# A REVIEW OF THE LOW-FREQUENCY RESPONSE OF THE PELAGIC ECOSYSTEM IN THE CALIFORNIA CURRENT

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## ABSTRACT

Recent analyses of CalCOFI data collected during the last three decades have revealed the existence of long-period fluctuations occurring in the California Current. This paper reviews the biological response of the ecosystem to these fluctuations in terms of zooplankton biomass, which is shown to have large-scale, low-frequency trends.

This low-frequency response is found to be coherent with interannual changes in flow pattern occurring in the Eastern Boundary Current. The ecological implications are that the California Current ecosystem might be permanently under nonequilibrium conditions, which in turn would suggest that the classical biologically interactive processes of competition and predation are only secondary mechanisms in regulating plankton abundance and species proportions.

## RESUMEN

Recientes análisis de los datos colectados durante las tres últimas décadas por CalCOFI han revelado la existencia de fluctuaciones de período largo en la Corriente de California. En este trabajo se reexamina la respuesta biológica del ecosistema a estas fluctuaciones en términos de la biomasa del zooplancton, datos que muestran modos de variación de gran escala y baja frecuencia.

La respuesta de baja frecuencia es coherente con cambios interanuales en el patrón de circulación que tienen lugar en toda la Corriente de Margen Oriental. Las implicaciones ecológicas son que el ecosistema de la Corriente de California estaría en forma permanente bajo condiciones de desequilibrio, lo que a su vez sugiere que los procesos biológicos interactivos clásicos, competencia y depredación, serían solamente mecanismos secundarios en la regulación tanto de la abundancia como de las proporciones de especies en el plancton.

## REVIEW

### Introduction

After the disappearance of the Pacific sardine fishery from the coast of California, The California

Cooperative Oceanic Fisheries Investigations (CalCOFI) were started with the intention of monitoring the reproductive success of the pelagic stocks inhabiting the region. Since 1949 CalCOFI has accumulated a huge amount of information on a series of physical and biological variables of the California Current System. The long time series resulting from this effort and the information contained are unique compared to the usual temporal scale of oceanographic observations.

From the point of view of fisheries research, it is of primary importance to predict with relatively high precision the changes of the stocks under exploitation. Fisheries models based on stock-recruitment relationships show adequate predictive abilities for some types of stocks, in particular demersal fish. However pelagic stocks seems to be more variable, and standard techniques do not provide consistently reliable answers for management purposes. From the theoretical side of the problem, a review of classical theory is long overdue in order to remove these models from the relative "ecological vacuum" where they were designed to function. From the empirical side, therefore, consideration of other aspects of the problem, such as density independence and other ecological factors, are still needed and useful. Analysis of the long time series of zooplankton biomass collected by CalCOFI provides some insights into the kind of variability observed at the ecosystem level in the interannual and interdecadal time scales. These have been shown to be important time scales for the fluctuation of some fish stocks (Parrish and MacCall 1978; Cushing 1976).

My work, together with that of Dudley Chelton, has coalesced into a single characterization of an important low-frequency mode of variability observed in this region that is coherent for the physical and biological components of the system. In this presentation I will discuss first the spatial and temporal scales relevant to the problem, then review the work done to characterize the low-frequency response of the ecosystem, and finally present evidence of the causal connections that this mode of variability seems to have and discuss its implications.

The work presented in this review has had several antecedents. Among them are the studies by Reid et

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al. (1958), Wickett (1967), and Colebrook (1977), all of which indicated that some large-scale, low-frequency events were occuring in the biota (see also the papers presented at the Symposium on The Changing Pacific Ocean in 1957-58, held at Rancho Santa Fe, June of 1958, in *CalCOFI Reports*, Volume VII, 1960). More recently, longer time series of data have been analyzed (Bernal 1979, 1980; Bernal and McGowan in press; Chelton 1980, 1981), and that work is reviewed here.

## Spatial Boundaries of the California Current Pelagic Ecosystem

At subtropical latitudes in the eastern half of the North Pacific there are at least two well defined oceanic plankton communities: the assemblage of the Central Water mass and the assemblage of the California Current System. These assemblages inhabit two drastically different environments, the former in oligotrophic waters showing a well developed halocline underlying high salinity and warm waters at the surface. The latter lies within waters of low salinity, cold, and with high nutrients and dissolved oxygen concentrations. Figure 1 shows a section extending from 74 km offshore the California coast to a point well out into the North Pacific Central Gyre. Shoreward of 126° W there is a well developed surface low-salinity minimum (upper panel), a feature typical of the California Current, and beginning at 138° W, 1,570 km offshore, the well developed halocline typi-
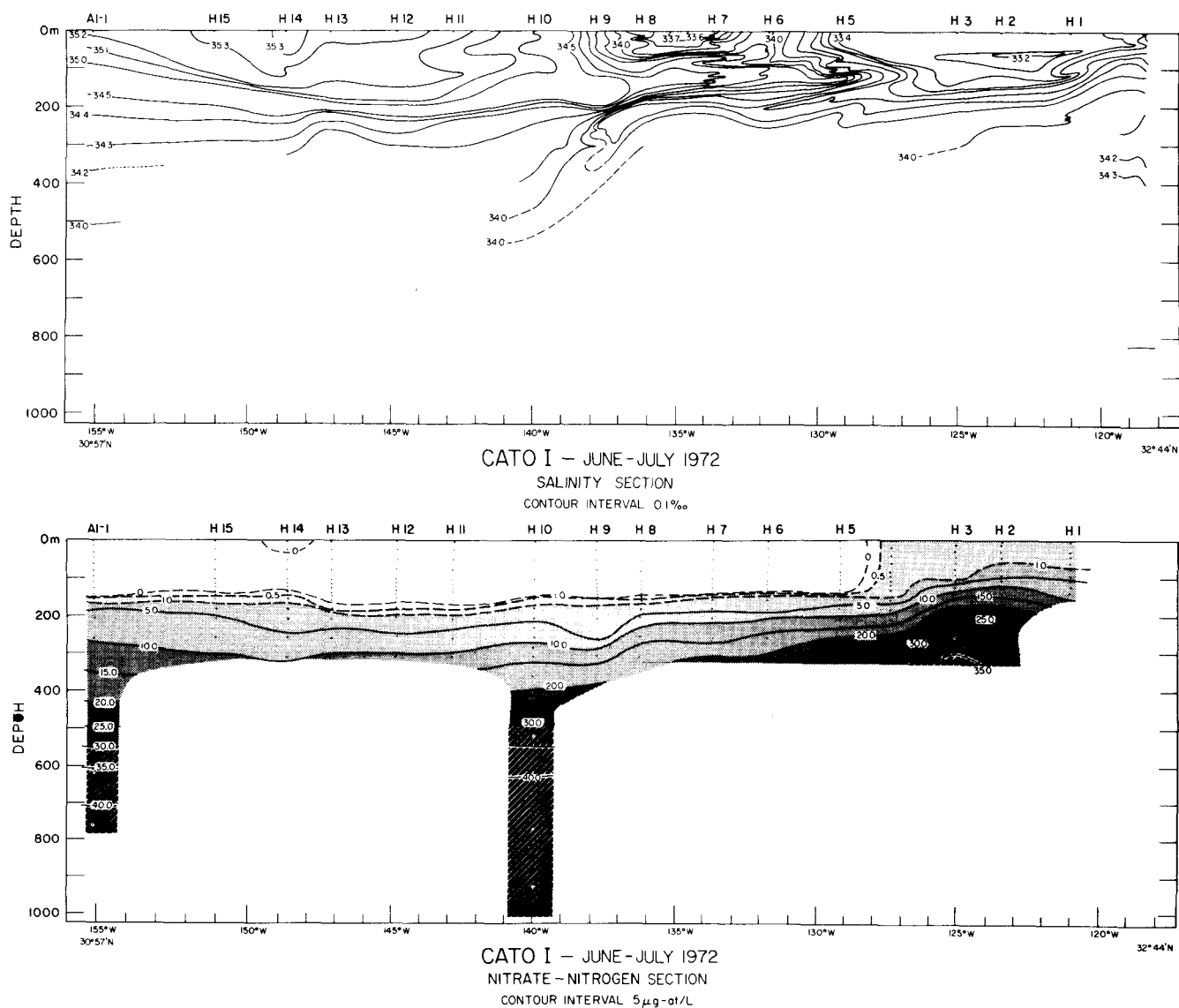


Figure 1. Sections of salinity and nitrate-nitrogen between San Diego and the Central Gyre of the North Pacific (155°W 30°57′N). *Upper panel:* distribution of salinity; between the most inshore station (right) and station H5, located 800 km offshore, waters of subarctic origin are present. *Lower panel:* distribution of nitrate-nitrogen expressed in μg-atoms/liter. Data collected during expedition CATO-I from Scripps Institution of Oceanography. (From Bernal and McGowan, in press.)

cal of the North Pacific Central Water mass appears. The nitrate concentration (lower panel) in the low-salinity area clearly differs from the oligotrophic Central Gyre, where the concentration of nitrate in the surface layer is uniformly below the level of detection of analytical techniques. Two interesting points are well illustrated here: first, that there is good agreement in the offshore extension of the surface low-salinity minimum and the area of enrichment in the California Current (nitrate above 0.5 $\mu$g-atom/liter) and second, that both boundaries lie about 820 km offshore (station H5).

To illustrate the typical cross-shore dimensions of the region of high production in the California Current ecosystem, two sets of replicate monthly samples of zooplankton collected along CalCOFI lines 60 and 90 during spring-summer are shown in Figures 2 and 3. These cross sections begin a few kilometers from the coast and extend more than 1,000 km offshore, thus sampling the western boundary of the ecosystem. These sections of zooplankton biomass are accompanied with information describing the cross-shore patterns of transport during July. The average integrated transport from 0 to 200 m was calculated from CalCOFI's dynamic heights data files (1950-78) assuming the existence of a level of no motion at 500 db. The units of transport are Sverdrups (Svd) per 100 km of cross section, positive values indicating

southward flow.

In Figure 2 the maximum of biomass occurs well offshore from the coast at about 180 km, and the region of high biomass (greater than 200 ml/1,000 m³) extends up to 500 km. Seaward than 800 km, the biomass reaches values typical of the Central Water mass of the North Pacific. Inshore of 180 km the dominant flow is northward, and its mass transport is about 0.45 Svd/100 km. Offshore of 180 km the flow is southward at about 1 Svd/100 km. In a comparison of upper and lower panels, it is noteworthy that the first maximum of biomass at 180 km (A in the figure) and a secondary maximum at 400 km offshore (B) coincide with areas where the cross-shore gradient of average transports is also maximum. In A the gradient is associated with the edge between the Davidson Current and the California Current itself; in B with the westward boundary of a region of intensified southward flow located between 350 and 400 km offshore. These maximum gradients of average flow, although not strictly comparable with maximum shear, point to regions where turbulent mixing might become a three-dimensional process and the vertical introduction of nutrients from below could be enhanced. In Figure 3 the patterns along CalCOFI line 90 are shown. These somewhat parallel those described for line 60, the high biomass zone (greater than 150 ml/1,000m³) extends from 100 to 350 km offshore with two maxima. The maximum inshore (A in the figure) here again coincides with the edge of the northward flow, but the second, in contrast with line 60, coincides with the maximum of southward flow at 270 km (B).

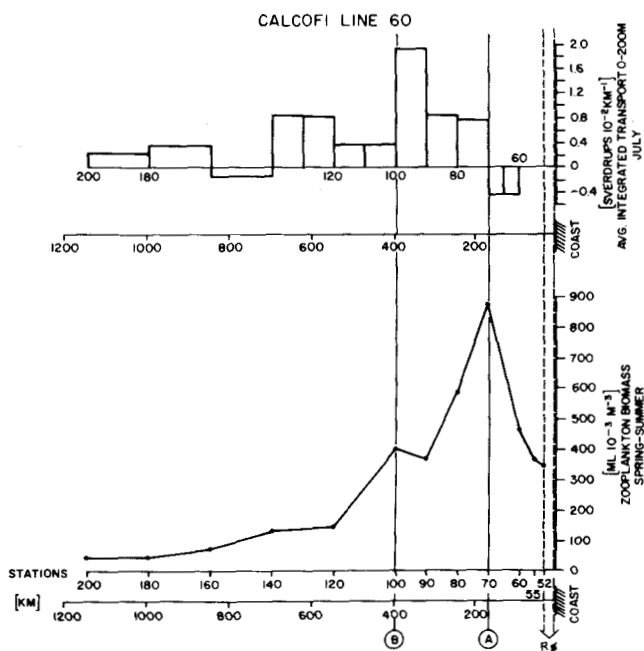An important feature common to both lines is the


Figure 2. Average longshore transport and zooplankton biomass across CalCOFI line 60 during spring and summer. Positive values of transport indicate southward flow. $R_d$ is the distance equivalent to one local baroclinic Rossby radius of deformation. A and B label regions discussed in text. (From Bernal 1980.)
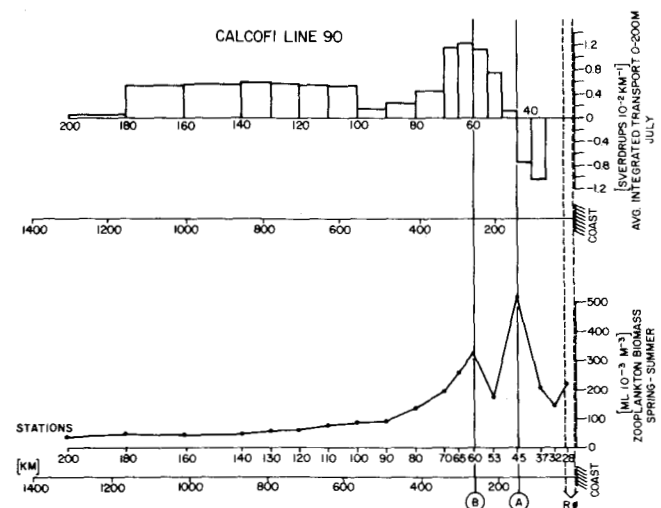

Figure 3. Average longshore transport and zooplankton biomass across CalCOFI line 90 during spring and summer. (From Bernal 1980.)

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relative scale of the zone influenced by coastal up-welling when compared with the width of the zone of high biomass, since for eastern boundary currents like the California Current, coastal upwelling is the process usually associated with the introduction of non-regenerative nutrients into the euphotic zone. Coastal upwelling occurs in a narrow boundary region with typical cross-shore horizontal scale of the same order of magnitude as the local baroclinic Rossby radius of deformation $R_\phi$ (Yoshida 1955; Allen 1973; O'Brien et al. 1977). Estimates of this length scale parameter are illustrated in Figures 2 and 3 by a band adjacent to the coastline. The width of this band is one order of magnitude smaller than the zone of high biomass. In Figure 3 there is a small maximum of zooplankton biomass, within one $R_\phi$-distance from the coast, which is separated from the bulk of the biomass and the two larger offshore maxima by a biomass minimum located at 70 km offshore. This feature does not appear in line 60.

Figure 4 shows the distribution patterns of phytoplankton and zooplankton biomass in the horizontal and the extension of the low-salinity water in the region during April of 1963. Despite significant meso-scale structure in the zooplankton distribution, these maps reflect the major trends and patterns described above for the sections. For example, in the northern region between San Francisco (line 60) and Point Conception (line 80) the contour of 0.10 mg/m³ of chlorophyll-$a$ is found up to 460 km offshore. Similarly, the region of high zooplankton biomass extends farther offshore than 350 km. The cross-shore dimension of the large extension of the low-salinity water of subarctic origin is quite apparent, extending at least 500 km offshore. There is another feature yet illustrated in this figure: the north-south trend of decreasing zooplankton biomass that can be seen (insert, zooplankton biomass map) where the average biomass per each 10 latitudinal lines are summarized in a bar graph. Between San Francisco and Point Conception the average values are over 600 ml/1,000 m³ whereas in the Southern California Bight and off Baja California values less than 200 ml/1,000 m³ are the norm. This trend is certainly one of the dominant features of the ecosystem since it persists when regional averages for the whole 1949-78 period are considered.

As the main conclusions of this section we can extract the following: First, the width of the region of high biomass characteristic of the California Current pelagic ecosystem extends a distance offshore at least eight and, depending on the latitude and season, ten times the local baroclinic Rossby radius of deformation, $R_\phi$, (500 km and 50 km respectively). Second, the locus of highest biomass in the cross-shore direc-
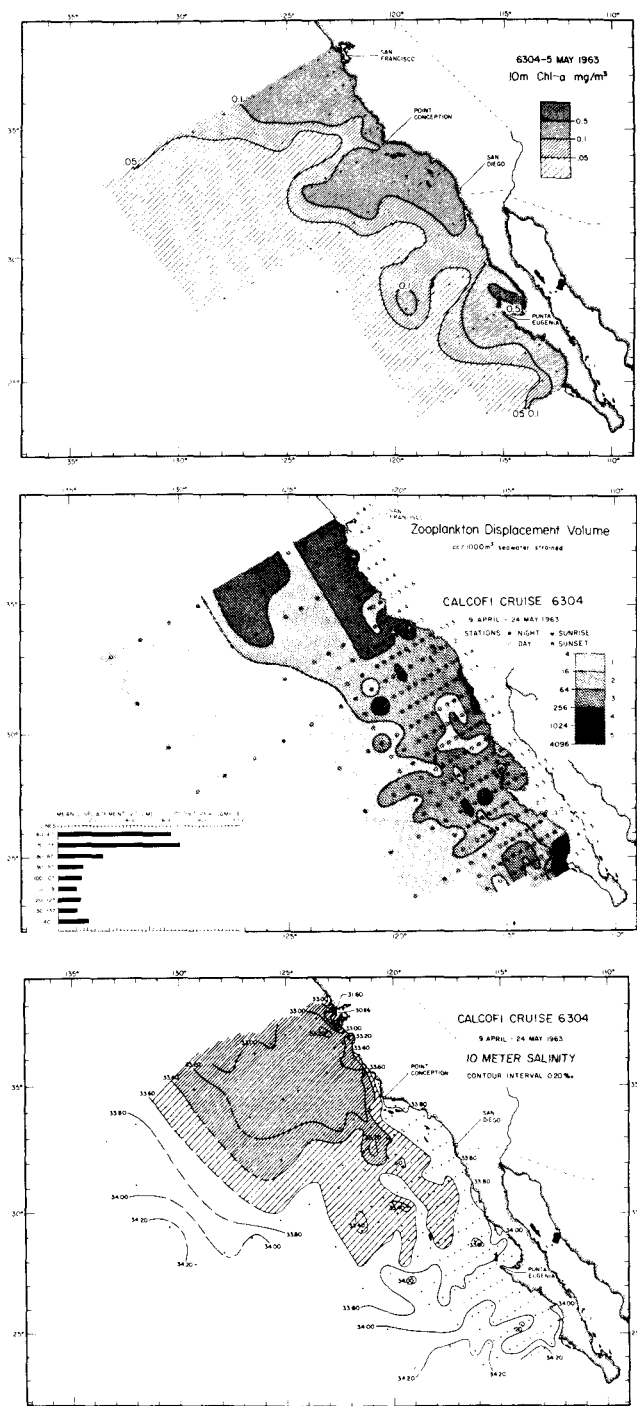


Figure 4. Horizontal distribution of phyto- and zooplankton biomass and 10-m salinity in the California Current region, April-May 1963 (CalCOFI cruise 6304). Top: phytoplankton biomass estimated as chlorophyll-a: units are mg/m³. Middle: zooplankton biomass in ml/1,000 m³. Bottom: salinity at 10-m contour intervals each 0.20 o/oo; dark shading indicates salinities less than 33.40 o/oo; light shading between 33.40 and 33.60 o/oo. (From Bernal and McGowan, in press.)

tion is consistently located offshore at a distance equivalent to at least 3 to 4 $R_\phi$. Third, the dimensions of the region with detectable nutrient concentrations and high phyto- and zooplankton biomass corresponds
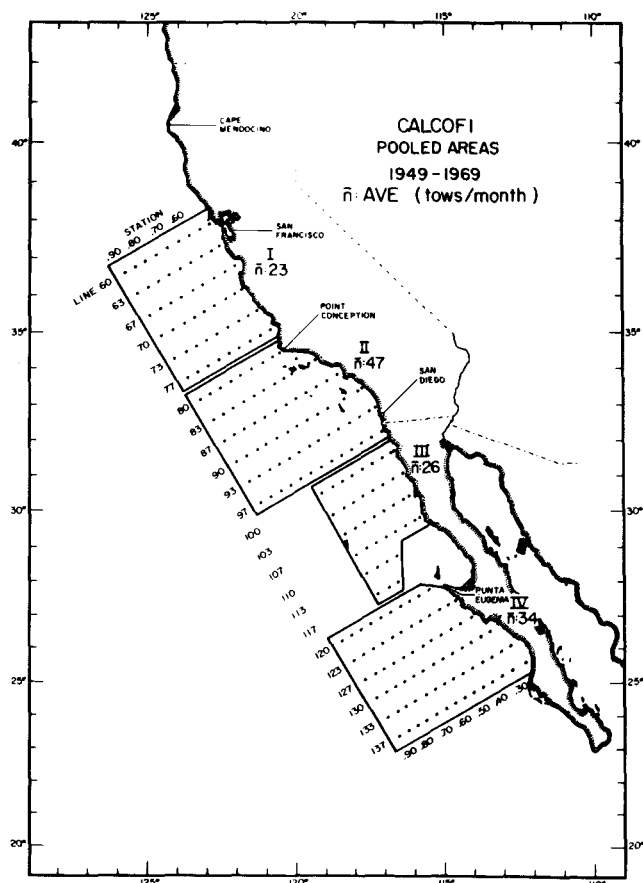
Figure 5. CalCOFI pooled areas. Dots mark positions of CalCOFI stations defined by line number on the left margin and by station number on top and bottom. Since not all stations within an area were occupied each cruise, average number of occupancies per month is given as n. (From Bernal 1980.)

with the areal extension of a water mass that has a northern origin. Fourth, there is a north-south trend of biomass with higher values in the north.

## The Low-Frequency Response of the Pelagic Ecosystem

In a previous paper (Bernal 1979), using the off-shore boundaries defined in the preceding paragraph and biogeographical information from the literature, I divided the CalCOFI sampling grid into four geographical areas and generated for each one of them time series of zooplankton biomass extending from 1949 to 1969. Figure 5 shows these areas. Each element of these time series is the average over space of the log-transformed zooplankton biomass of all the stations occupied within each area on a given month. This treatment filters out the short-term and small-scale spatial variability.

Since in the California Current ecosystem there is a well defined seasonal response, an evaluation of its importance was made. In Table I, the total and seasonal variability of the series are compared. The pro-

## TABLE 1
### Total and Seasonal Variability Per CalCOFI Area

|  | Uncorrected series sum squares | Seasonally corrected sum squares | Seasonality sum squares | % total |
|---|---|---|---|---|
| Area I | 43.9 | 30.7 | 13.2 | 30.0 |
| Area II | 79.9 | 61.7 | 18.2 | 22.7 |
| Area III | 84.6 | 77.5 | 7.1 | 8.4 |
| Area IV | 44.8 | 38.7 | 6.1 | 13.6 |

cedure used consisted of calculating the total variance, subtracting the seasonal component from the series, and recomputing the variance of the new seasonally corrected series. By difference an estimate of the magnitude of the seasonal component for each area is obtained. The seasonal component is more important in the northern part of the region (Area I, 30%) and is less important to the south (about 10%). On the average for the whole California Current ecosystem, seasonality represents less than 20% of the total variability, and given the pattern of distribution of biomass in the cross-shore direction and the very large extent of the areas upon which the series were constructed (between 100,000 to 200,000 km$^2$ each), it can be concluded that the nonseasonal variability is the dominant and most important component of the total response of the ecosystem.

Figure 6, illustrating the four seasonally corrected time series for Areas I through IV, shows that there are large-scale, low-frequency (i.e. long periods) trends. Particular years, 1950, 1953, and 1956, have simultaneous maxima in at least two of the areas; years 1958 and 1959 show coherent sets of minima in all four areas. A more systematic and objective inspection was performed using spectral analysis, the results of which are reproduced in Table 2. The main feature of the spectra is that a large fraction of the total variance lies within the low-frequency band, i.e. less than $1.6 \times 10^{-3}$ cycles/day, or with characteristic periods larger than 608 days. The north-south trend of biomass is paralleled by an increasing proportion of the total variance clustered in the low-frequency band. We have discussed elsewhere (Bernal and McGowan, in press) the reasons why we think this phenomenon represents the response of the ecosystem to external driving. If

## TABLE 2
### Percentage of Total Variance in Low-Frequency Bands of the Spectra

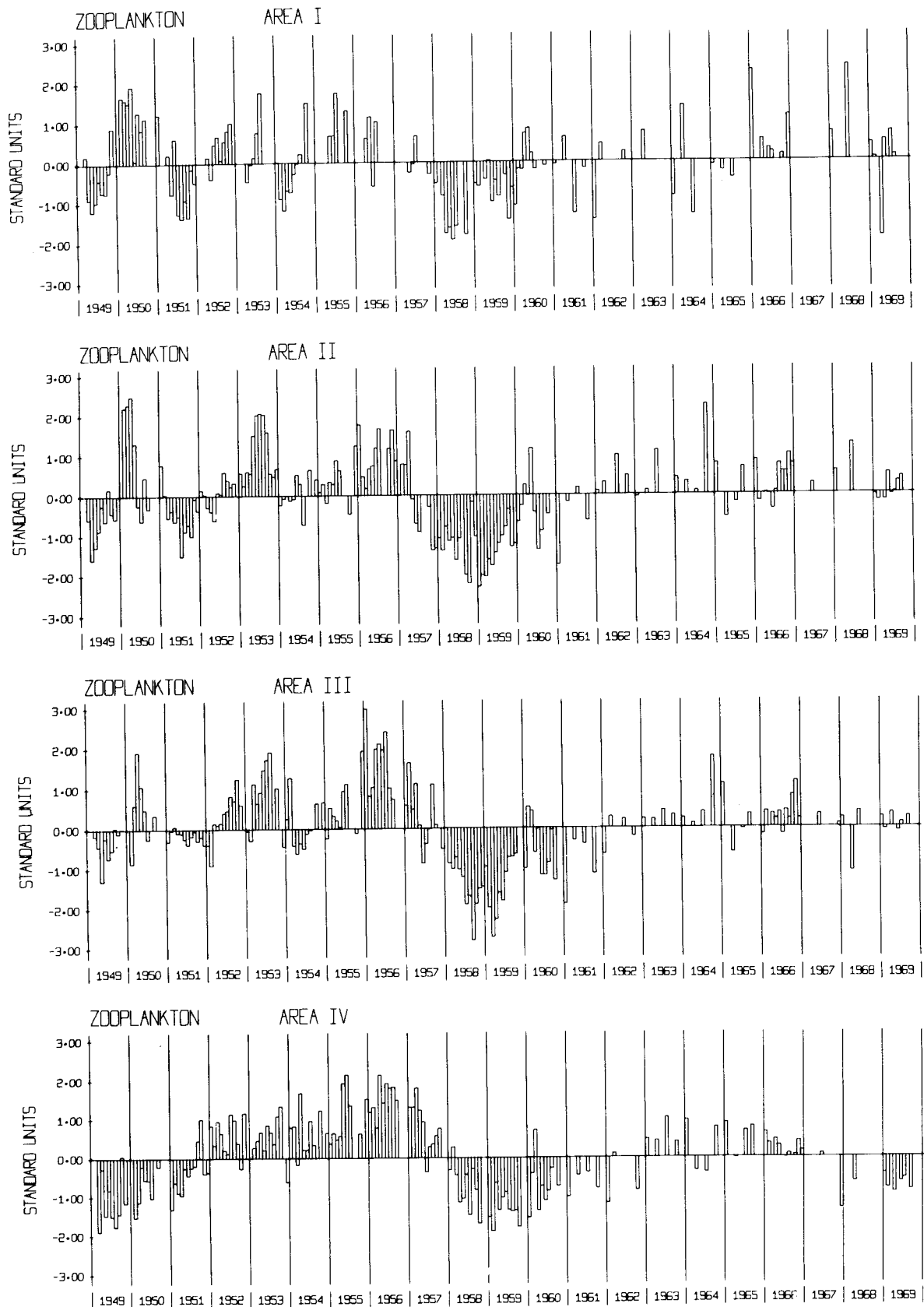|  | Frequency (cycles/day) | | |
|---|---|---|---|
|  | <0.0008 | 0.0008-0.0016 | <0.0016 |
| Area I | 16.75 | 18.17 | 34.93 |
| Area II | 44.72 | 11.72 | 56.43 |
| Area III | 46.10 | 8.18 | 54.28 |
| Area IV | 53.97 | 3.27 | 57.24 |
| Characteristic periods (days) | >1217 | 1217-608 | >608 |

Figure 6. Seasonally corrected time series of zooplankton biomass. These are anomalies calculated as difference with respect to corresponding long-term monthly average. Magnitude of this variable given in standard units; hence, value of 1.00 is equivalent to one standard deviation from the mean. (From Bernal 1980.)

this assumption is correct, the results of the spectral analysis say that a significant proportion of the total variability of planktonic biomass should be driven by a low-frequency physical process dominant on an inter-annual time scale, in any case with characteristic periodicity greater than 608 days.

Walsh and Howe (1976) and Walsh (1977) have proposed a hypothetical spectrum of physical forcing functions, presumably connected to the major biotic compartments of the pelagic ecosystem in Eastern Boundary Currents. The spectrum proposed by these authors predicts a broad spectral peak between 0.016 and 0.060 cycles/day, associated with the zooplankton response. Our results strongly contradict this hypothesis, since Table 2 show that close to 50% of the nonseasonal variability is clustered below 0.0016 cycles/day, an entire order of magnitude below the prediction. Furthermore, the low-frequency component cannot be an artifact of the elimination of seasonality, since this component only accounted for 20% of the total variance, meaning that at least 40% of the total variance, seasonality included, is clustered in the low-frequency band.

## Coastal Upwelling and Horizontal Advection as Forcing Functions of the Low-Frequency Response of the Ecosystem

The presence of a dominant low-frequency response of the pelagic ecosystem of the California Current poses the question: what is the forcing mechanism driving the system in this frequency domain? The first step to answer this question is provided by the existence of a significant negative correlation between sea-surface temperatures and zooplankton biomass (Reid et al. 1958; Reid 1962). However this correlation by itself, interesting as it is, does not allow us to differentiate between the two causal mechanisms potentially involved with the input of nonregenerative nutrients; namely coastal upwelling and large-scale horizontal advection from the north, since both processes by lowering the sea-surface temperature, could have forced the statistical association. I have attempted to resolve this dichotomy by assuming, first, that variations in coastal upwelling intensity are the dominant process and, second, by assuming that large-scale advection (and eventual mixing) of cold, low-salinity, high-nutrient water from the north is the dominant process. The method used was, first, to perform time-lagged correlations with the time series of zooplankton biomass as the dependent variable and the index of coastal upwelling derived from the Ekman layer model (Bakun 1973, 1975) and second, to perform the same correlations with indices of horizontal advection as independent variables. Two separate in-

dices of advection were used.

Figure 7 shows the time series of coastal upwelling indices computed at locations within each of the four areas described above. These series were treated in the same way as zooplankton data; i.e. seasonality was subtracted by the same methods and they were standardized to mean zero and unit standard deviation. Figure 8 shows the cross-correlation functions of zooplankton and upwelling, with time lags from 0 to 18 months. Almost none of the values were significantly different from zero at the 95% level. This result represents a strong rejection of the hypothesis that coastal upwelling is the principal physical mechanism responsible for the input of nonregenerative nutrients into the ecosystem. For the sake of completeness and brevity, I will only mention that a measure of offshore or average upwelling, a type of vertical motion driven by the local curl of the wind offshore (Yoshida 1955), is also uncorrelated with the biomass series (Bernal 1980).

Since there is abundant circumstantial evidence that large amounts of cold, low-salinity, high-nutrient water enters the system from the north and northwest, it is reasonable to attempt the same kind of analysis with measures of horizontal transport from the north. I have used the 33.40 o/oo isohaline as an index of the degree of penetration of these northern waters. Figure 9, modified from Wyllie and Lynn (1971), shows the sections of average salinity across four CalCOFI lines, where the extension and depth of the surface low-salinity minimum and its gradual disappearance to the south are evident. Using this marker, its variability, and the CalCOFI data files of steric heights, an index of transport of northern waters was calculated. First, for each month the geostrophic transport across a section off Point Conception (line 80) was computed, then with the information from the observed salinity field along the same section, the transport associated with waters less than 33.40 o/oo in the upper 200 m was obtained by numerical integration. These transport estimates, expressed in Sverdrups per 100 km of cross-shore distance, were also seasonally corrected and standardized to zero mean and unit standard deviation. Figure 10 shows the time series of this index, and Figure 11 the cross-correlation functions with zooplankton biomass as dependent variable. The results for northern Area I, although having some significant but very low correlations at lags 2 and 5 months, indicate that here the zooplankton is not predicted very well by the index: this might be due to the fact that line 80 lies downstream from the area. However, in Areas II and III the cross-correlation function attains highly significant values of $r$ $(t)$ [$r(t) \neq 0$; $P \leq 0.05$] uniformly in lags from 0 to 7 months in
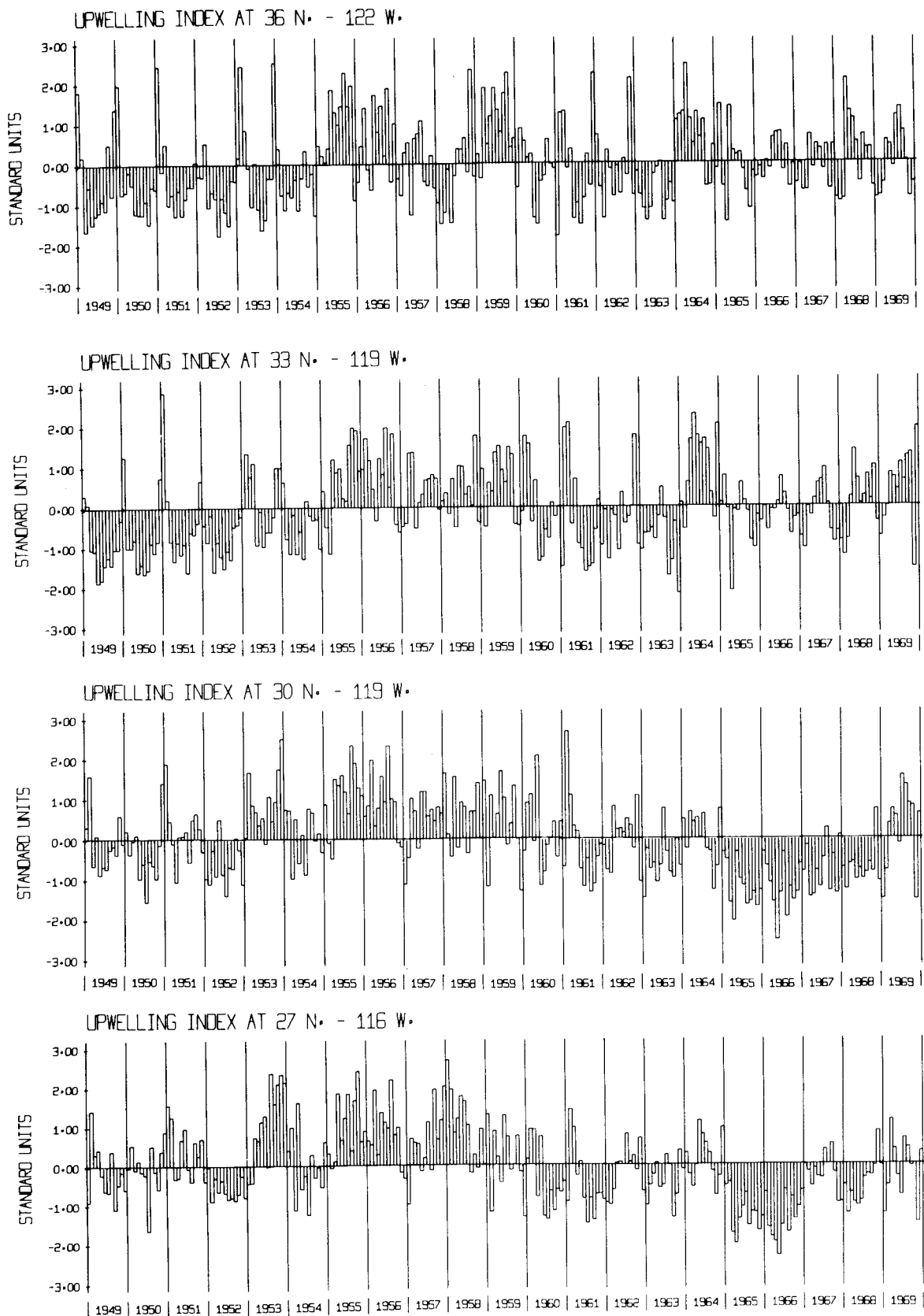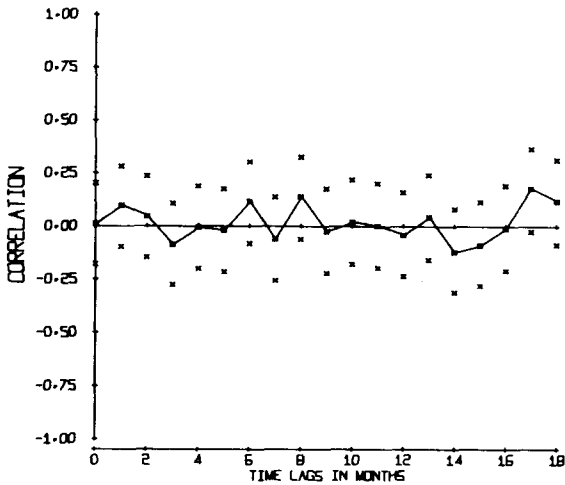
Figure 7. Seasonally corrected time series of upwelling indices. These indices derived by Bakun (1973, 1975), using a wind-driven coastal Ekman layer model. The series have been standardized and therefore have zero mean and unit standard deviation. (From Bernal 1980.)
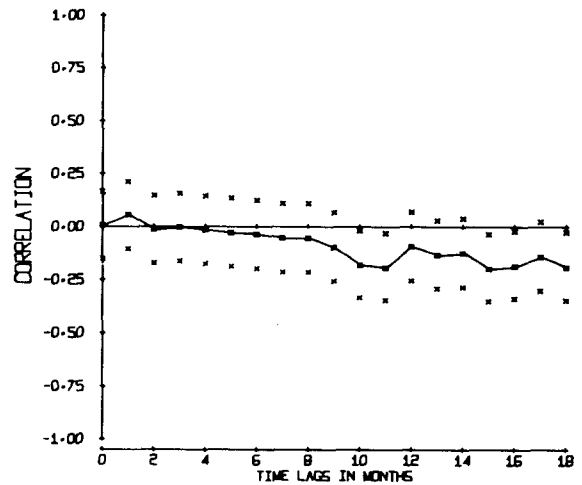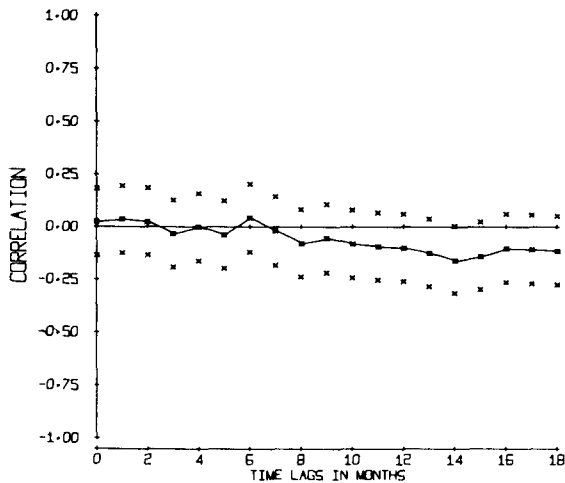
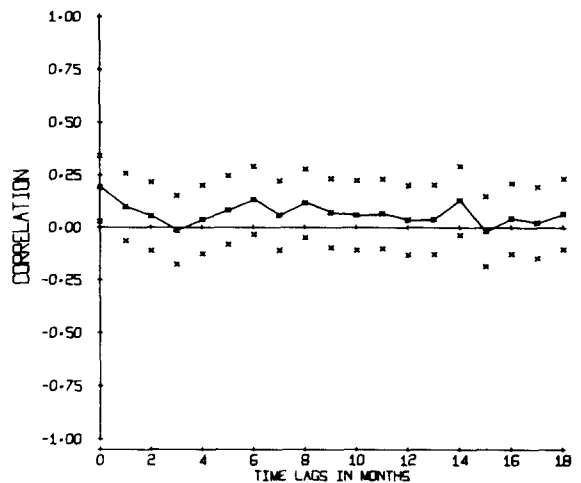Figure 8. Cross-correlation functions between upwelling indices and zooplankton biomass. Time lags in months; 95% confidence limits [r(t) ≠ 0; P ≤ 0.05] represented by crosses above and below continuous line. (From Bernal 1980.)

Area II and in lags from 0 to 5 months in Area III. In Area IV the correlation values become smaller again but are still significantly different from zero in 0 to 5 months lag. These correlations, although significant, are small since they account for only 25 to 30% of the variance. Nevertheless, the main point to stress here is that this index of advection is a much better predictor than the indices of nearshore vertical motion and its predictive performance with respect to biomass is close to or better than that of sea-surface temperatures (Bernal 1980).

The second index of horizontal advection was derived by Chelton (1981) by means of an objective analysis of the steric-heights information collected by CalCOFI from 1950 to 1978. Using an orthogonal decomposition of the time-space mean-products matrix, Chelton defined a restricted set of time-invariant spatial patterns of steric heights, patterns that account for a large proportion of the total variance present in the record. Hence, each time-invariant pattern or spatial Empirical Orthogonal Function (EOF) represents dominant modes of variability of the steric height field and therefore dominant patterns of flow in the California Current that are uncorrelated to each other. Figure 12 shows, on the left, the spatial averages of steric heights in the region and, on the right, the first mode of variation or EOF number one, which in this case accounts for 35% of the total variance of the field. For each month for which there are observations, each EOF has a time amplitude coefficient associated with
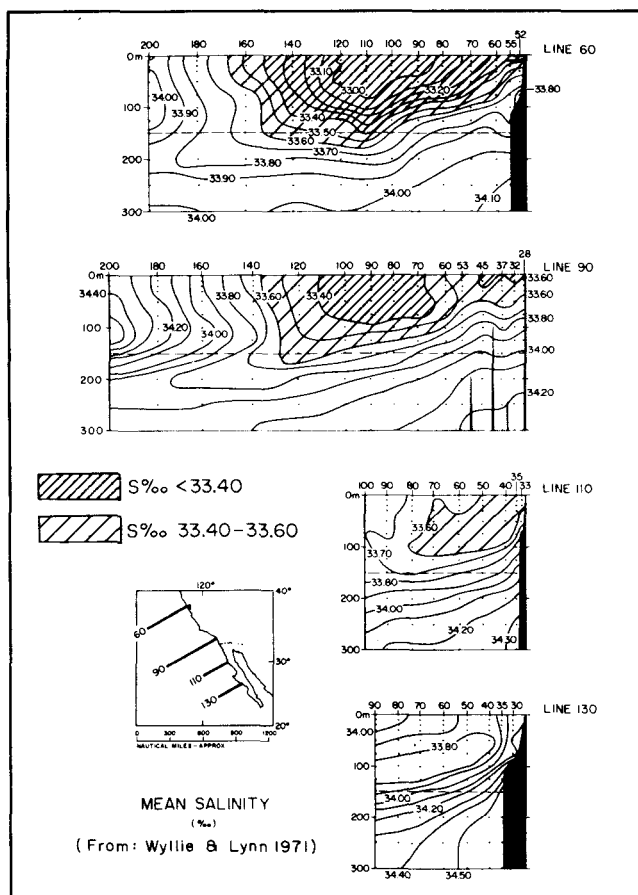
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Figure 9. Average vertical sections (1949-69) of salinity across CalCOFI lines 60, 90, 110, and 130. Contour interval, 0.20 o/oo. (Modified from Wyllie and Lynn, 1971.)

it that tell us how important or dominant was that particular spatial pattern during that month. Figure 13 shows the time series of the amplitude coefficients for EOF number one. The sign convention with respect to the average patterns is such that a positive value represents an intensification of the flow in the direction of the arrows in Figure 12 and a negative value of the coefficient a reversal of the direction of the flow along the level lines. For example, during years 1958 and 1959 the flow pattern was reversed with respect to the map in the figure. A zero or close to zero value of the coefficient means that flow along this pattern did not exist or contributed very little to the total observed flow pattern during a given month. The results of the cross-correlation analysis with this index of horizontal advection predicting the changes in zooplankton biomass are shown in Figure 14. In all four areas the positive correlation values are uniformly significant from 0 to 11 months lag, and the proportion of the variance accounted for by the highest correlations

TABLE 3
Maximum Values of Correlation and Coefficients of Determination between Zooplankton Biomass and Anomalous Steric Height (EOF Number 1)

|  | $r(t)^1$ | $N$ | $t = $ lag | $r^2(t)$ |
|---|---|---|---|---|
| Area I | 0.57 | 70 | 1 | 0.33 |
| Area II | 0.65 | 97 | 1 | 0.42 |
| Area III | 0.68 | 95 | 1 | 0.46 |
| Area IV | 0.60 | 84 | 7 | 0.36 |

[1]maximum values in the range 0 to 18 months lag.

INTEGRATED TRANSPORT 0-200 M    LESS THAN 33.40 O/OO SALINITY
SECTION ALONG CALCOFI LINE 80
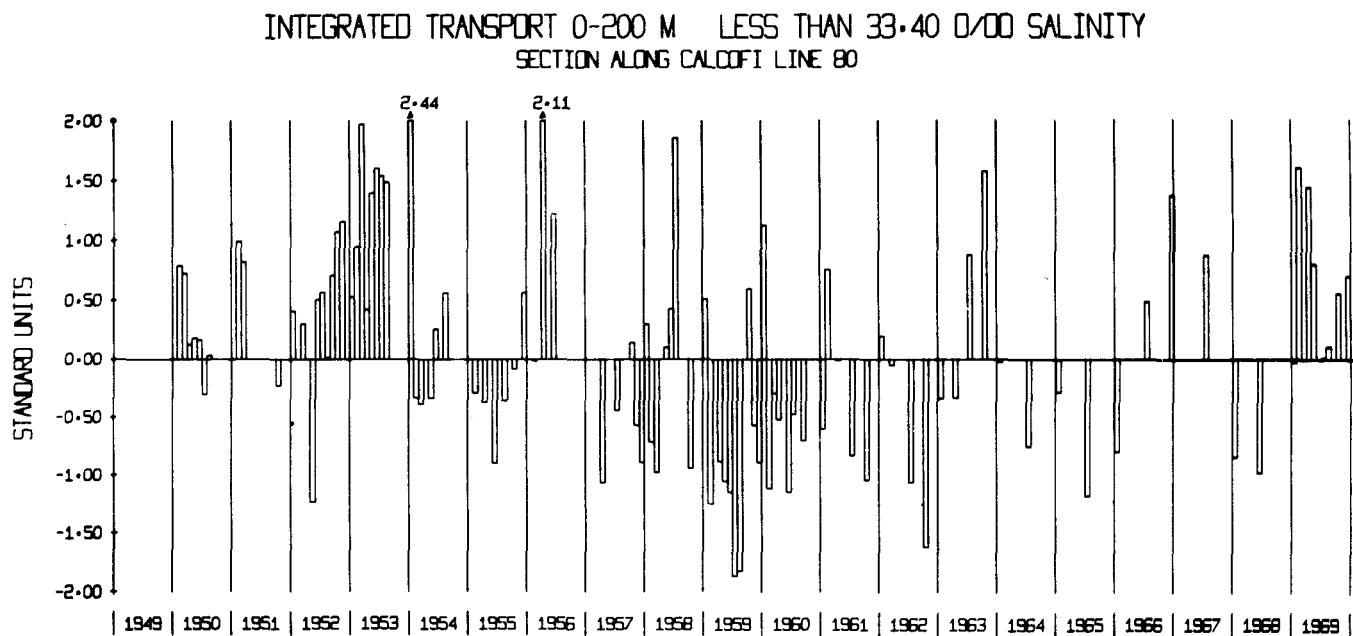


Figure 10. Seasonally corrected time series of index of advection from the north. These indices are estimates of the geostrophic transport across CalCOFI line 80, associated with waters of salinity less than 33.40 o/oo. Series have been standardized and therefore have zero mean and unit standard deviation. (From Bernal 1980.)
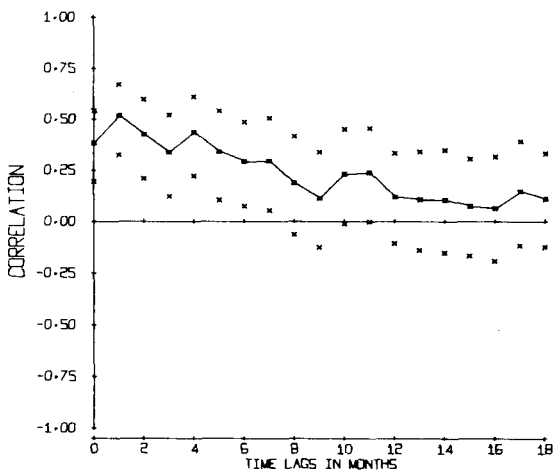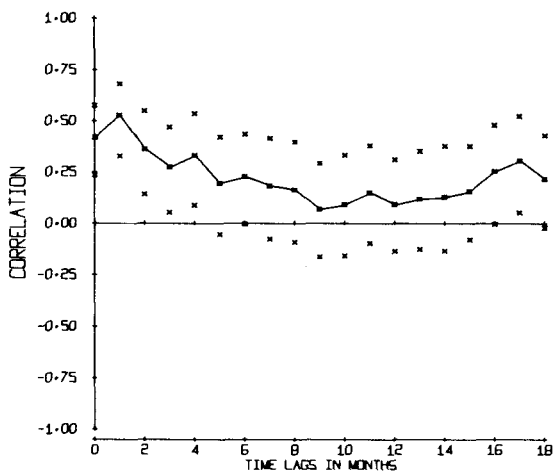
## CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00    LINE 80
LEADS ZOOPLANKTON    AREA I
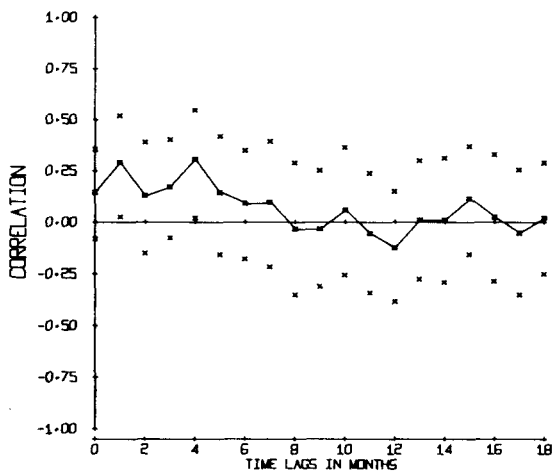
## CROSS-CORRELATION FUNCTION

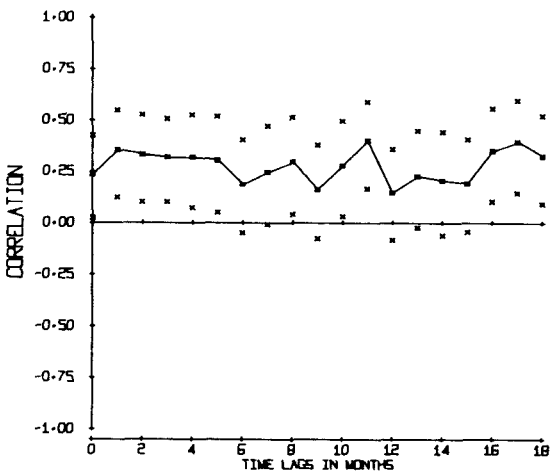NORTHERN TRANSPORT LESS THAN 33-40 0/00    LINE 80
LEADS ZOOPLANKTON    AREA II

## CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00    LINE 80
LEADS ZOOPLANKTON    AREA III

## CROSS-CORRELATION FUNCTION

NORTHERN TRANSPORT LESS THAN 33-40 0/00    LINE 80
LEADS ZOOPLANKTON    AREA IV

Figure 11. Cross-correlation functions between index of advection from the north and zooplankton biomass. Time lags in months; 95% confidence limits [$r(t) \neq 0$; $P \leq 0.05$] represented by crosses above and below continuous line. (From Bernal 1980.)
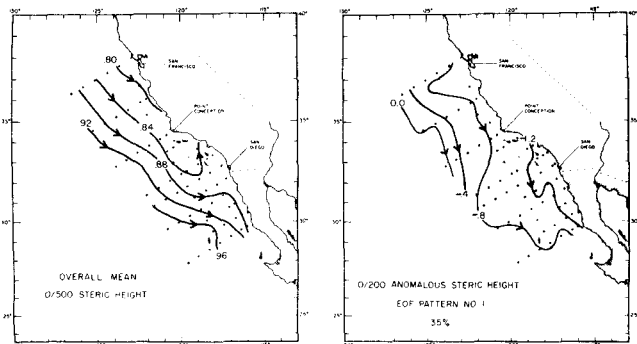
Figure 12. Spatial patterns of dynamic heights (flow) in the California Current. *Left*: long-term (1950-78) average dynamic height integrated from 500 db to surface; units are dynamic meters. *Right*: First spatial empirical orthogonal function of dynamic height. This spatial pattern is the first (35% of variance) mode of variation of dynamic height field. Negative values labeling contours indicate slanting of surface from offshore high to inshore low. (Modified from Chelton 1980.)

ranges from 33 to 46% as summarized in Table 3. These results mean that the low-frequency response of the ecosystem is coherent, with changes of the flow pattern occurring in the whole Eastern Boundary Current. Haury et al. (1978) presented a conceptual model of the time-space scales of zooplankton variability in the world oceans. In their description the spectral region in the neighborhood of the response described here is not very active and includes only El Niño-type of events. It is very likely that fluctuations in this spectral region are more important than previously thought and that interannual fluctuations in the strength of eastern boundary currents and concomitant changes in the flow patterns determine to a large degree the behavior of the resident ecosystems. From an ecological point of view, this conclusion also has
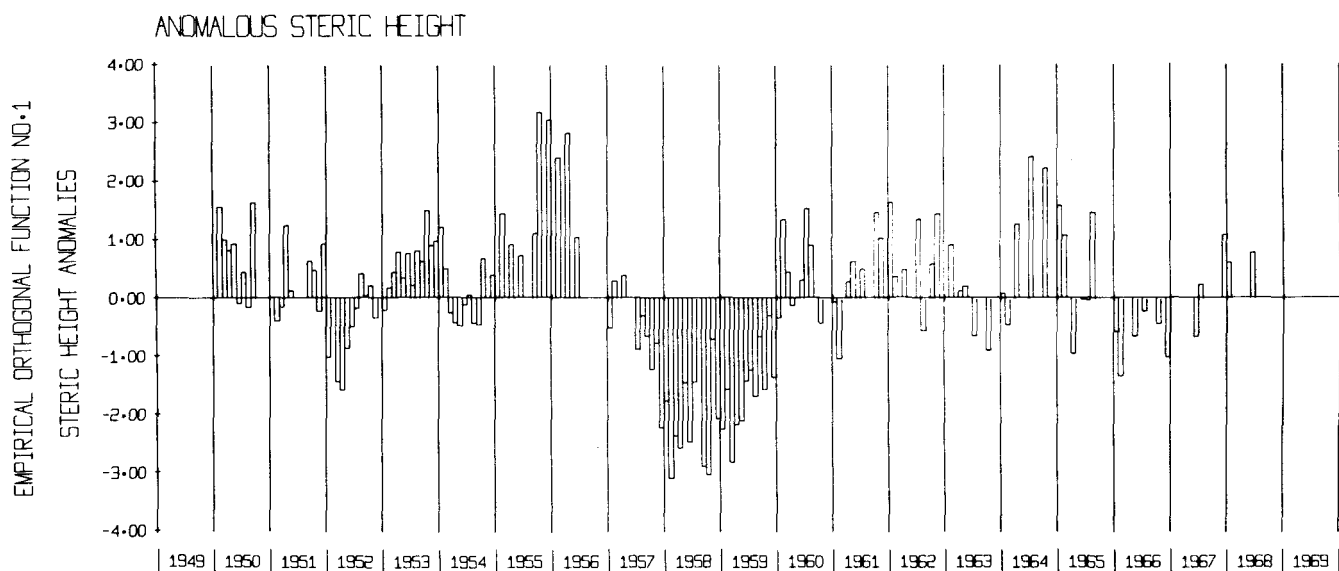
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Figure 13. *Time series of the monthly amplitude of the first Empirical Orthogonal Function. Coefficients, according to the sign convention used in Figure 12, are positive when flow is southward along EOF contour lines, negative when flow is reversed. (From Bernal 1980.)*

important implications, since these ecosystems might be permanently under nonequilibrium conditions. For ecosystems like this, it has been proposed (McGowan 1974) that classical biological interactive processes, such as competition and predation, will be secondary as regulatory mechanisms, since they might not have much of an opportunity to play a dominant role in modulating the changes in abundance of the species, due to the disruptive effect of physical conditions. This contention is not unreasonable, because a strict planktonic population drifting with the average current would have a residence time within the system of only 100 days and its demographic response to environmental and biological factors influencing its reproductive success while inside it would be lost out of the system. Strict planktonic populations might not really exist in nature, and certainly it may be fair to assume that the species assemblage of the California Current pelagic ecosystem has evolved complex adaptations to make full use of this highly variable environment. However this last comment has uncomfortable tautological overtones that need to be removed by formulating testable hypotheses and perhaps developing a new theory. Little is known about the causal mechanism that might drive the low-frequency component of the flow. The fact that the first EOF of dynamic heights displays a flow pattern with a dominant north-south directional component is consistent with both the presence of perturbations originating in the equatorial region (McCreary 1976; Smith 1978) and with basin-wide fluctuations influencing the general pattern of circulation around the North Pacific Ocean. There is some evidence indicating that winter
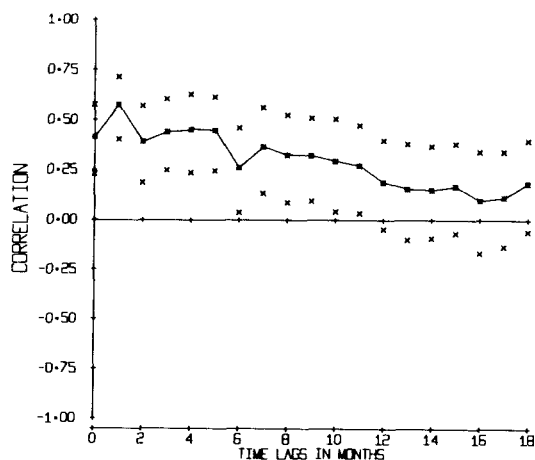
temperature anomalies are conserved in their transit around the subtropical Central Gyre of the North Pacific (Namias 1970) and that extreme years in a time series of very large-scale wind anomalies (expressed as the wind torque over the Gyre) coincide with extreme years in the sea-surface temperature-anomalies record. This suggests that coherent large-scale advection of heat and perhaps momentum are also taking place on basin-wide and interannual scales.
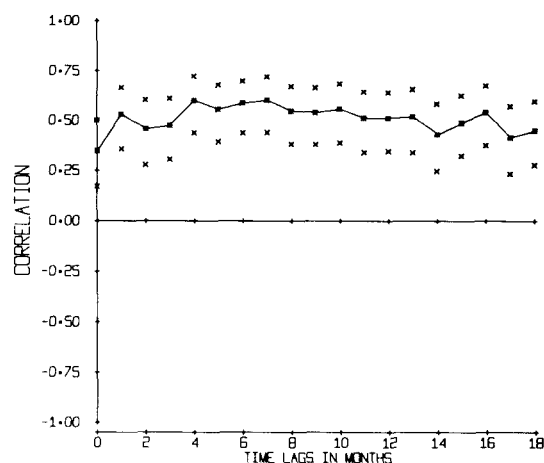
## ACKNOWLEDGMENTS

Figure 14. Cross-correlation functions between amplitude of the first EOF of dynamic height and zooplankton biomass. Time lags in months; 95% confidence limits [$r(t) \neq 0; P \leqslant 0.05$] represented by crosses above and below continuous line. (From Bernal 1980.)

## LITERATURE CITED

Allen, J.S. 1973. Upwellling and coastal jets in a continuously stratified ocean. J. Phys. Oceanogr. 3(3): 245–257.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. U.S. Dep. Comm., NOAA Tech. Rep. NMFS, SSRF-671, 103 p.

Bakun, A. 1975. Daily and weekly upwelling indices, west coast of North America, 1967–73. U.S. Dep. Comm., NOAA Tech. Rep. NMFS, SSRF-693, 114 pp.

Bernal, P.A. 1979. Large-scale biological events in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 20:89–101.

Bernal, P.A. 1980. Large-scale biological events in the California Current: the low-frequency response of the epipelagic ecosystem. Ph.D. thesis, Univ. Calif. San Diego. (University Microfilm, Ann Arbor, Michigan USA) 184 p.

Bernal, P.A., and J.A. McGowan (in press) Advection and upwelling in the California Current. In F. Richards (ed.), Proc. IV Internat. Coastal Upwelling Sym.

Chelton, D.B. 1980. Low frequency sea level variability along the west coast of North America. Ph.D. dissertation, Scripps Institution of Oceanography, Univ. Calif. San Diego, 212 p.

Chelton, D.B. 1981. Interannual variability of the California Current—physical factors. Calif. Coop. Oceanic Fish. Invest. Rep. 22: (this volume).

Colebrook, J.M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955-59. Fish.Bull., U.S. 75: 357-368.

Cushing, D.H. 1976. The biological response in the sea to climatic changes. Adv. Mar. Biol. 14:1–122.

Haury, L.R., J.A. McGowan, and P.H. Wiebe 1978. Patterns and processes in the time-space scales of plankton distributions. *In* J.H. Steele (ed.), *Spatial pattern in plankton communities*, NATO Conf. series IV: Marine Sciences, Plenum Press, New York, p. 277–327.

McCreary, J. 1976. Eastern tropical ocean response to changing wind systems: with application to El Niño. J. Phys. Oceanogr. 6:632–645.

McGowan, J.A. 1974. The nature of oceanic ecosystems. *In* C.B. Miller (ed.), *The biology of the oceanic Pacific*, Oregon State Univ. Press, Corvallis, p 9–28.

Namias, J. 1970. Macroscale variations in sea-surface temperatures in the North Pacific. J. Geophys. Res. 75(3): 565–582.

O'Brien, J.J., R.M. Clancy, A.J. Clarke, M. Crepon, R. Elsberry, T. Gammelsrød, M. MacVean, L.P. Röed, and J.D. Thompson. 1977. Upwelling in the ocean: two- and three-dimensional models of upper dynamics and variability. *In* E.B. Kraus (ed.), Modelling and prediction in the upper layers of the ocean, Pergamon Press, Oxford, p. 178–228.

Parrish, R.H., and A.D. MacCall. 1978. Climatic variation and exploitation in the pacific mackerel fishery. Calif. Dept. Fish Game, Fish Bull. 167:1–110.

Reid, J.L. 1962. On circulation, phosphate-phosphorous content and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7(3):287–306.

Reid, J.L., G.I. Roden, and J.G. Wyllie. 1958. Studies of the California Current System. Calif. Coop. Oceanic Fish. Invest. Rep. 6:28–56.

Smith, R.L. 1978. Poleward propagating perturbations in currents and sea levels along the Peru coast. J. Geophys. Res. 79:435–443.

Walsh, J.J. 1977. A biological sketchbook for an eastern boundary current. *In* E.D. Goldberg et al. (eds.), The Sea, Volume VI: Marine Modeling, Wiley & Sons, New York, pp. 47–61.

Walsh, J.H., and S.O. Howe. 1976. Protein from the sea: a comparison of the simulated nitrogen and carbon productivity in the Peru upwelling ecosystem. *In* B.C. Patten (ed.) System analysis and simulation in ecology, Vol. IV, Academic Press, New York, p. 47–61.

Wickett, W.P. 1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J. Fish. Res. Board Can. 24:581–594.

Wyllie, J.G., and R.J. Lynn. 1971. Distribution of temperature and salinity at 10-meters, 1960-1969, and mean temperature, salinity and oxygen at 150 meters, 1950-1968, in the California Current. Calif. Coop. Oceanic Fish. Invest. Atlas 15, v-vii, charts 1–188.

Yoshida, K. 1955. Coastal upwelling off the California Coast. Recds. Oceanogr. Works in Japan 2(2): 8–20.