problem.

However, the earlier idea—that is, the survival rate from the egg stage to the late larvae—demands special attention. If sardine abundance is determined this way, and is also related to temperature regimes, then some temperature-related factor should affect the egg-to-larvae process in a way that is reflected in abundance. Thus the egg-to-larvae proportion should be quite different between warm and cold regimes; a constant proportion would be, at least, difficult to explain.

Another possibility is that spawning itself may be related to temperature, and thus variable. Even with a constant ratio between eggs and larvae (i.e., a constant survival rate), abundance may be temperature-determined. Regarding the California sardine, Ahlstrom (1965) identified a rather constant rate between eggs and larvae through different years. In figure 7 we show the average proportion of positive stations for both eggs and larvae of sardine for the area between lines 80 and 100 and from the coast to station 100 of the CalCOFI grid, covering the Southern California Bight. In the same figure, we have placed the detrended GSAT regime index. Despite minor deviations, it is clear that there are more sardine eggs (and thus increased spawning) during the warm regime, and the relative abundance of both eggs and larvae is essentially similar.

If a rather constant egg-survival ratio is found to be a general phenomenon for sardine, as it seems to be for the area and period analyzed here, it would mean that spawning itself is variable, and depends on environmental conditions, as previously proposed (Lluch-Belda, Lluch-Cota et al. 1991). However, it should be stressed that the approaches are not mutually exclusive, since climate variations may directly determine spawning, and also modify the egg-survival rate. Many of the proposed mechanisms could be reconciled through this point of



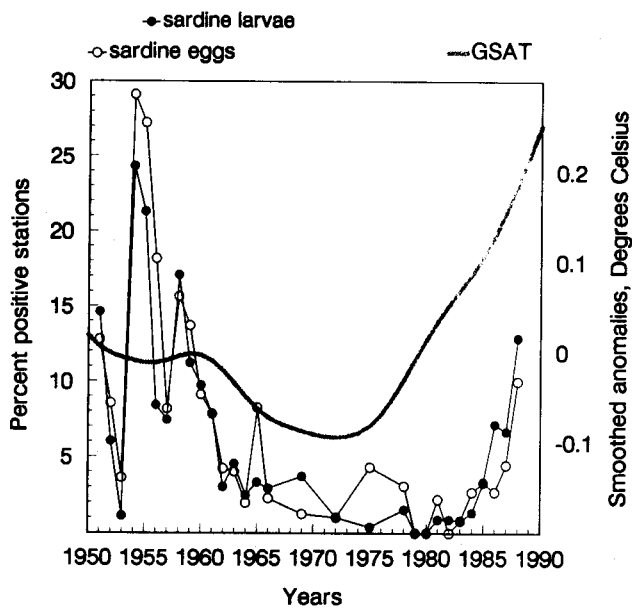


Figure 7. Average proportion of positive stations for sardine eggs and larvae for the area between lines 80 and 100 and from the coast to station 100 of the CalCOFI grid, together with the detrended GSAT from Jones and Wigley (1990).

view, although the relative contributions of both processes to the final abundance level remain a topic for future discussion.

Finally, the relation between the regime problem and the fishery problem may be more evident at the time the populations are being depleted. Diminished spawning due to environmental changes may result in poor recruitment. If a fishery is at the same time harvesting the nonspawning population, its total abundance would diminish much faster than as the result of natural mortality alone (which makes fishery regulation particularly important under these conditions). It would also seem reasonable that a smaller population resulting from intensive exploitation would take longer to grow, even under favorable climatic conditions. However, the events in the Japanese fishery, with a population growing explosively even under intense exploitation (Kawasaki 1983), seem to show otherwise and give insights into the high potential of population growth.

Up to now, there has been no agreement between the different authors, although some factors such as food supply; oceanic circulation patterns; changing winds and resulting upwelling patterns; and larval food access as related to turbulence, temperature, and habitat selection have been considered important. The difficulty in discriminating among these factors is that they are closely related and mostly change simultaneously. Despite the specific mechanism through which climatic regimes and abun-

dance regimes may be related, no doubt should remain as to the existence of more than one "problem" at the root of the sardine population's fluctuations. However, the relative importance of these problems may be quite different, and a great deal of research must be done to reach more definitive conclusions.

### LITERATURE CITED

Ahlstrom, E. H. 1965. A review of effects of the environment of the Pacific sardine. ICNAF Spec. Publ. 6:53-76.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* 247(12):198-201.

Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends in abundance estimates for the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33 (this volume).

Cayan, D. R., D. R. MacLain, W. D. Nichols, and J. S. DiLeo-Stevens. 1991. Monthly climatic time series data for the Pacific Ocean and western Americas. U. S. Geol. Surv. Open-File Rep. 91-92, 380 pp.

Clark, F. N., and J. C. Marr. 1955. Population dynamics of the Pacific sardine. Calif. Coop. Oceanic Fish. Invest. Progress Rep. 4:11-48.

Gribbin, J. 1986. El clima futuro. Biblioteca Científica Salvat Editores, 241 pp.

Hansen, J., D. Johnson, A. Lacis, S. Lebedeff, P. Lee, D. Rind, and G. Russell. 1981. Climate impact of increasing atmospheric carbon dioxide. *Science* 213(4511):957-966.

Hjort, J. 1914. Fluctuations in the great fisheries of the North Europe viewed in the light of the biological research. Cons. Perm. Int. Explor. Mer. Rapp. and Proc. Verb. 20, 228 pp.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with change in ocean temperature. *J. Mar. Res.* 7(3): 459-482.

Jones, P. D., and T. M. Wigley. 1990. Global warming trends. *Sci. Amer.* 263(2):66-73.

Kawasaki, T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuations from the viewpoint of the evolutionary ecology. In Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, April 1983. Sharp, G. D. and J. Csirke, eds. FAO Fish. Rep. 291(3):1065-1080.

Kawasaki, T., and M. Omori. 1988. Fluctuations in the three major sardine stocks in the Pacific and the global trend in temperature. In Long term changes in marine fish populations, T. Wyatt and M. G. Larrañeta, eds. Vigo; Instituto de Investigaciones Marinas de Vigo: 37-57 (Proceedings of a symposium held in Vigo, November 1986).

Kondo, K. 1980. The recovery of the Japanese sardine—the biological basis of stock-size fluctuations. Rapp. P-V. Réunion. Cons. Int. Explor. Mer. 177:332-354.

Lange, B. C., S. K. Burke, and W. H. Berger. 1990. Biological production off southern California is linked to climatic change. *Clim. Change* 16(3):319-330.

Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years 1975 through 1978. Rapp. P-V. Réunion. Cons. Int. Explor. Mer. 178:375-388.

Lasker, R., and A. MacCall. 1983. New ideas on the fluctuations of the clupeoid stocks off California. In C.N.C./SCOR proc. of the Joint Oceanographic Assembly 1982—general symposia. Ottawa, Can. Pp. 110-120.

Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. World wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* 8:195-205.

Lluch-Belda, D., S. Hernández-Vázquez, and R. A. Schwartzlose. 1991. A hypothetical model for fluctuation of the California sardine population (*Sardinops sagax caerulea*). In Long-term variability of pelagic fish populations and their environment, T. Kawasaki et al., eds. Pergamon Press, pp. 293-300.

- Lluch-Belda, D., D. B. Lluch-Cota, S. Hernández-Vázquez, C. A. Salinas-Zavala, and R. A. Schwartzlose. 1991. Sardine and anchovy spawning as related to temperature and upwelling in the California Current system. *Calif. Coop. Oceanic Fish. Invest. Rep.* 32:105-111.
- MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. *Calif. Coop. Oceanic Fish. Invest. Rep.* 20: 72-82.
- . 1986. Change in the biomass of the California Current ecosystem. *In* Variability and management of large marine ecosystems, K. Sherman and L. M. Alexander, eds. A.A.A.S. Select. Symp. Ser. No. 99, pp. 33-54.
- Murphy, G. I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc. Calif. Acad. Sci. Fourth Series* 34:(1)1-84.
- Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* 1:175-203.
- Radovich, J. 1982. The collapse of the California sardine fishery: What have we learned? *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:56-78.
- Smith, P. E. 1990. Monitoring interannual changes in spawning area of Pacific sardine (*Sardinops sagax*). *Calif. Coop. Oceanic Fish. Invest. Rep.* 31:145-151.
- Soutar, A., and J. D. Isaacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 13: 63-70.
- . 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off the Californias. *Fish. Bull.* 72:257-273.
- Wolf, P. 1992. Management of the recovery of the Pacific sardine and the recent California fishery. *Calif. Coop. Oceanic Fish. Invest. Rep.* 33 (this volume).