LARGE-SCALE BIOLOGICAL EVENTS IN THE CALIFORNIA CURRENT

PATRICIO A. BERNAL
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, CA 92093

INTRODUCTION

In addition to the seasonal signal, which can be statistically resolved for both physical and biological variables, the California Current system undergoes large-scale non-periodical fluctuations. Based on the record of varved sediments of biological origin preserved in anærobic basins, these fluctuations seem to have been the rule rather than the exception in the past (Soutar 1967, 1971; Soutar and Isaacs 1969, 1974). For example, the combined biomass of the Pacific sardine, *Sardinops caerulea,* the northern anchovy, *Engraulis mordax*, the Pacific hake, *Merluccius productus*, and the Pacific saury, *Colalabis saira,* have experienced fluctuations of at least one order of magnitude during the last 150 years (Soutar and Isaacs 1974). Thecosomatous pteropods and heteropod molluscs, members of the planktonic assemblage of the California Current, also showed large departures from their long-term density in the sediments, with maxima up to four times the mean (A. Soutar, personal communication).

Since 1949 the CalCOFI project has been collecting zooplankton samples on which zooplankton displacement volumes are routinely determined. These volumes represent a readily available estimate of the biomass of zooplankton, and with some caution they can be interpreted as an index of the secondary production of the epipelagic ecosystem in the region. Smith (1971) presented detailed monthly charts of displacement volumes for the period 1951 through 1966, discussing in detail the methods and major trends present in the record.

In an effort to identify periods of unusually high or low secondary production in the epipelagic ecosystem, this report reexamines the CalCOFI record of zooplankton displacement volumes for the 21-year period extending from 1949 through 1969, using the techniques of time-series analysis.

MATERIALS AND METHODS

A good summary of the methods and techniques used in field and laboratory to obtain the zooplankton displacement volumes is given in Kramer et al. (1972), and they will not be repeated here.

The five geographical areas of the California Current chosen for this study are shown in Figure 1. In delimiting them, consideration was given to the hydrographic (Reid et al. 1958) and faunistic (Brinton 1962; Alvariño 1964; Fleminger 1967; McGowan 1968) patterns present in the region. Although this is a region of confluence for different faunas, these areas represent a partition of the CalCOFI sampling grid with some faunistic meaning. Area I in the north should be dominated by subarctic and transitional forms. Areas III (in part) and IV present a fauna that becomes increasingly dominated by equatorial forms. Area II, on the other hand, is an area where intense stirring and mixing of different water masses and a parallel mixture of faunas occur; here representatives of the three regimes already mentioned are found interspersed in the samples. Area V, lying close to the outer boundary of the current, is dominated by species that belong to the assemblage of the Subtropical Central Pacific Water mass.

Time series of zooplankton biomass for each area were derived, with each element of the series-vector being the average over space of the stations within that area occupied on a given month. This procedure filters out the short-term (daily) and the small-scale spatial (patchiness) variability. The time series were standardized to give a mean of zero and unit standard deviation, and then they were codified into integer values with one unit being equivalent to ± 0.2 standard deviation units; hence, a codified value of ± 5.0 is equivalent to one standard deviation. The absolute unit used by CalCOFI to report zooplankton displacement volumes is ml/1000 m^3; the necessary information to convert codified values back to absolute units is given in the Appendix, which follows this report.

Because the station-to-station data and the averaged values for the five areas have frequency distributions that are clearly non-normal, a logarithmic transformation taking the natural logarithm of each sample was applied to the original data base, and areal averages were recomputed. The improvement toward normality that resulted from the transformation was quite apparent when frequency distributions were compared by plotting them on probability paper. It should be noted that in the log-transformed series, the average corresponds to the geometric mean of the original values (Bagenal 1955).

Preliminary work and previously published information (Smith 1971; Kramer and Smith 1972) indicated the presence of a seasonal signal in the record. Because my interest was in long-term fluctuations, a set of seasonally corrected series was computed. The correction consisted of calculating the monthly deviations of the areal

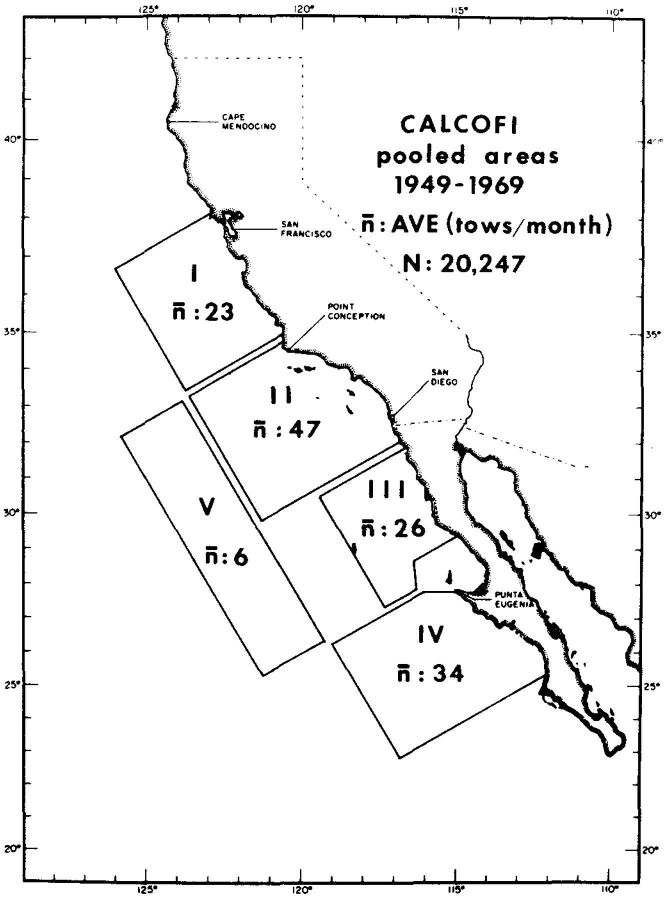

Figure 1. Geographical areas in the California Current over which spatial averages of zooplankton volume were computed: "n" is the average number of samples pooled into a typical monthly estimate; "N" is the total number of plankton tows used in the study.

averages by subtracting the 21-year monthly average and standardizing it with the corresponding 21-year monthly standard deviation. This is equivalent to eliminating the average seasonal cycle term by term.

Autocorrelation functions plus auto- and cross-spectral estimates were computed for the seasonally corrected series for Area I through IV. Area V was excluded because very few observations were available.

The autocorrelation function is the serial correlation of a series with itself, and it provides information of how neighbouring points are correlated. In our case a high autocorrelation value means that a high or low biomass will tend to broadcast its influence in the future of the series, producing more high or low values than expected if no autocorrelation existed. Broadly speaking, it measures the "inertia" of the series.

Spectral analysis performs a decomposition of the total variance of a series into independent—orthogonal—components as a function of frequency or period. The area under the spectral curve is equivalent to the total variance; hence, peaks in the spectral density function signal out frequencies or periods that account for a high proportion of the variance, and the frequency or period at which these peaks occur indicates how the maxima (or minima) are spaced in the time domain. For example if a peak occurs at a frequency of 0.05 cycles/month, this means that maxima (or minima) of biomass tend to occur every 0.05^{-1} months apart, i.e. 20 months.

Spectral analysis also permits the comparison of two or more time series. The coefficient of spectral coherency is the ratio of the cross-spectrum of two series and the geometric mean of both auto-spectra (Robinson 1967). Accordingly, spectral coherence measures the common variance at any given frequency of the two time series being compared. If the series maintain, for any given frequency, a fixed phase relationship, this ratio attains its maximum value of 1: the complete "coherent" case. Conversely, if the phase relationship changes randomly, the ratio becomes zero: the completely "incoherent" case. A high coherency at a given frequency between two time series means that peaks in their spectra coincide at that frequency and that the spacing between maxima (or minima) of biomass is more or less the same.

RESULTS

The five time series of untransformed codified values are presented in Figure 2. The series show some very high peaks of biomass that occur simultaneously for more than two areas. During 1950 there are extreme values in Areas I, II, III, and V; during 1953 there are extreme values in Areas II and III; 1956 shows distinct maxima in all areas except II. On the other hand, the biomass values remained consistently below the long-term mean during most of 1958 and parts of 1957 and 1959.

The log-transformed time series are presented in Figure 3. The major features are essentially preserved and the transformation reveals more clearly the minima in the record, especially during years 1957 through 1959.

The seasonally corrected series in Figure 4 show the long-term variation of biomass in the California Current. It is apparent that underlying the seasonal signal there are long-term trends that occur in more than one area at the same time. In particular, years 1950, 1953, and 1956 present simultaneous maxima in at least two areas; and years 1958 and 1959 show a coherent set of minima in four areas.

Figure 5 shows the autocorrelation functions for the four areas upon which the techniques of spectral analysis were applied. The rate at which the autocorrelation function decays as a function of time lag is inversely proportional to the time constant of the process being analyzed, i.e. a fast decay corresponds to a process with a short time constant and vice versa. From Figure 5 it is clear that the characteristic time scale varies from area to area. Area I, the northernmost area in the region, has a

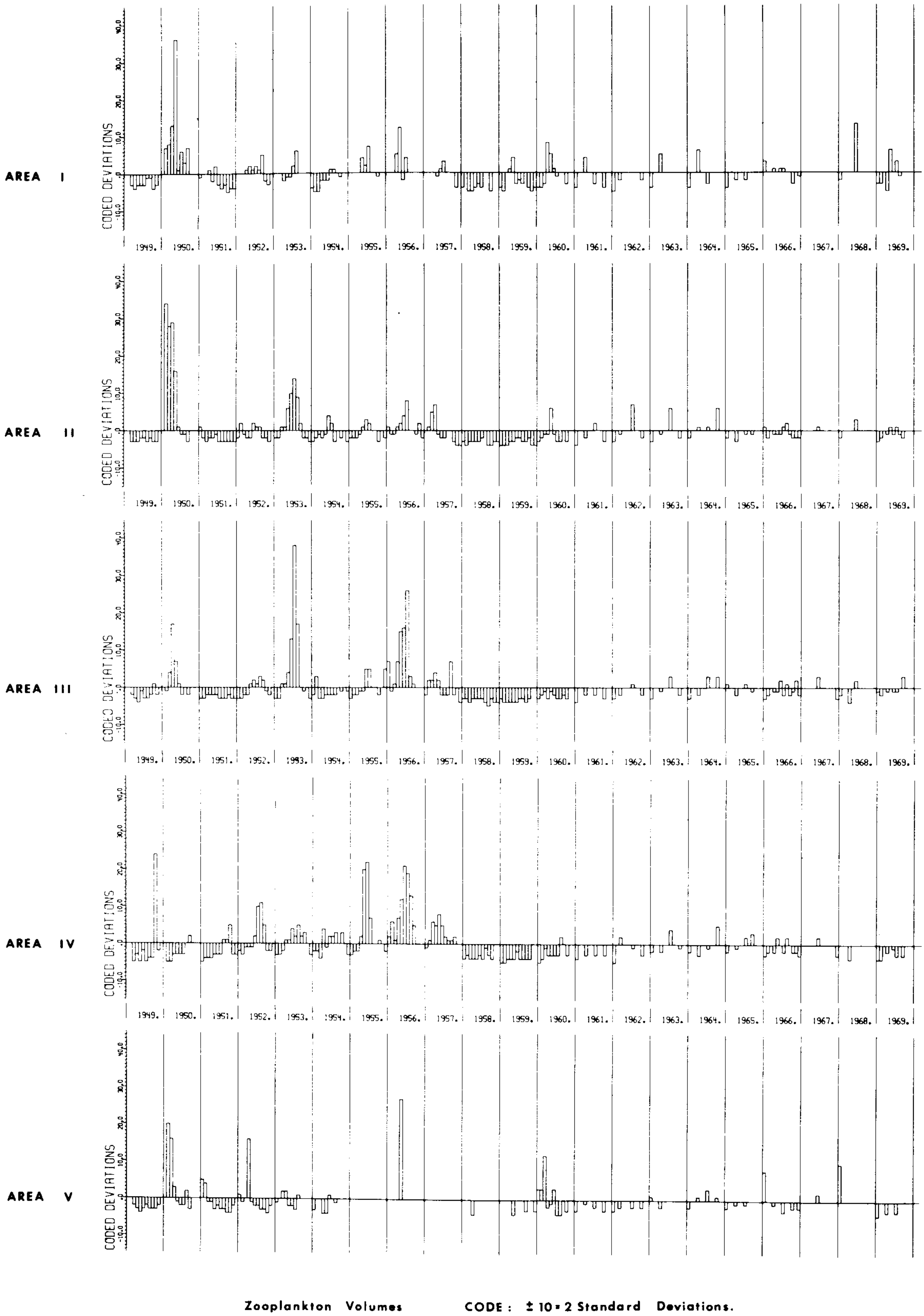

Figure 2. Time series of untransformed monthly averages of zooplankton volume for all five areas. Values plotted are codified deviations from the 21-year mean. Means and standard deviations for all areas are given in the Appendix.

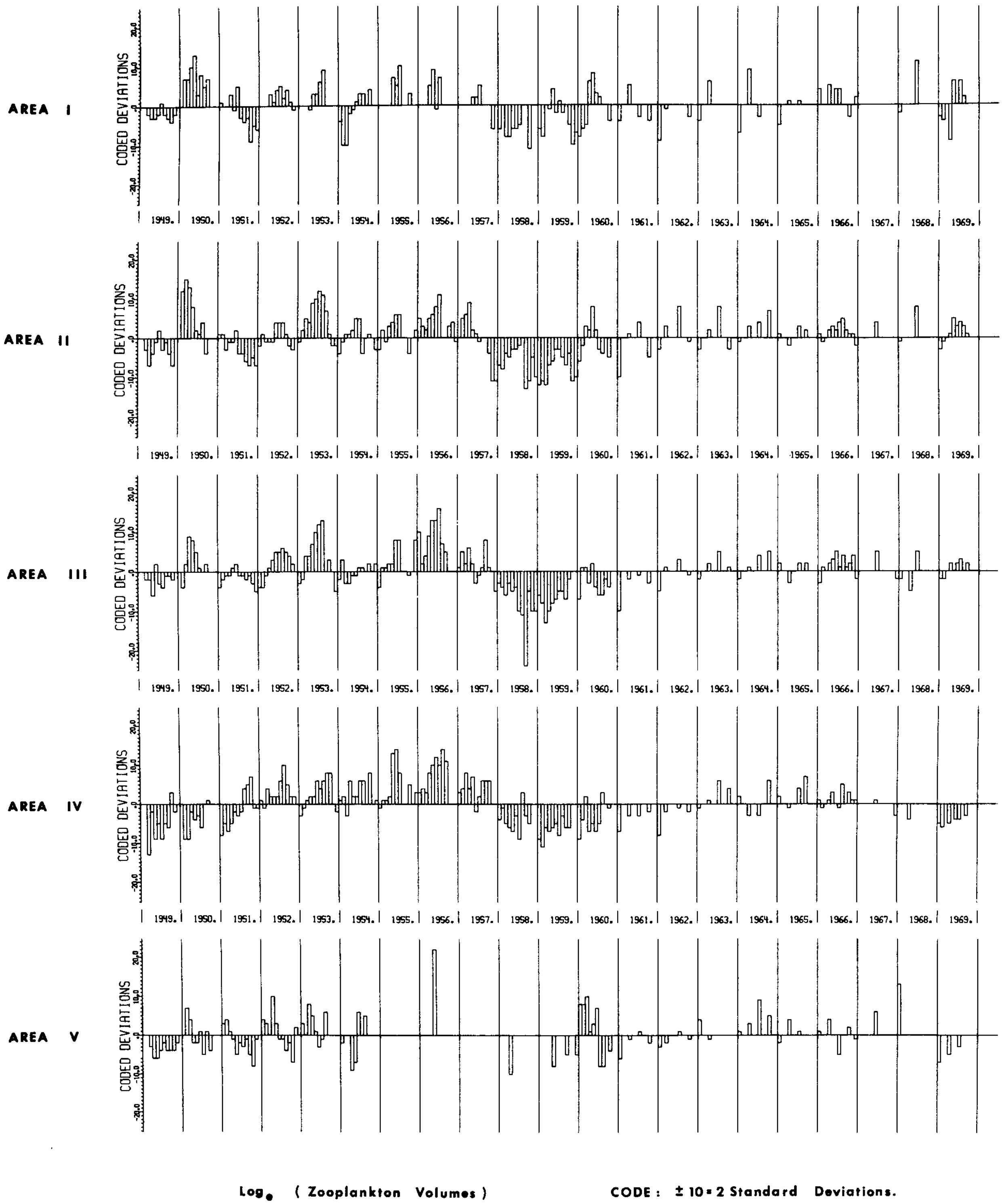

Figure 3. Time series of monthly averages of log$_e$ zooplankton volume for all five areas. Values plotted are codified deviations from 21-year mean. Means and standard deviations of log$_e$ zooplankton volume for all five areas are given in the Appendix.

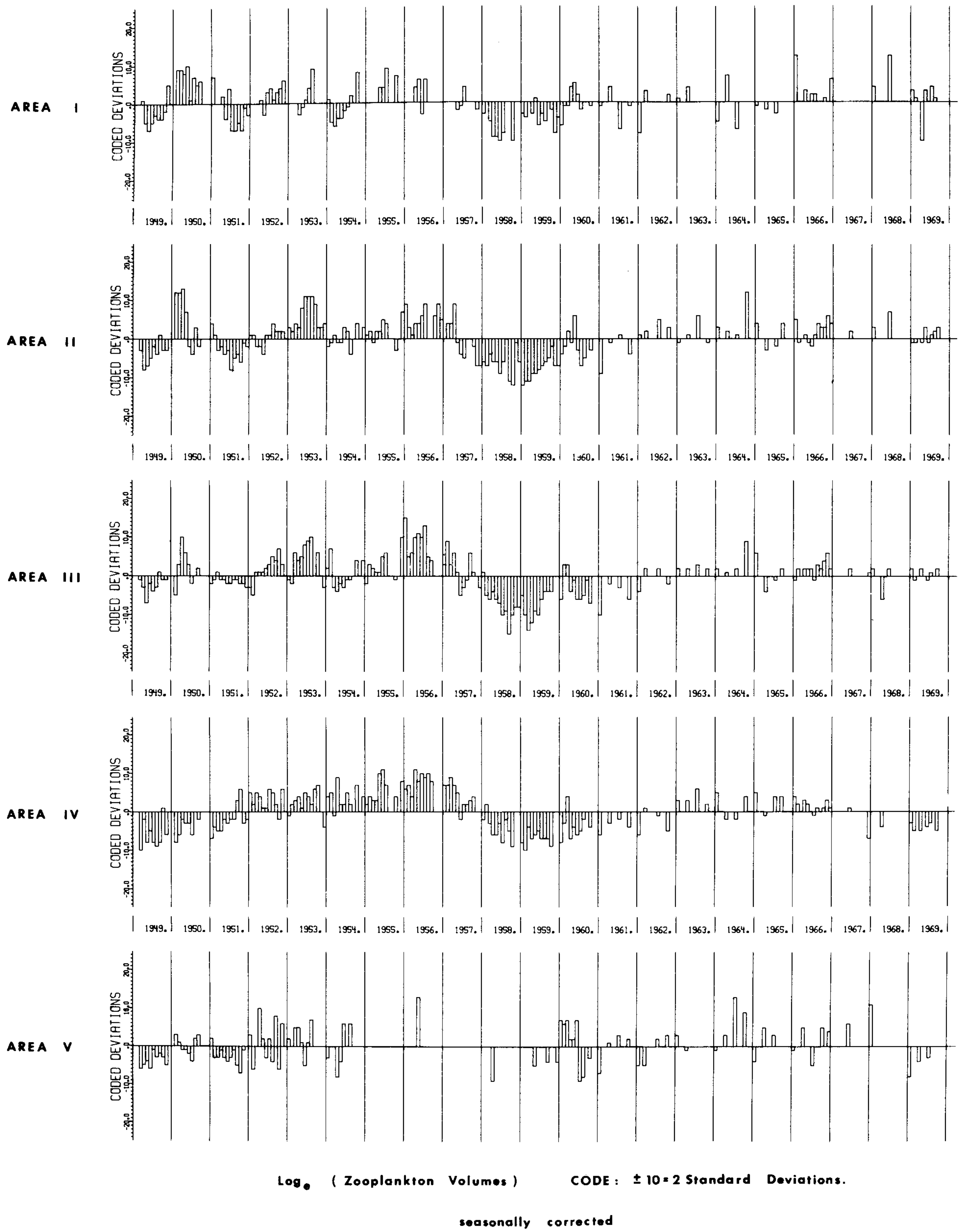

Figure 4. Time series of seasonally corrected monthly averages of $\log_e$ zooplankton volume for all five areas. Values plotted are codified deviations from the 21-year monthly averages standardized against 21-year monthly standard deviation. Monthly means and standard deviations are given in the Appendix.

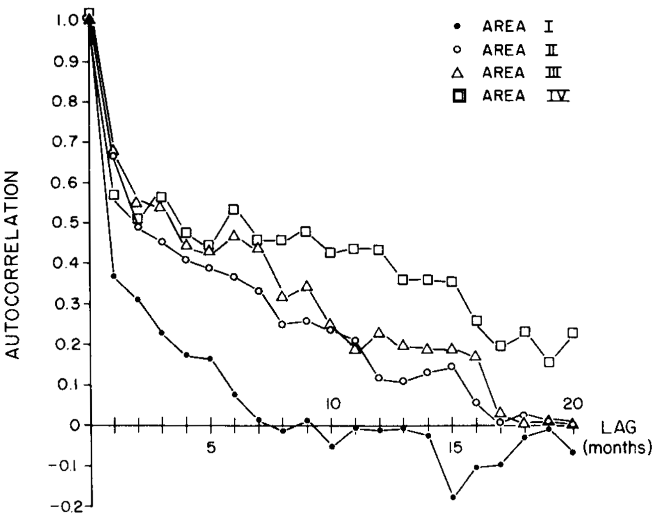

Figure 5. Autocorrelation functions for Areas I through IV: Y-axis in product-moment correlation coefficient units; X-axis in months.

much shorter time scale, less than 7 months, than the rest. Areas II and III have an intermediate temporal scale of about 17 months, and Area IV has a rather long time scale of about 23 months, a value not shown in the figure.

Area I has consistently higher absolute values of biomass than the other four areas, and its monthly averages form a high peaked function, with its maxima occuring during the month of May. The fact that the dominant time scale of this seasonally corrected series is still of the order of 7 months might be interpreted as an expression of the strong influence of seasonally related effects superimposed on lower frequency components. Because the seasonal correction used is rather insensitive to phase shifts, year-to-year changes of phase ("early" or "late" biomass maxima) might account for this behaviour; furthermore, the effects of phase shifts might be more important here because this time series has the highest root mean square of all. Nevertheless, the possibility that the short time scale might be a spurious result introduced by the frequency of sampling cannot be ruled out.

The series in Figure 4 show a low frequency sine-wave pattern in the southernmost areas, which is most developed in Area IV. The emergence of this pattern is consistent with the north-south trend of increasing temporal scale suggested by the autocorrelation functions.

Figure 6 shows the four auto-spectral plots. The main feature of these plots is that a large fraction of the total variance lies within the low-frequency band, i.e. frequencies less than 0.05 cycles/month or with periods larger than 20 months. Table 1 gives some relevant numerical results from this analysis. The north-south trend of increasing temporal scale of biomass fluctuations that was evident from the autocorrelation functions is

TABLE 1
Percentage of the Total Variance in First Maximum and Selected Bands. Frequency unit: cycles/month

	First Maximum		Frequency Bands		
	Frequency	% Variance	<.025	0.025-0.050	<0.050
Area I	0.033	4.95	16.75	18.17	34.93
Area II	0.0083	12.59	44.72	11.72	56.43
Area III	0.0083	14.36	46.10	8.18	54.28
Area IV	0.0083	21.44	53.97	3.27	57.24

paralleled here by an increasing proportion of the total variance clustered in the low-frequency band. This means that as one moves from north to south an increasing amount of variability is accounted by some slow-response, large-scale process. Another result that points in the same direction is the increasing proportion of the total variance associated with the first maximum in each spectrum, a proportion that increases from 4.95% in Area I to 21.44% in Area IV.

Figure 7 shows the spectral coherency plots for the three area pairs that are contiguous in a north-south direction, with the corresponding 90% confidence limits. Although the coherence ratio fluctuates as a function of frequency, it is clear that the series pairs reach highly significant coherencies in the low-frequency band. This means that the separation in time between maxima and minima of biomass tends to be the same for the different areas.

Based on these results, I have defined five discrete events characterized by the occurrence of very high or low biomass over large extents of the California Current region. They were identified by applying the additional statistical criteria of lying outside the interval bounded by ±8 codified units (±1.6 standard deviation units), and by this standard we can accurately call them unusual events. Table 2 summarizes the main features of these events.

DISCUSSION

It is my strong opinion that, because of their magnitude and areal extent, the periods with very high or low biomass represent very important ecological events that cannot be the result of the unforced, free response of the local epipelagic ecosystem. For example, the biomass of copepods, which represent on the average one third of the total macrozooplankton biomass, diminished one order of magnitude (44.85 gm/1000 m^3 to 4.15 gm/1000 m^3) from October 1955 to October 1958 (Isaacs et al. 1969). This change is equivalent to a power flux of 4×10^{12} watts in the California Current alone (Isaacs 1975). During these unusual periods, changes in horizontal advection, as well as other physical processes associated with an external input of nutrients, must be acting as forcing functions for the epipelagic ecosystem.

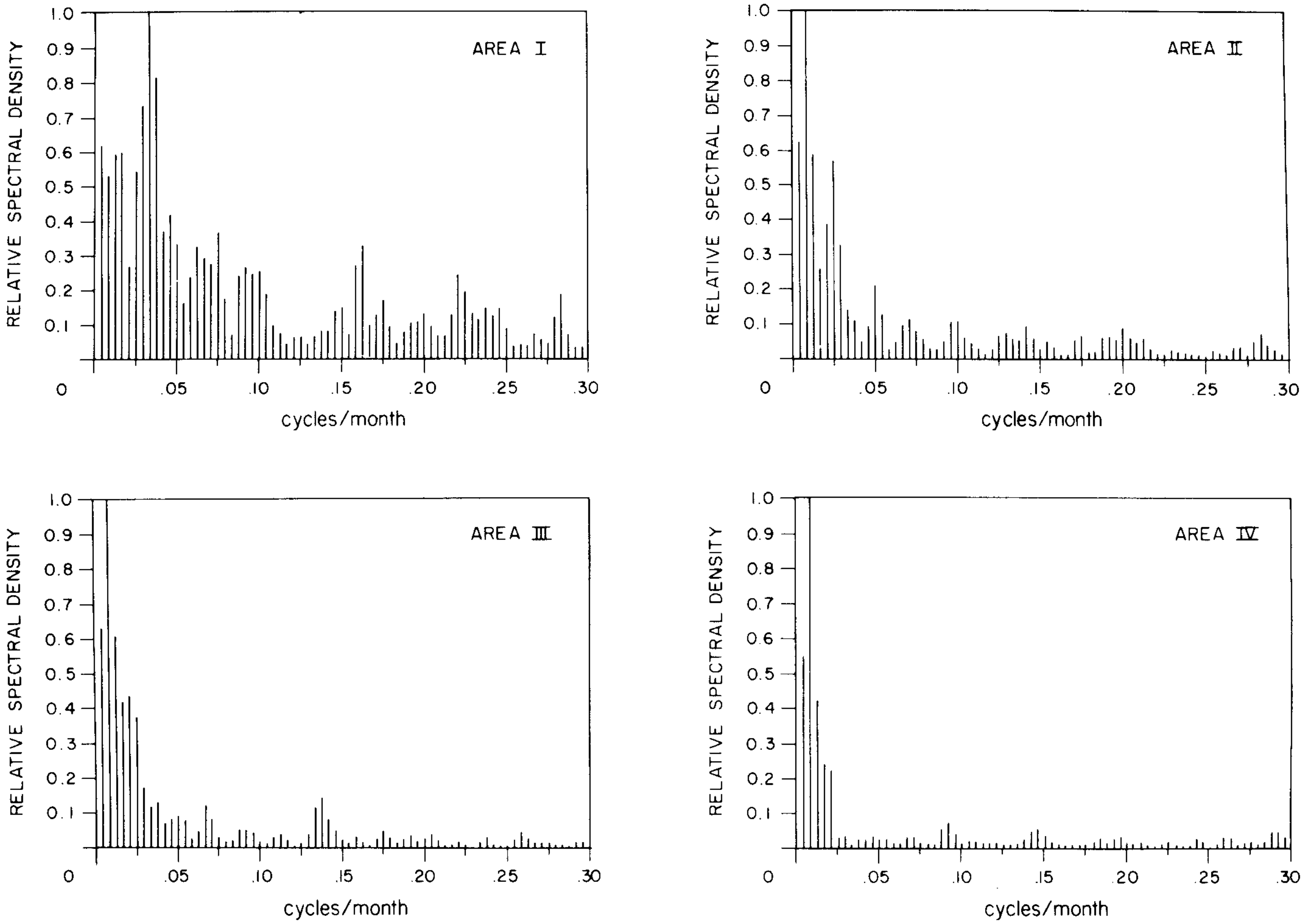

Figure 6. Auto-spectra for Areas I through IV. Y-axis is labeled "Relative Spectral Densities" because all densities were scaled with respect to the largest value: thus, the highest density in each spectrum = 1.0. Frequency in cycles/month. Equivalent periods unit $(\text{cycles/month})^{-1}$

Colebrook (1977) studied the year-to-year fluctuations in biomass of 17 taxonomic categories in the California Current during 1955-59, using principal component analysis. The results of this study indicated that changes in biomass show a remarkable coherence among categories and among different geographic localities. In other words, a large element of the year-to-year fluctuations in biomass is common to all geographic areas in the region and to a vast majority of taxa. Although the increase in numbers of certain taxonomic categories at the expense of others could be explained by internal readjustments within the local ecosystem, such an explanation is untenable when all categories tend to increase or decrease their numbers simultaneously.

Indirect evidence that advection is playing a role can be inferred from changes of hydrographic characteristics between years of high and low biomass. As an indicator of advection of northern waters, from the subarctic and transitions zones, I have chosen the 33.40 ^{o}/oo isohaline at 10 m. This is a salinity value that characteristically lies in the middle of the halocline in the subarctic Pacific Ocean (Tully and Barber 1960). Toward lower latitudes this isohaline approaches the surface layers of the ocean as the halocline itself becomes shallower, and at the surface it marks the midpoint of a zone of transition between the typical salinity structures of the subarctic and subtropical domains.

In order to summarize the information available, I have plotted the position of the 33.40 ^{o}/oo isohaline for all the months available in the years of interest (data from Anonymous 1963; Wyllie and Lynn 1971). The areal range of all observed positions of the 33.40 ^{o}/oo isohaline are presented in Figure 8 a and b. In a given year, the envelope usually defines an area to the north where the surface waters were always "fresher" than 33.40 ^{o}/oo and an equivalent area to the south and inshore where the surface waters were never "fresher" than 33.40 ^{o}/oo. The envelope itself is a conservative estimate, because in several cases the isohalines, during most of the year, were closely packed together and only a few extreme observations made the areal range wider. As a reference I have used the statistically determined position of the isohaline published by Lynn (1967).

The years 1950, 1953, and 1969 show intrusions of

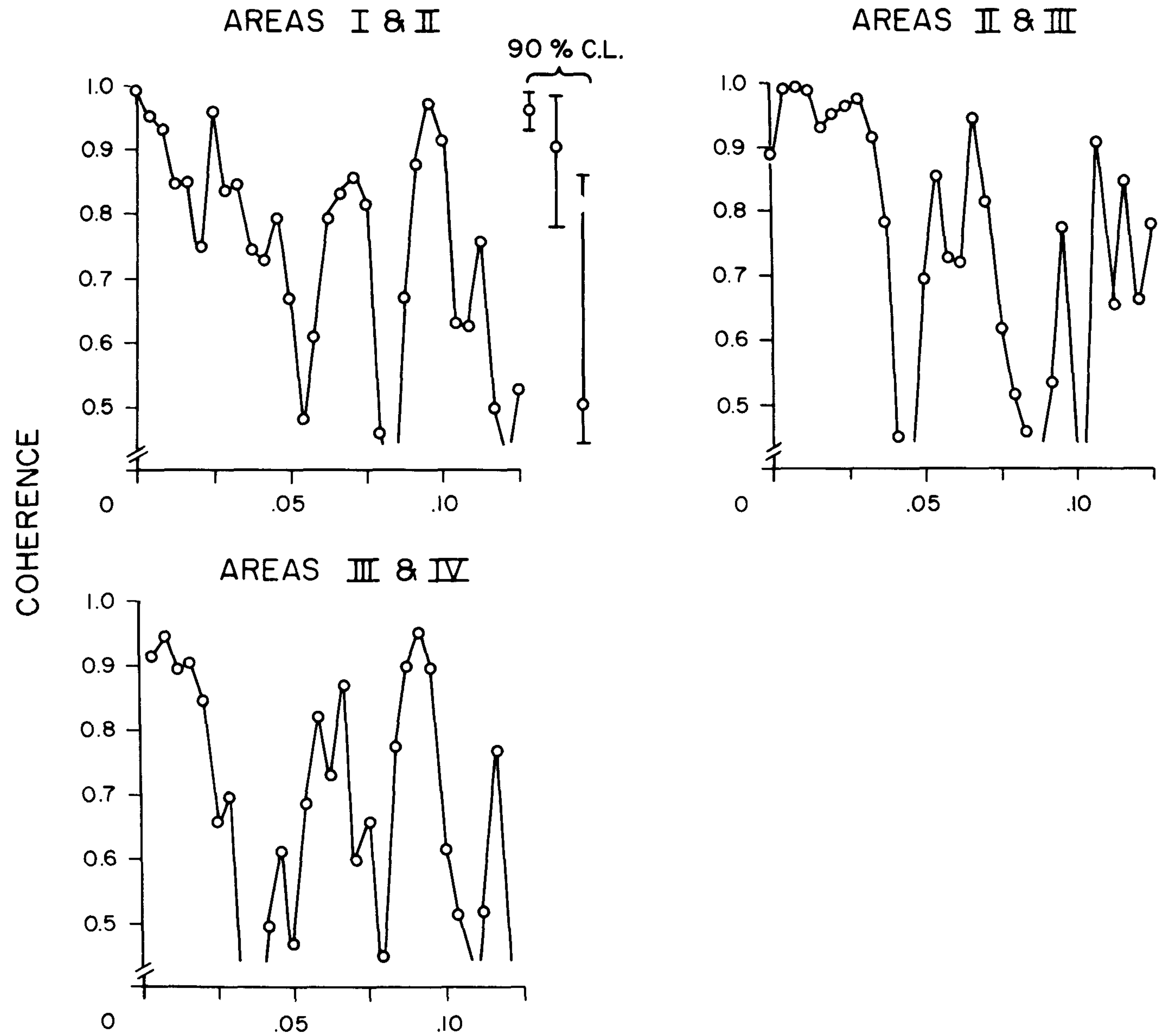

Figure 7. Spectral coherency plots for the three north-south area pairs. Coherence is a measure of the common variance between two series at any given frequency; 90% confidence limits for three selected values are presented beside the first plot. These limits were computed following the standard asymptotic approximations.

northern waters much farther south than the normal range. In 1958 and 1964 the isohalines did not appreciably extend further south than their average position. Although we used the salinity values at 10 m, these intrusions are not restricted to a thin surface layer. Figure 9 shows a time series of salinity versus depth for CalCOFI Station 90.60, located in Area II (32° 30' N, 120° W). Two major features are evident in the figure; the year-to-year variability and the depth range of northern waters, which extends to 100 m at this latitude. Thus, during the same years that anomalous biomass maxima or minima were present, hydrographic changes could also be detected in the California Current.

Unfortunately a continuous record of nutrient concentration does not exist for the region, so that a direct quantitative comparison is not possible. Nonetheless, Zentara and Kamykowski (1977), analyzing the information available for the eastern Pacific Ocean, found that nitrate, phosphate, and silicate follow an inverse monotonic relationship with temperature. Between 65° N and 35° S, their nutrient scatter diagrams intercept the temperature axis, indicating nutrient depletion above cer-

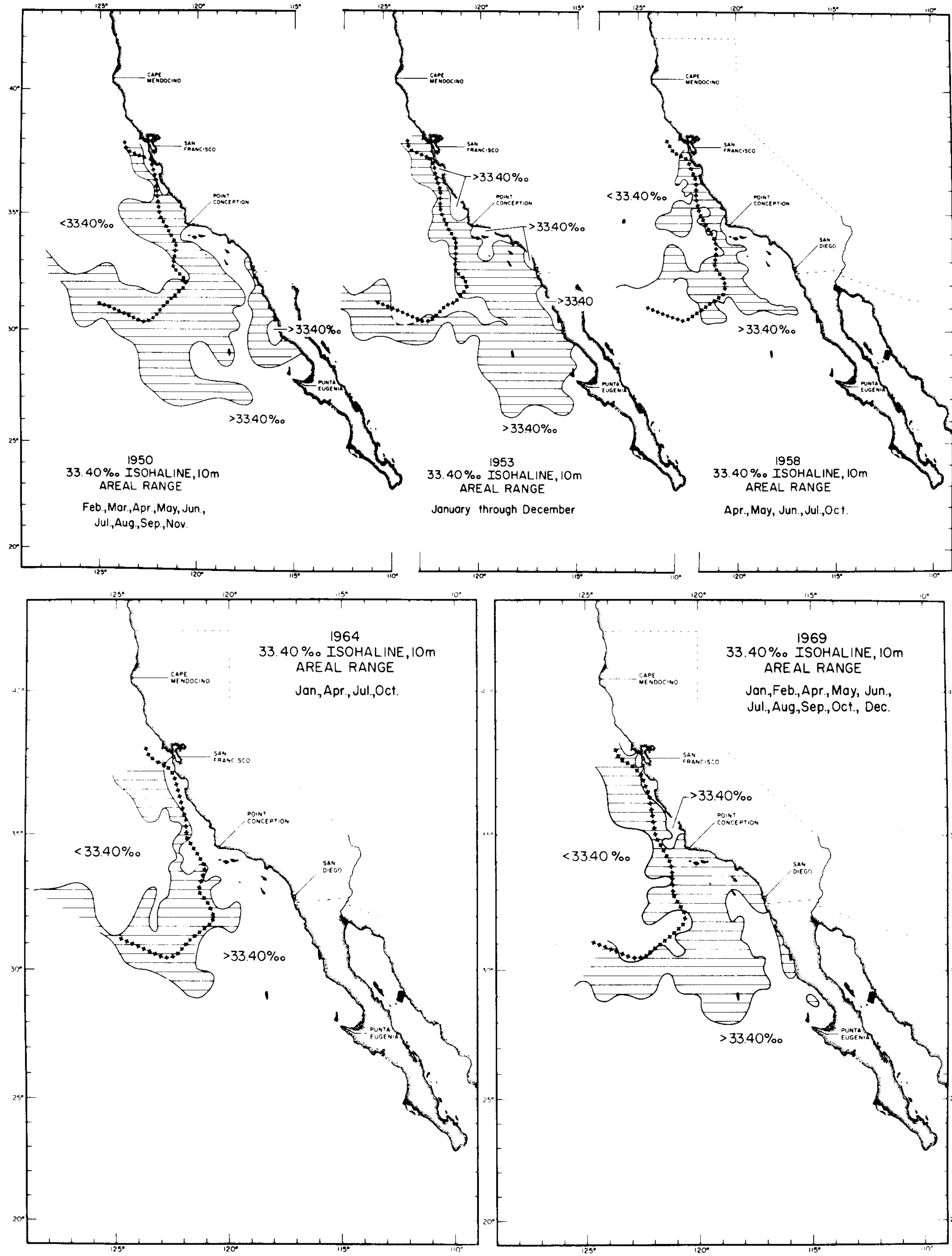

Figure 8. Extension of water masses of northern origin into the California Current. (a) Areal range of 33.40 $^{o}/oo$ isohaline for years 1950, 1953, and 1958. (b) Areal range of 33.40 $^{o}/oo$ isohaline for years 1964 and 1969. The stippled area includes all positions of the 33.40 $^{o}/oo$ isohaline observed for the period. The statistically computed average position of the isohaline is delineated by crosses.

TABLE 2.

Summary of Main Features of Five Discrete Events Characterized by Extensive Occurrence of Biomass Extremes over the California Current Region.

Event	Area	Max/min value[1] ml/1000m[3]	# Extreme Values[2]	Run length[3] months	Run: Start/End
1	I	1109.3 (5005)*	3 (5002, 03, 05)	11 (18)	4911-5104
	II	723.4 (5004)	3 (5002, 03, 04)	4	5002-5005
	III	279.2 (5004)	1 (5004)	4	5003-5006
2	I	642.9 (5308)	1 (5308)	4 (8)	5306-5401
	II	646.8 (5307)	4 (5306, 07, 08, 09)	18 (19)	5206-5312
	III	497.2 (5308)	2 (5307, 08)	7 (8)	5303-5310
	IV	170.5 (5310)	–	9	5302-5310
	V	91.0 (5308)	–	2	5307-5308
3	I	741.0 (5507)	1 (5507)	8 (22)	5408-5605
	II	506.7 (5607)	4 (5601, 07, 11, 5704)	14 (17)	5512-5704
	III	768.9 (5607)	7 (5512, 5601, 04, 05, 06, 07, 5702)	15 (18)	5512-5705
	IV	306.1 (5506)	8 (5404,5505,06,5604, 06,07,08,5703)	30 (36)	5404-5705
	V	437.9 (5605)	1 (5605)	....	....
4	I	123.1 (5806)	4 (5804,05,06,5810)	11 (18)	5711-5904
	II	25.4 (5901)	8 (5806,09,10,5901, 02,03,04,05,06)	31 (34)	5705-6002
	III	2.8 (5809)	9 (5807,08,09,10, 5902,03,04,05,06)	22 (24)	5802-6001
	IV	23.9 (5902)	2 (5810, 5902)	20 (24)	5803-6002
	V	20.7 (5804)	1 (5804)	4 (21)	5804-5912
5.....	II	315.1 (6410)	1 (6410)	5 (13)	6401-6501
	III	154.3 (6410)	1 (6410)	9 (25)	6301-6501
	V	120.3 (6407)	1 (6407)	3 (7)	6404-6410

[1]This is the maximum or minimum value of biomass within the run.
[2]Number of months above (below) ±9 codified units.
[3]Is the number of consecutive months above or below 21-year monthly means. In parentheses are given the numbers of months obtained by interpolation, assuming that blanks in the record had anomalies of the same sign.
*Cruises are identified by 4 digits; the first two indicate the year and the last two the month.

tain temperatures. A similar relationship has been reported for nitrate concentrations and ambient temperature (Strickland et al. 1970; Kamykowski 1973; Eppley et al. 1978). Typically the water mass lying to the north of the 33.40 ⁰/oo isohaline has temperature values well below these intercepts, less than 13° C between 40° and 35° N, for example, suggesting that it represents an important source of nutrients for the system.

There is also published evidence pointing to the importance of advection. Wickett (1967) found a positive correlation ($r = 0.84$; $p < 0.01$) between southward Ekman transport at 50° N and the zooplankton biomass off southern California one year later, suggesting that the zooplankton may be responding to a nutrient input taking place very far upstream. McGowan and Williams (1973) computed a budget of inorganic phosphorus for the subarctic Pacific and found an excess of 0.13 mg-atoms PO_4/m^2/day. Because there is no evidence that phosphorus is accumulating in the upper layers of the ocean at those latitudes, these authors concluded that the balance must be achieved by a net transport of phosphorus from the subarctic Pacific into the California Current. Colebrook (1977) concluded that "whatever influence or in-

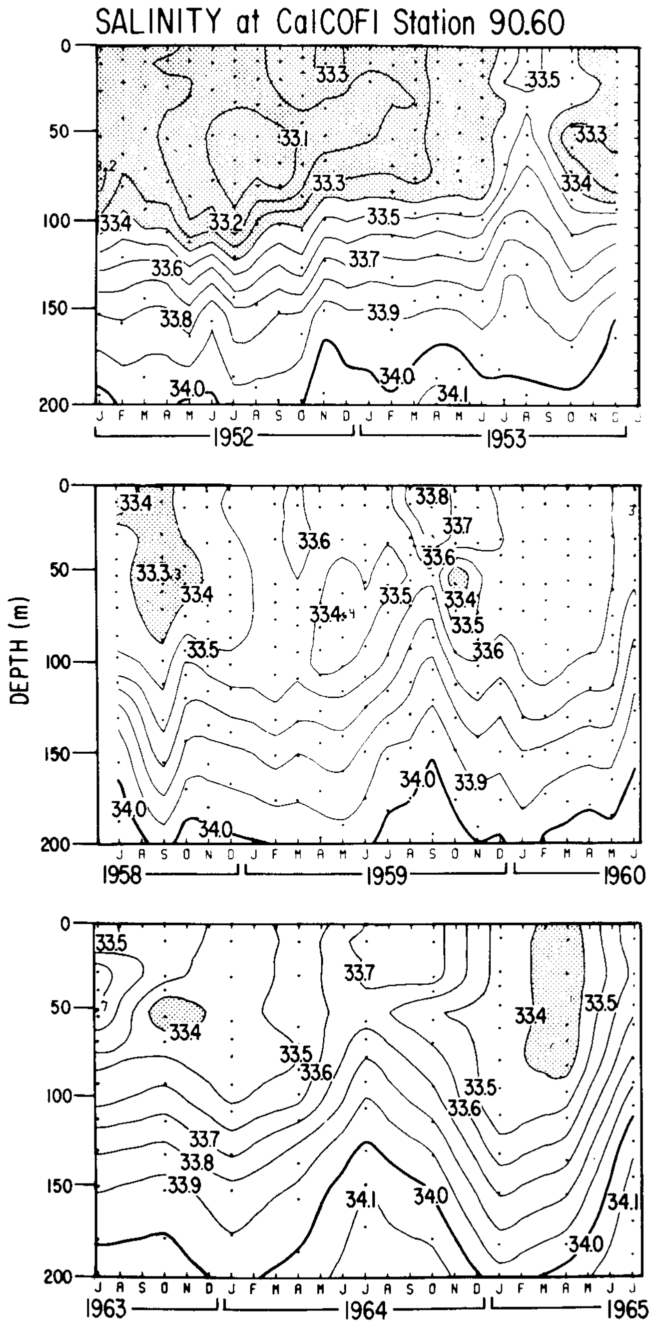

Figure 9. Time series of salinity versus depth at CalCOFI Station 90.60 (32° 30' N, 120° W) during some selected years. Salinities less than 33.40‰ are stippled (Modified from Eber 1977).

fluences are responsible for the fluctuations in the plankton either have their origin in the north of the survey area or have a greater effect on those categories with northern patterns of distribution."

Other large-scale physical phenomena might also be playing an important role. Recent work by McCreary (1976), simulating the "El Niño" phenomenon, predicts that changes originating over the interior of the Pacific

Ocean in the equatorial region influence both eastern boundary currents, i.e. the Peru-Chile and California Currents. This phenomenon is accompanied by a deepening of the thermocline, a perturbation that according to the model travels poleward as coastally trapped Kelvin waves. In theory, according to the critical depth model (Sverdrup 1953), a deepening of the mixed layer, other things being equal, should result in a decrease of biological production. The zooplankton provides the first link in the marine food web, and a time lag in its response to this kind of external driving should be detectable.

In order to test this hypothesis, I have taken from Allison et al. (1971) a time series of quarterly sea-surface temperature anomalies computed for the equatorial band lying between 5° N-5° S and 80°-180° W. This series has been used as an indicator for "El Niños" events off the South American coast. By comparing it with the series of quarterly standardized anomalies of zooplankton biomass in Area III, I obtained a highly significant negative correlation ($r = -0.40; p < 0.01$) when the zooplankton lagged the temperature anomalies by three quarters (Figure 10). Although this evidence is not overwhelming, it is nonetheless an indication that some of the ecological events described, in particular the one occuring during the warm years of 1957 and 1958, might represent true "Californian El Niños." In any case, it indicates that McCreary's hypothesis deserves further study.

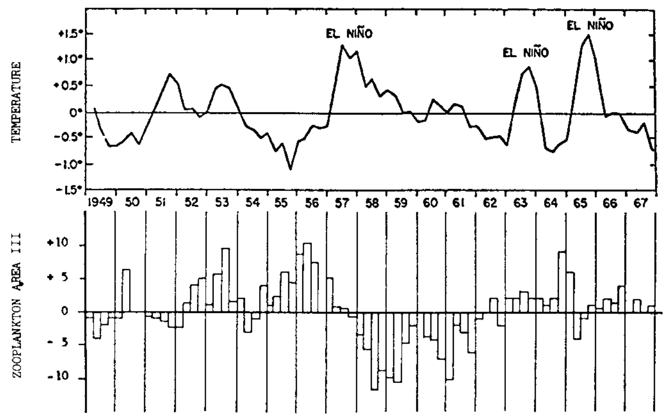

Figure 10. Californian "El Niños." Upper panel: Quarterly sea surface temperature anomalies for the equatorial band between 5° N - 5° S and 80° - 180° W. Well recognized "El Niños" events off Peru and Chile are shown as warm peaks (Allison et al. 1971). Lower panel: Codified standardized deviations of $\log_e$ zooplankton volume/quarter in Area III.

ACKNOWLEDGMENTS

I would like to express my thanks for the encouragement and support provided by Drs. J.A. McGowan and M.M. Mullin during this research. Ms. Patricia Walker and Dr. Thomas L. Hayward read the manuscript and made valuable suggestions for its improvement. This research has been supported by the Marine Life Research program, the Scripps Institution of Oceanography part of the California Cooperative Oceanic Fisheries Investigations, which is sponsored by the Marine Research Committee of the State of California, and by a grant from the Ford Foundation through the University of Chile-University of California Cooperative Program.

REFERENCES

Allison, L.J., J. Steranka, R.J. Holub, F.A. Gobshall, and C. Prabhakara. 1971. Air-sea interactions in the tropical Pacific Ocean. Goddard Space Flight Center, Preprint X-651-71-191., Greenbelt, Maryland (NTIS-Microfiche: N71-27648).

Alvariño, A. 1964. Zoogeografía de los Quetognatos, especialmente de la Regiȯn the California, *Ciencia* (Mex.), 23: 51-74.

Anonymous. 1963. CalCOFI Atlas of 10-meter temperatures and salinities, 1949 through 1959. Calif. Coop. Oceanic Fish. Invest., Atlas 1, ii-iv, charts 1-297.

Bagenal, M. 1955. A note on the relations of certain parameters following a logarithmic transformation. J. Mar. Biol. Assoc. U.K., 34: 289-296.

Brinton, E. 1962. The distribution of Pacific Euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif., 8(2): 51-270.

Colebrook, J.M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955-59. Fish. Bull. U.S., 75(2): 357-368.

Eber, L.E. 1977. Contoured depth-time charts (0 to 200 m., 1950 to 1966) of temperature, salinity, oxygen and sigma-t at 23 CalCOFI stations in the California Current. Calif. Coop. Oceanic Fish. Invest., Atlas 25, ii-ix, charts 1-231.

Eppley, R.W., C. Sapienza, and E.H. Renger. 1978. Gradients in phytoplankton stocks and nutrients off southern California in 1974-76. Estuar. Coast. Mar. Sci., 7: 291-301.

Fleminger, A. 1967. Distributional atlas of calanoid copepods in the California Current region. Part II. Calif. Coop. Oceanic Fish Invest., Atlas 7, iii-xvi, charts 1-213.

Isaacs, J.D. 1975. Assessment of man's impact on marine biological resources. *In*: Marine pollution and marine waste disposal. Pearson and Frangipane, eds., Pergamon Press, Oxford and New York, p. 329-340.

Isaacs, J.D., A. Fleminger, and J.K. Miller. 1969. Distributional atlas of zooplankton biomass in the California Current region: Spring and fall 1955-1959. Calif. Coop. Oceanic Fish. Invest., Atlas 10, v-xxv, charts 1-252.

Kamykowski, D. 1973. Some physical and chemical aspects of the phytoplankton ecology of La Jolla Bay. Dissertation. University of California, San Diego. 269 p.

Kramer, D., M.J. Kalin, E.G. Stevens, J.R. Thrailkill, and J.R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dept. Commerce, NOAA Tech. Rep.. NMFS Circ-370, iii-iv, 1-38.

Kramer, D., and P.E. Smith. 1972. Seasonal and geographic characteristics of fishery resources. California Current region, VII. Zooplankton. Commer. Fish. Rev., 34: 33-40.

Lynn, R.J. 1967. Seasonal variation of temperature and salinity at 10 meters in the California Current. Calif. Coop. Oceanic Fish. Invest., Rep. 11: 157-186.

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. 1968. The thecosomata and gymnosomata of California. The Veliger 3 (Supplement): 103-122.

McGowan, J.A., and P.M. Williams. 1973. Oceanic habitat differences in the North Pacific. J. Exp. Mar. Biol. Ecol., 12: 187-217.

Reid, J.L., G.L. Roden, and J.G. Wyllie. 1958. Studies in the California Current system. Calif. Coop. Oceanic Fish. Invest., Rep. 6: 27-57.

Robinson, E.A. 1967. Multichannel time series analysis with digital computer programs. Holden-Day, San Francisco, 298 p.

Smith, P.E. 1971. Distributional atlas of zooplankton volume in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest., Atlas 13, ii-xvi, charts 1-144.

Soutar, A. 1967. The accumulation of fish debris in certain California coastal sediments. Calif. Coop. Oceanic Fish. Invest., Rep. 11: 136-139.

———. 1971. Micropaleontology of anærobic sediments and the California Current. *In*: The micropaleontology of oceans, Funnel and Reidel, eds., Cambridge University Press, Cambridge, p. 223-230.

Soutar, A., and J.D. Isaacs. 1969. History of fish populations inferred from fish scales in anærobic 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 anærobic sediments off the Californias. Fish. Bull., U.S., 72: 257-273.

Strickland, J.D.H., L. Solorzano, and R.W. Eppley. 1970. General introduction, hydrography and chemistry. *In*: "The ecology of the plankton off La Jolla, California, in the period April through September, 1967. (J.D.H. Strickland, ed.), Bull. Scripps Inst. Oceanogr., Univ. Calif., 17: 1-22.

Sverdrup, H.U. 1953. On conditions for the vernal blooming of phytoplankton. J. Cons. Int. Explor. Mer, 18: 287-295.

Tully, J.P., and F.G. Barber. 1960. An estuarine analogy in the subarctic Pacific Ocean. J. Fish. Res. Board Can., 17(1): 91-112.

Wickett, W.P. 1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J. Fish. Res. Board, Canada, 24(3): 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.

Zentara, S.J., and D. Kamykowski. 1977. Latitudinal relationships among temperature and selected plant nutrients along the west coast of North and South America. J. Mar. Res., 35: 321-337.

APPENDIX

The absolute unit used by CalCOFI to report zooplankton displacement volumes is ml/1000 m^3. Any standardized and codified value can be converted back to absolute units using the following relationship:

$$\text{absolute value} = (\text{codified value} \times 0.2 \times \text{standard deviation}) + \text{mean}$$

Because the codification transforms a continuous variable into discrete integers, some precision is lost due to rounding errors. This Appendix gives the necessary statistical parameters to perform such conversion. In the case of log-transformed series, the mean of $\log_e$ zooplankton volume corresponds to the geometric mean in absolute units. Symbols: "N" is the number of months with at least one observation, "$\bar{X}$" is the mean, "s" is the standard deviation, and G.M. is the geometric mean.

Zooplankton volumes:

	Area I	Area II	Area III	Area IV	Area V
N	115	164	162	155	91
$\bar{X}$	417.04	243.67	153.89	138.22	81.50
s	367.62	314.27	181.86	115.35	80.49

$\log_e$ zooplankton volumes:

N	115	164	162	155	91
$\bar{X}$	5.471	4.795	4.399	4.321	3.947
s	0.621	0.701	0.725	0.539	0.504
G.M.	237.70	120.90	81.37	75.26	51.78

Zooplankton volumes, N:

JAN	13	17	18	17	13
FEB	5	13	13	13	4
MAR	6	13	13	13	6
APR	16	18	19	19	14
MAY	13	14	13	13	9
JUN	14	16	16	14	8
JUL	17	19	19	19	12
AUG	8	10	11	11	7
SEP	4	10	12	11	5
OCT	11	16	15	15	8
NOV	5	9	5	4	3
DEC	3	9	8	6	2

	Area I	Area II	Area III	Area IV	Area V
Zooplankton volumes, $\overline{X}$:					
JAN	227.76	137.59	94.42	79.84	92.87
FEB	281.77	338.97	107.30	91.04	179.25
MAR	308.33	329.50	121.90	102.70	148.76
APR	526.03	305.47	154.66	117.28	83.98
MAY	735.20	320.01	187.71	176.19	101.46
JUN	456.02	302.10	212.92	205.67	73.38
JUL	445.45	326.31	255.27	156.87	55.20
AUG	439.73	221.03	171.53	191.06	60.37
SEP	570.92	142.38	141.30	144.08	38.11
OCT	224.84	149.06	116.52	171.27	48.25
NOV	169.04	110.16	102.62	95.85	55.31
DEC	229.54	101.21	96.59	88.43	48.25
Zooplankton volumes, s:					
JAN	145.99	72.31	79.42	35.69	64.76
FEB	339.13	618.27	58.78	58.38	148.37
MAR	325.69	502.91	74.30	66.39	120.69
APR	342.42	447.42	106.16	66.97	74.94
MAY	761.70	300.41	177.45	159.31	155.75
JUN	268.48	186.93	188.11	189.19	30.25
JUL	208.93	261.43	380.72	129.62	25.65
AUG	297.88	202.47	205.30	116.40	29.24
SEP	300.71	85.67	109.00	70.47	4.45
OCT	92.74	120.20	50.15	152.39	19.03
NOV	64.70	82.05	64.51	10.38	4.04
DEC	140.40	52.44	88.33	13.41	14.50
$\log_e$ Zooplankton volumes, $\overline{X}$:					
JAN	5.014	4.450	4.084	4.061	4.075
FEB	4.996	4.809	4.258	4.100	4.454
MAR	5.115	4.904	4.285	4.104	4.246
APR	5.686	4.963	4.449	4.234	3.899
MAY	5.833	5.085	4.587	4.365	3.955
JUN	5.719	5.190	4.755	4.374	4.069
JUL	5.755	5.216	4.636	4.306	3.829
AUG	5.659	4.889	4.463	4.761	3.882
SEP	5.622	4.542	4.274	4.538	3.577
OCT	5.015	4.507	4.390	4.556	3.744
NOV	4.945	4.160	4.143	4.328	3.938
DEC	5.022	4.160	4.094	4.308	3.710

	Area I	Area II	Area III	Area IV	Area V
$\log_e$ Zooplankton volumes, s:					
JAN	0.419	0.528	0.560	0.421	0.512
FEB	0.793	0.721	0.456	0.485	0.241
MAR	0.722	0.649	0.605	0.576	0.518
APR	0.636	0.649	0.618	0.425	0.518
MAY	0.610	0.610	0.782	0.664	0.884
JUN	0.468	0.494	0.746	0.632	0.405
JUL	0.490	0.606	0.835	0.583	0.397
AUG	0.464	0.707	0.919	0.539	0.458
SEP	0.553	0.733	1.145	0.583	0.122
OCT	0.508	0.557	0.369	0.439	0.396
NOV	0.415	0.666	0.698	0.106	0.137
DEC	0.541	0.624	0.701	0.165	0.269
$\log_e$ zooplankton volumes, G.M.					
JAN	150.50	85.63	59.38	58.03	58.85
FEB	147.82	122.61	70.67	60.34	85.97
MAR	166.50	134.83	72.60	60.58	69.82
APR	294.71	143.02	85.54	68.99	49.35
MAY	341.38	161.58	98.20	78.65	52.19
JUN	304.60	179.47	116.16	79.36	58.50
JUL	315.76	184.20	103.13	74.14	46.02
AUG	286.86	132.82	86.75	116.86	48.52
SEP	276.44	93.88	71.81	93.50	35.76
OCT	163.20	90.65	80.64	95.20	42.27
NOV	140.47	68.17	62.99	75.79	51.31
DEC	151.71	64.07	59.98	74.29	40.85