ANNUAL FLUCTUATIONS IN BIOMASS OF TAXONOMIC GROUPS OF ZOOPLANKTON IN THE CALIFORNIA CURRENT, 1955-59

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ABSTRACT

Year-to-year fluctuations in the abundance of the zooplankton of the California Current region, from 1955 to 1959, have been studied. The abundance of zooplankton was measured in terms of the biomass of each of 17 major taxonomic categories (generally Class or Order). Principal components analysis was used to produce concise descriptions of the major elements of the fluctuations in the abundance of the categories in each of 14 areal subdivisions of the survey area. Considerable coherence with respect to annual changes was found both between the taxonomic categories and between the areas. The principal common element in the fluctuations could be associated with a marked increase in the temperature of the surface waters which occurred in 1957 and persisted through 1958 and 1959. A less pronounced but still quite clear common element in the fluctuations could be associated with year-to-year fluctuations in the amount of coastal upwelling in the area.

Since 1949, the regular surveys conducted by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program have yielded information about a variety of physical, chemical, and biological parameters (see, e.g., Marine Research Committee 1957). For the CalCOFI survey cruises during January, April, July, and October for each of the years from 1955 to 1959, samples of zooplankton were analyzed to provide estimates of the biomass for each major taxonomic category within the zooplankton (Isaacs et al. 1969).

These data were generously made available to the author by J. D. Isaacs to provide material for a study of year-to-year changes in the abundance of the major components of the zooplankton. As stated by Isaacs et al. (1969), "Selection of the years 1955 through 1959 for analysis of biomass distribution was dictated by interest in the occurrence and nature of patterns of seasonal and annual variability among the functional groups of zooplankton. During this time, yearly mean temperatures above the thermocline shifted upward from the relatively cold years of 1955 and 1956 to the relatively warm years of 1958 and 1959."

The object of the study described in this paper is to describe the annual changes, from 1955 to 1959, in the abundance of the zooplankton of the CalCOFI survey area in as much detail as is available from the survey data in order to discover whether observed changes can be associated with environmental fluctuations.

MATERIAL

The details of the procedures for deriving biomass estimates have been described by Isaacs et al. (1969), who also give the reasons for the selection of the particular set of taxa (listed in Table 1). It was their intention to provide estimates of the "nutrient quality" of the standing crop of zooplankton as well as an index of "trophodynamic complexity." The categories were chosen to represent the quality and quantity of zooplankton as food for fish rather than as indicators of variability of the zooplankton as such.

TABLE 1.—A list of the taxa from CalCOFI cruises for which biomass estimates are available. They are listed in alphabetical order and a code used in Figures 7 and 10 is given.

Taxa	Code	Taxa	Code
Amphipoda	AMPH	Larvacea	LARV
Chaetognatha	CHET	Medusae	MEDS
Cladocera	CLAD	Mysidacea	MYSD
Copepoda	COPD	Ostracoda	OSTR
Crustacea larvae	CRST	Pteropoda	PTER
Ctenophora	CTEN	Radiolaria	RADL
Decapoda	DECP	Siphonophora	SIPH
Euphausiacea	EUPH	Thaliacea	THAL
Heteropoda	HETP		

The collection method for the standard CalCOFI plankton samples has been described in

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detail by, e.g., Ahlstrom (1954) and Fleminger (1964). Very briefly, the net is 1 m in diameter at the mouth and 5 m long, the filtering section having a mesh size of about 0.5 mm. The net is towed obliquely, from a ship traveling at a speed of about 2 knots, from the surface down to a depth of 140 m and then returned to the surface. The volume of water fitered varies from about 400 to 600 m^3.

Charts of the distribution of biomass for each taxon have been given by Isaacs et al. (1969) for the April and October cruises, by Isaacs et al. (1971) for the January cruises, and by Fleminger et al. (1974) for the July cruises. The station data are held on a magnetic tape file at the Southwest Fisheries Center, National Marine Fisheries Service.

DATA PROCESSING METHODS

For the purposes of presenting summaries of CalCOFI data in a compact form and to permit some smoothing of the data by taking average values, P. E. Smith's proposal for subdividing the survey area into 23 zones was used in this study (Figure 1). The extent of the survey and hence the number of stations occupied varied from cruise to cruise. The station patterns for the cruises included in this study are given in Smith (1971), and a summary showing the numbers of samples in each zone is given in Table 2.

The biomass data are available as grams/1,000 m^3 and estimated to two decimal places. The range of estimates is from zero to over 5,000 g, and within each taxon they are heavily positively skewed.

The results presented here were expressed in terms of relative changes in biomass in time and space within each taxonomic category, and extensive averaging was employed. It was decided, therefore, to apply a logarithmic transformation to the original estimates. Averages based on log transformed values are weighted in favor of the more numerous low values as opposed to arithmetic means, the values of which may be determined largely by small numbers of high estimates.

In order to give zero a value on the transformed scale it is normal to add 1 to the observation prior to transformation. In this case, where the biomass has been estimated to two decimal places, a number of options is available, either 1.0, 0.1, or 0.01 can be added prior to transformation. Trials

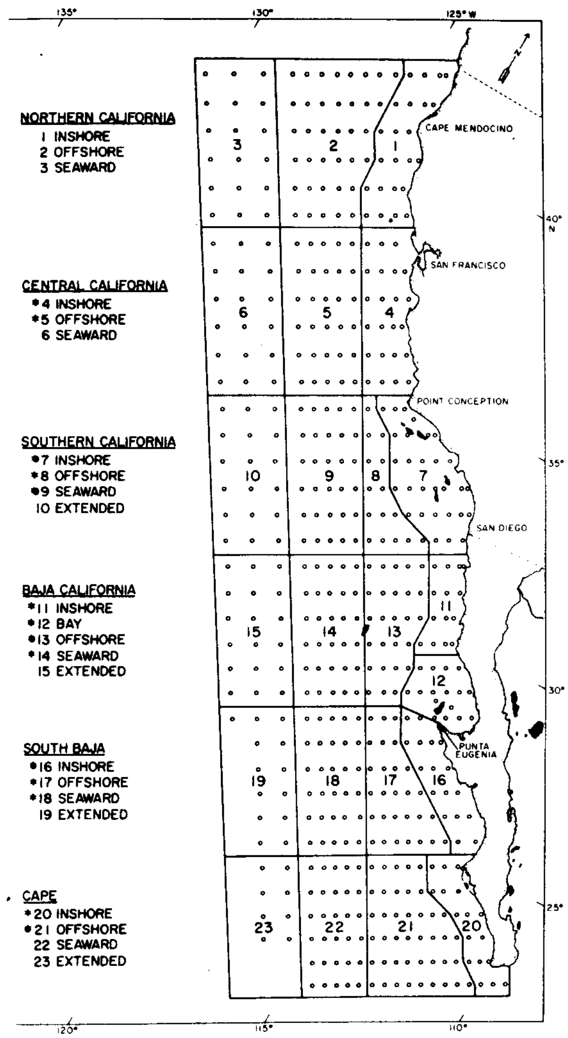


FIGURE 1.—A chart of the area of the CalCOFI survey showing the grid of station positions on which were based the cruises during the period 1955-59. Also shown is the subdivision of the area into the standard zones used in this study. The well-sampled zones for which annual means of biomass were calculated are marked with an asterisk (see Table 2).

involving the calculation of means for each zone for each cruise for a subset of the taxonomic categories indicated that adding 1.0 produced a considerable loss of resolution for means corresponding to less than 1 g/1,000 m^3, and adding 0.01 produced a resolution of low means that appeared to be greater than was warranted by the accuracy of the data. Therefore throughout this study a transformation of the form

$$Y = \log_{10}(10X + 1)$$

TABLE 2.—The numbers of samples collected during each of the January (Jn), April (Ap), July (Jl), and October (Oc) CalCOFI cruises for the years 1955-59 in each of the standard zones (see Figure 1). Annual totals are given in boldface and the grand total is printed in italic.

	1955					1956					1957					1958					1959					
Zone	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Jn	Ap	Jl	Oc	To-tal	Grand total
Central California:																										
Inshore	0	0	13	13	**26**	0	18	16	0	**34**	0	0	16	0	**16**	9	21	23	20	**73**	15	20	24	18	**77**	*226*
Offshore	0	0	9	6	**15**	0	9	18	0	**27**	0	0	10	0	**10**	2	21	20	17	**60**	12	14	30	18	**74**	*186*
Southern California:																										
Inshore	20	17	27	22	**86**	21	22	29	27	**99**	0	25	26	26	**77**	18	27	26	29	**100**	29	28	28	27	**112**	*474*
Offshore	4	6	14	6	**30**	4	6	13	9	**32**	0	7	12	6	**25**	5	13	14	9	**41**	6	12	14	9	**41**	*169*
Seaward	3	17	20	6	**46**	5	13	26	6	**55**	0	17	23	17	**57**	11	21	27	17	**76**	11	30	29	17	**87**	*321*
Baja California:																										
Inshore	12	12	13	12	**50**	12	12	14	0	**38**	8	13	12	13	**46**	12	13	11	13	**49**	13	14	13	14	**54**	*237*
Bay	12	13	14	11	**50**	11	12	15	0	**38**	12	15	16	14	**57**	10	16	14	16	**56**	15	16	17	16	**64**	*265*
Offshore	11	13	26	4	**54**	11	11	22	0	**44**	10	20	26	11	**67**	10	25	25	18	**78**	18	26	24	16	**87**	*330*
Seaward	4	12	24	5	**45**	6	16	20	0	**42**	2	16	19	13	**50**	10	30	23	18	**81**	18	29	29	18	**94**	*312*
South Baja:																										
Inshore	16	15	16	14	**61**	13	13	14	0	**40**	16	15	17	17	**65**	15	16	17	17	**65**	17	11	19	17	**64**	*295*
Offshore	8	12	13	6	**39**	8	8	13	0	**29**	8	21	18	12	**59**	12	22	19	20	**73**	19	17	27	20	**83**	*283*
Seaward	3	2	2	3	**10**	1	2	2	0	**5**	1	12	13	13	**39**	3	15	6	7	**31**	8	7	12	8	**35**	*120*
Cape:																										
Inshore	15	0	0	0	**15**	16	16	0	0	**32**	0	19	0	0	**19**	17	0	0	17	**34**	20	10	0	0	**30**	*130*
Offshore	1	0	0	0	**1**	1	10	0	0	**11**	0	22	0	0	**22**	10	0	0	24	**34**	31	14	0	0	**45**	*113*

has been employed. By this transformation, means corresponding to greater than about 0.2 g/1,000 m^3 are virtually on a logarithmic scale while lower means show a progressive transition to an arithmetic scale.

Quarterly means were calculated by averaging the data for the stations in each zone and then these were averaged to give annual values. For those occasions when less than five stations were occupied in any zone, the station data were ignored and a quarterly mean was interpolated by the following method:

1. For each taxonomic category the set of overall zone means (the sum of all the observations for all the cruises in each zone divided by the total number of stations occupied in the zone) was calculated. The set of overall quarterly means (the sum of all the observations for all the cruises in each quarter divided by the number of stations in each quarter) was calculated.
2. For each missing value the sum of the remaining means for the other zones for the cruise and the sum of the corresponding overall zone means were calculated. The latter was weighted by the ratio of the relevant overall quarterly mean to the grand mean and the missing value then calculated as the product of the remaining zone means for the cruise and the weighted sum of the overall zone means.

From these quarterly means, annual means were calculated for each taxon for each of a set of regularly sampled zones (those marked with an asterisk in Figure 1); and principal components analysis was used to extract from these data the main patterns of year-to-year change in biomass. This is a technique of multivariate analysis (see, e.g., Kendall 1957) which generates a sequence of variables known as components with, in this case, values for each year, which are the weighted sums of the standardized data variables, in this case sets of annual means of the taxonomic categories. The sets of weighting factors, with values for each taxonomic category, are the successive latent vectors of the correlation matrix derived from the original data, in this case the table of correlations between the annual variations in abundance of all possible pairs of taxonomic categories. The first latent vector generates a component which has the largest possible variance. The second vector generates a component which has the largest possible variance in relation to the residual following the removal of the variability associated with the first component, and so on. If the original data are coherent to any extent, it is normal for the first few components to account for a large proportion of the variability of the original data array.

GEOGRAPHICAL DISTRIBUTIONS

To provide some geographical background to the study of year-to-year changes in biomass, charts of the overall mean for each taxon in each standard zone were prepared. In order to search for possible relationships between the geographical distributions of the taxonomic categories, these data were subjected to a principal components analysis.

Figure 2 is a graph of the first latent vector plotted against the second. The graph has a point for each taxonomic category, and the disposition of points represents in a spatial form the relationships between the geographical distributions of the taxonomic categories with respect to the first two components which, in this case, account for 61% of the variability of the original geographical distributions. The interrelationships are probably best regarded in the form of a more or less circular sequence; only the point for Medusae falls well off the sequence.

Figure 3 shows charts of the first two components. The first component shows a very clear north to south, alongshore gradient; and the second shows an equally clear inshore to offshore gradient, indicating that the sequence of categories in Figure 2 runs from categories with northern distributions (Siphonophora to Radiolaria) to inshore distributions (Euphausiacea to Cladocera) to southern and inshore distributions (Larvacea to Mysidacea) to offshore distributions (Heteropoda to Ostracoda). Figure 4 shows the

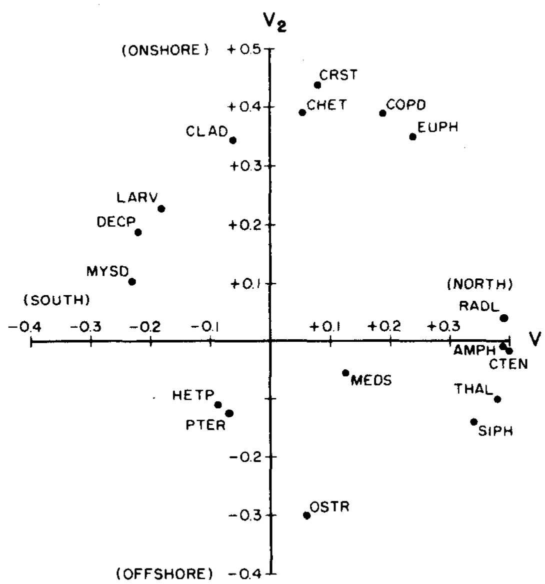


FIGURE 2.—A plot of the first vector against the second vector derived from a principal components analysis of the geographical distributions of the taxa. A key to the abbreviations of the names of the categories is given in Table 1.

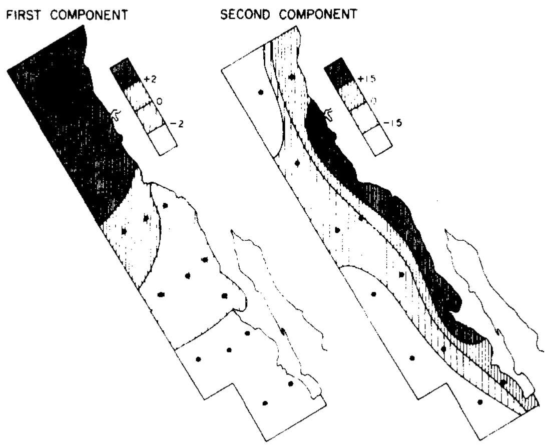


FIGURE 3.—Charts of the first and second components derived from a principal components analysis of the geographical distributions of the taxa.

distributions of the taxonomic categories arranged in this sequence. They are based on averages of the transformed data, for each zone, for each quarterly cruise for the period 1955-59, excluding zones for which fewer than five stations were occupied. These distributions show variability other than that involved in their relationships with the first two components; nevertheless, the north to inshore to south to offshore sequence can be seen fairly clearly. Heteropods and Pteropods are firmly placed in the sequence of taxonomic categories in the vector plot in Figure 2. They have, however, fairly low values compared with the other categories, and only parts of their distributions conform with the south to offshore transition indicated by their position in the vector plot. The distribution of Medusae (Figure 4) can be seen to include areas of relatively high biomass both in the north and in the south, and clearly it does not fit into the sequence of the other categories.

It is obviously unrealistic to attempt to classify the internally diverse taxonomic categories used here in terms of geographical distribution types such as Brinton (1962) found for Euphausiacea. Brinton found that the alongshore axis of the California Current in the CalCOFI survey area was characterized by transitions from "subarctic" species in the north to "transition" species in the region between lat. 30° and 40°N to "equatorial" species in the south. "Central" species occurred offshore and some "boundary" species occurred inshore in the area. McGowan (1971) has shown that these patterns are reflected generally in the distribution of the plankton of the Pacific Ocean. It may, nevertheless, be significant that the pattern of distribution of the taxonomic categories reflects both the alongshore and the inshore-offshore transitions in the distribution of the Euphausiacea.

YEAR-TO-YEAR FLUCTUATIONS IN BIOMASS

Annual means of biomass were calculated, as described above, for each taxonomic category (Table 1) for each of the well-sampled standard zones (Figure 1) for each of the years 1955-59. Two sets of principal components analyses were carried out, firstly for each of the 14 standard zones on the annual fluctuations in biomass of each taxonomic category and secondly for each taxonomic category on the annual fluctuations in abundance in each of the standard zones. The same data are involved in both sets of analyses.

Graphs of the first principal components for each of the zone analyses are given in Figure 5. Table 3 shows that these components accounted for between just under one-half and about three-quarters of the total variability; it also shows that all but a very few of the categories showed positive relationships with the components. The graphs show considerable similarity between the various zones. These results indicate that a large element of the year-to-year fluctuation in biomass is common to all the zones and to a vast majority of the taxonomic categories. Nearly all the zones show a relatively high biomass (relative to a mean of zero) in 1955 and 1956 and a low biomass in 1958 and 1959. The data for 1957 vary from zone to zone, perhaps tending to be higher in the northern and offshore zones and lower in some of the southern and inshore zones.

A table was prepared of the corresponding vectors with the taxonomic categories arranged, by trial and error, to give the high positive terms at the top, and the low positive and the few negative terms at the bottom of the table. The final ranking of categories and the vector values are given in Table 4. This rank was compared with the rank of taxa based on the relationships between their geographical distributions (Figure 2) starting with the northern distributions, with Siphonophora and Thaliacea, working round the sequence and ignoring Medusae (also left out of Table 4) to finish with Pteropoda and Ostracoda.

TABLE 3.—For each zone (*a*) the percentage of the total variability of the original data accounted for by the first component and (*b*) the number of taxa with positive first vector values (maximum = 17). The code names for the zones used in Table 4 and Figures 6 and 9 are also given.

Zone	Code	*a*	*b*
Central California:			
Inshore	CCALIN	74	17
Offshore	CCALOF	71	17
Southern California:			
Inshore	SCALIN	63	14
Offshore	SCALOF	58	17
Seaward	SCALSW	58	15
Baja California:			
Inshore	BCALIN	70	15
Bay	BCALBY	66	16
Offshore	BCALOF	52	14
Seaward	BCALSW	48	13
South Baja:			
Inshore	SBAJIN	64	16
Offshore	SBAJOF	56	16
Seaward	SBAJSW	45	12
Cape:			
Inshore	CAPEIN	54	15
Offshore	CAPEOF	53	16

TABLE 4.—The first vectors of principal component analyses for each standard zone with the taxonomic categories ranked as described in the text. Also the rank of the categories derived from Figure 2.

Taxa	CCALIN	CCALOF	SCALIN	SCALOF	SCALSW	BCALIN	BCALBY	BCALOF	BCALSW	SBAJIN	SBAJOF	SBAJSW	CAPEIN	CAPEOF	"Atlas" rank
Copepoda	0.28	0.28	0.30	0.31	0.36	0.29	0.29	0.30	0.34	0.30	0.30	0.31	0.27	0.30	7
Thaliacea	0.27	0.27	0.30	0.28	0.31	0.28	0.29	0.32	0.33	0.29	0.31	0.29	0.30	0.31	2
Amphipoda	0.27	0.28	0.30	0.32	0.31	0.27	0.28	0.31	0.33	0.28	0.28	0.22	0.29	0.28	4
Siphonophora	0.27	0.28	0.22	0.29	0.23	0.29	0.29	0.25	0.29	0.28	0.30	0.32	0.28	0.28	1
Radiolaria	0.28	0.27	0.30	0.29	0.31	0.28	0.28	0.30	0.28	0.23	0.28	0.20	.02	0.00	5
Ctenophora	0.26	0.27	0.30	0.26	0.28	0.26	0.26	0.26	0.33	0.27	0.26	0.06	0.16	0.05	3
Decapoda	0.25	0.25	0.26	0.29	0.29	0.27	0.24	0.31	0.29	0.24	0.28	0.29	0.30	0.33	12
Euphausiacea	0.27	0.26	0.28	0.26	0.26	0.28	0.21	0.14	0.17	0.24	0.28	0.18	0.18	0.31	6
Chaetognatha	0.28	0.27	0.30	0.28	0.28	0.27	0.24	0.11	0.27	0.24	0.25	.26	0.31	0.32	9
Crustacea larvae	0.25	0.06	0.30	0.27	0.22	0.25	0.24	0.17	.09	0.25	0.31	.25	0.29	0.11	8
Heteropoda	0.15	0.24	0.14	0.18	0.23	0.16	0.29	0.20	0.07	0.19	0.29	0.19	0.27	0.28	14
Larvacea	0.28	0.27	0.17	0.13	0.24	0.27	0.29	0.21	.05	0.22	.08	0.29	0.22	0.23	11
Ostracoda	0.22	0.26	.01	0.26	0.23	0.12	0.18	0.23	0.13	0.18	0.11	.21	0.21	0.24	16
Cladocera	0.12	0.19	.03	0.01	0.03	.23	0.03	.25	0.06	0.23	0.17	0.11	0.09	.08	10
Pteropoda	0.19	0.13	0.10	0.08	.02	0.04	0.12	.02	.19	.06	0.05	.08	.17	0.21	15
Mysidacea	0.15	0.17	.28	0.09	.15	0.08	0.11	.12	.27	0.26	0.14	.33	0.29	0.16	13

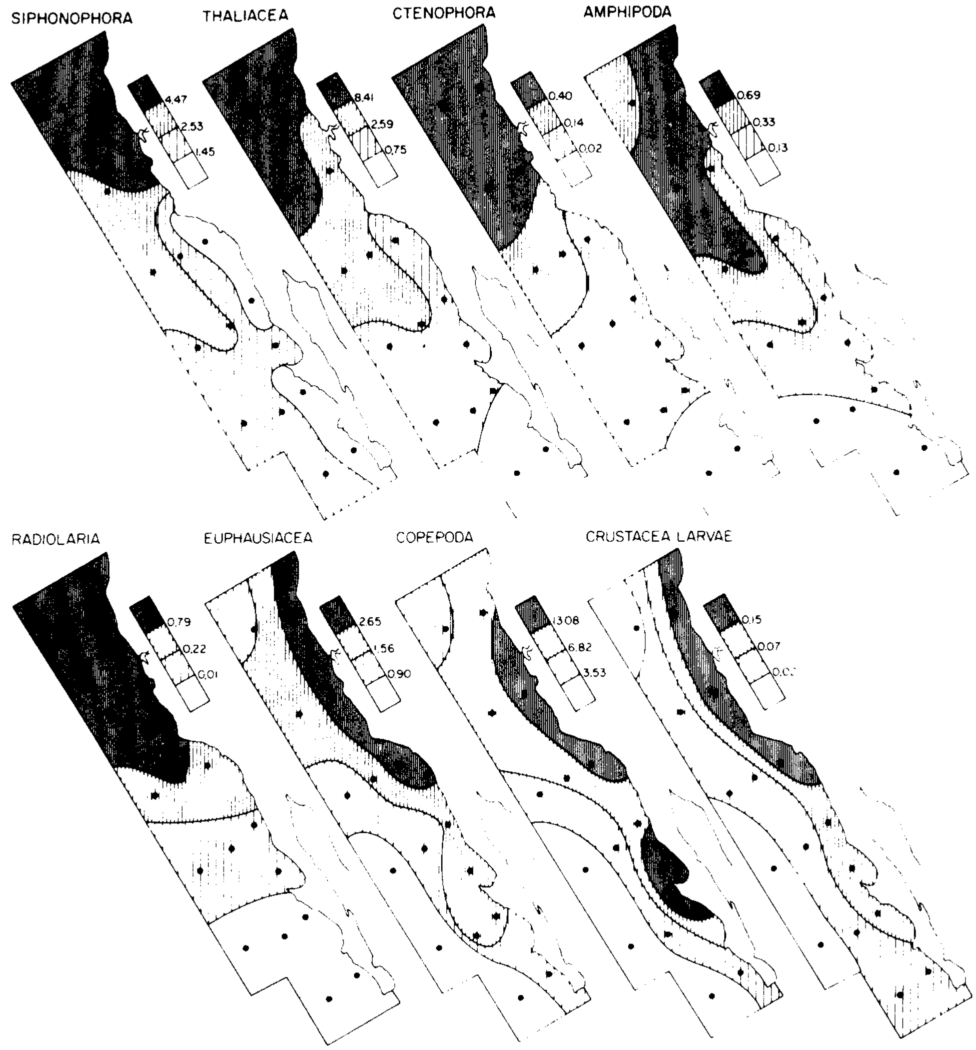


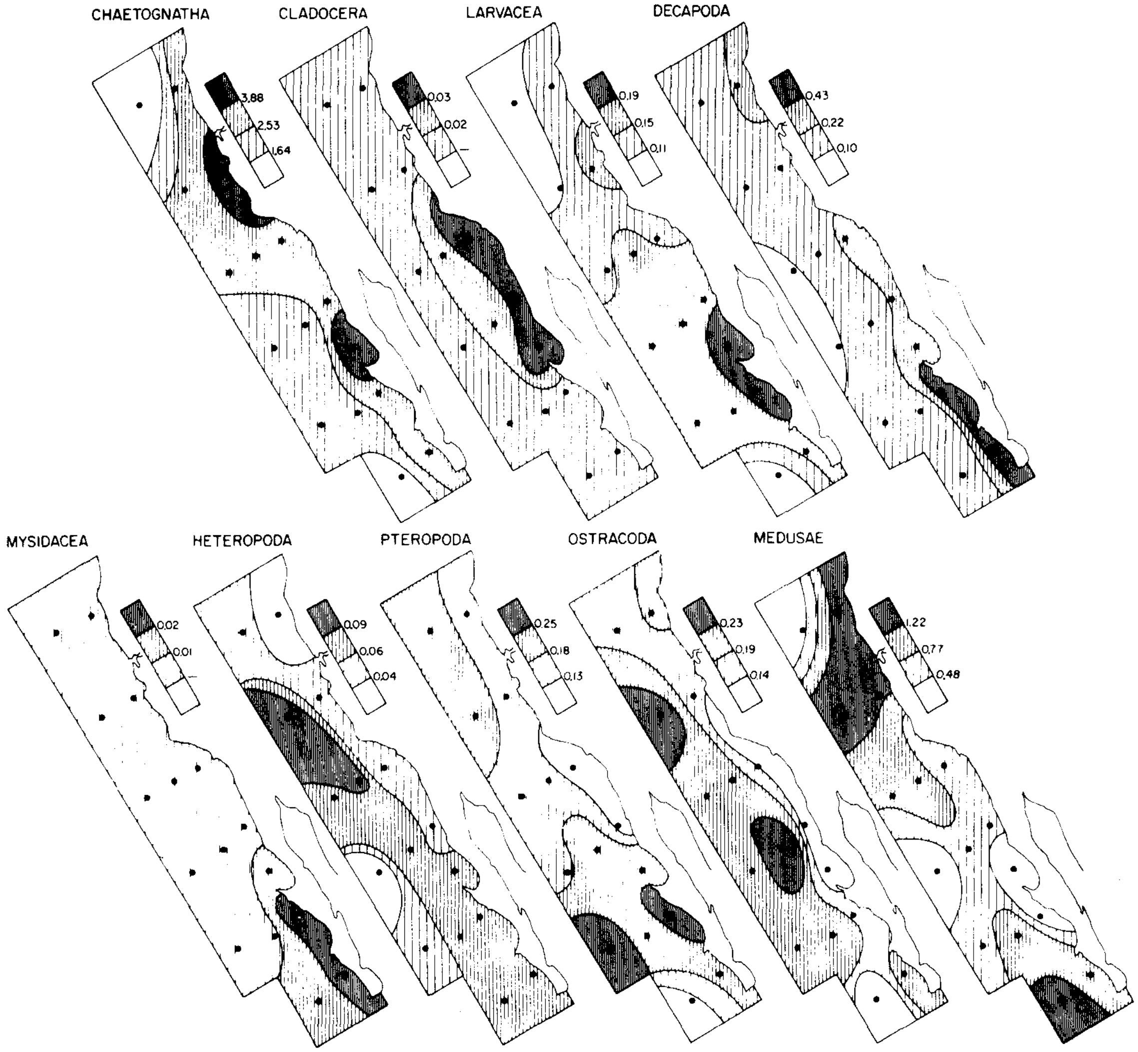
FIGURE 4.—Charts of the geographical distribution of biomass for each of the taxa based on logarithmic means for each standard zone (see Figure 1) for all the CalCOFI cruises for 1955-59. Contours are drawn at levels correspond-

The ranks are given in Table 4, and the value of Spearman's rank correlation coefficient between the two ranks is +0.806 which is significant at the 0.1% level.

Figure 6 shows graphs of the first principal components of the analyses for each taxonomic category with the categories ranked in the same order as in Table 4. All the northern and inshore categories, down to Crustacea larvae in Figure 2, show the same form of year-to-year fluctuations in biomass as do the zones, with relatively high biomass in 1955 and 1956 and low biomass in 1958 and 1959. The remaining categories show some features of this pattern with only Cladocera showing a negative relationship.

These results suggest that whatever influence or influences 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. It is, at least, fairly safe to infer that there is some commonality between the influences which determine geographical distribution and those which are responsible for the form of the year-to-year changes in biomass.

The years from 1955 to 1959 were deliberately



ing to the mean + 1 SD, the mean, and the mean − 1 SD. The keys to the contour levels for each category give the arithmetic values, as grams per 1,000 m^3, corresponding to these levels.

chosen for the production of biomass data to cover a period of marked change in physical conditions and in the distribution of many species in the CalCOFI area. The main features of these changes have been described in the proceedings of a special symposium (Sette and Isaacs 1960). The most striking feature was a considerable warming of the surface waters which started in the south in 1956 and spread through the area during 1957 (see, e.g., Longhurst 1967).

The general form of the change can be typified by the variation in temperature in the top 50 m in the southern California offshore area shown in Figure 7. Favorite and McLain (1973) showed that this is part of a widespread change in surface temperature affecting almost the whole of the North Pacific Ocean. The reasons for the change are not yet completely clear. The initial warming in 1957 appears to be associated with a reduction in the flow of the California Current which occurred between the late summer of 1957 and midsummer 1958. As an index of the flow of the California Current, Saur (1972) used the difference in sea level between Honolulu and San Francisco. A plot of monthly means (with a linear trend removed and adjusted to normal atmo-

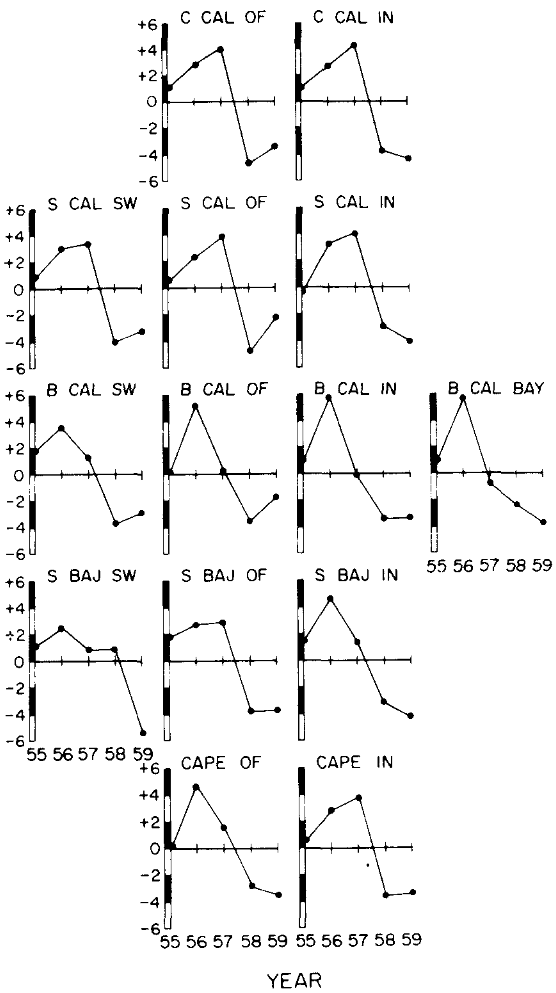


FIGURE 5.—Graphs for each of the well-sampled CalCOFI zones (see Figure 1) of the first principal component of the year-to-year fluctuations in biomass of all the 17 taxa. Each graph is drawn with a mean of zero and the vertical scale is in SD units.

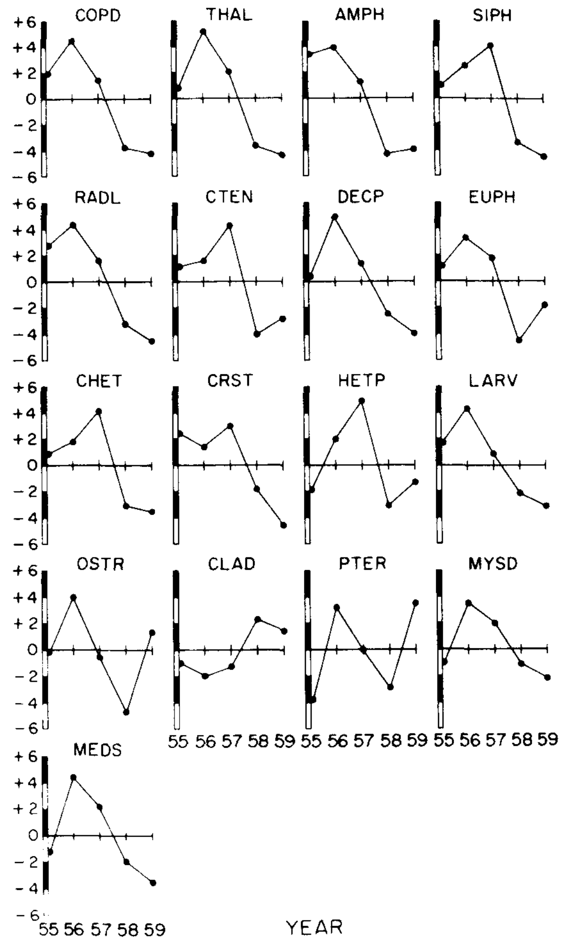


FIGURE 6.—Graphs for each taxon of the first principal component of the year-to-year fluctuations in biomass for all the well-sampled CalCOFI standard zones. A key to the abbreviations of the names of the taxa is given in Table 1. They are in the same order as in Table 4 (see text). Each graph has a mean of zero and the vertical scale is in SD units.

spheric pressure) for 1955-59 is shown in Figure 7. Differences greater than 58 cm are believed to indicate a stronger than normal flow and differences less than 58 cm a less than normal flow. It can be seen that the period of less than normal flow in 1957-58 corresponds well with the timing of the increase in temperature in the southern California offshore zone. In the California Current region, and indeed over most of the eastern North Pacific, the increase in temperature persisted through 1958 and 1959 while the sea level differences indicate a normal or above average flow during this time. The period of below normal flow corresponds with El Niño off the coast of Peru and perhaps with an anomalous weakening of the trade winds of the southern hemisphere and a concurrent reduction of equatorial upwelling (Bjerknes 1966; Favorite and McLain 1973).

Wickett (1967) found a relationship between the year-to-year changes in zooplankton volume for the CalCOFI survey (Thrailkill 1963) and the mean meridional Ekman transport (Fofonoff 1962) for January to August in the previous year at lat. 50°N, long. 140°W (over 1,000 miles upstream from the CalCOFI survey area) for the years 1952-59. He suggested that a major cause of variation in the abundance of zooplankton in the California Current region is the change in the

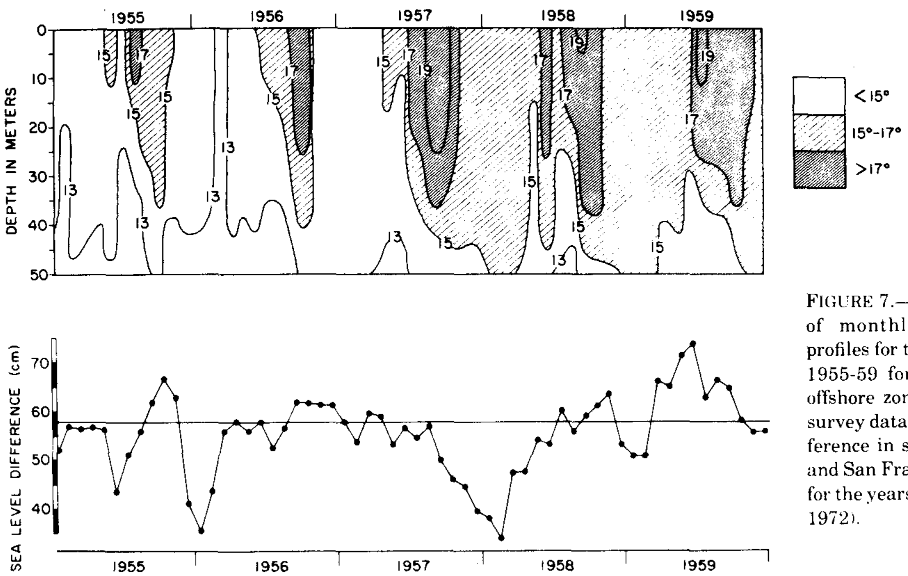


FIGURE 7.—Top) A contoured diagram of monthly vertical temperature profiles for the upper 50 m for the years 1955-59 for the southern California offshore zone (see Figure 1). CalCOFI survey data. Bottom) A graph of the difference in sea level between Honolulu and San Francisco at monthly intervals for the years 1955-59 (plotted from Saur 1972).

proportion of the superficial wind-driven water that is swept southward out of the North Pacific subarctic circulation.

There seems little doubt that the change in temperature in 1957 and its persistence through 1958 and 1959 is related to the relative reduction in biomass of the zooplankton associated with the first principal components of all zones and most of the taxonomic categories. The data presented by Wickett showed a marked reduction in southward transport at lat. 50°N, long. 140°W during 1958 and 1959 and this, coupled with the reduction in the flow of the California Current in 1957 and 1958 (Figure 7), would appear to support Wickett's suggestion of a direct influence by water movements. The relationship between the north to south geographical gradient (Figure 3) and the first principal components is also entirely consistent with this hypothesis.

An examination of the remaining components for each of the zones indicated the existence of a second pattern of fluctuation common to most of the zones. In Figure 8 are given graphs of a component, other than the first, for each zone selected to give the best approximation to a form common to all the zones. In 8 of the 14 zones it is the second component; in the remaining zones it is either the third or the fourth component. Given the quantity and the quality of the original data and considering the large proportion of the variability of the data associated with the first components, the lack of consistency in the position of the common pattern among the components is perhaps not surprising. Figure 9 shows the same for each taxonomic category; again the majority are second components and only one, for Radiolaria, is the fourth component. The main features of the pattern are a low in 1957 and highs in 1956 and 1958; 1955 and 1959 tend to be low but their positions vary somewhat within both the zones and the taxonomic categories.

Coastal upwelling is a feature of the California Current region, and Bakun (1973) has produced estimates of relative fluctuations in upwelling at a number of positions along the west coast of North America. They are based on estimates of the offshore component of the Ekman transport which is in turn estimated from atmospheric pressure fields.

Monthly means of the upwelling index for five positions off the coast at latitude and longitude 36°N, 122°W; 33°N, 119°W; 30°N, 116°W; 27°N, 116°W; and 24°N, 113°W, for the period 1955-58 were extracted from Bakun's report. Uncertainties about the differences in absolute terms between the estimates at different positions particularly off southern California, discussed by Bakun, suggested that principal components might provide a good method of summarizing the data from this set of positions. For each calendar month, analyses were carried out on the index estimates for the five positions and the 5 yr. Examination of the components showed that a pattern common to the first 7 mo of the year was

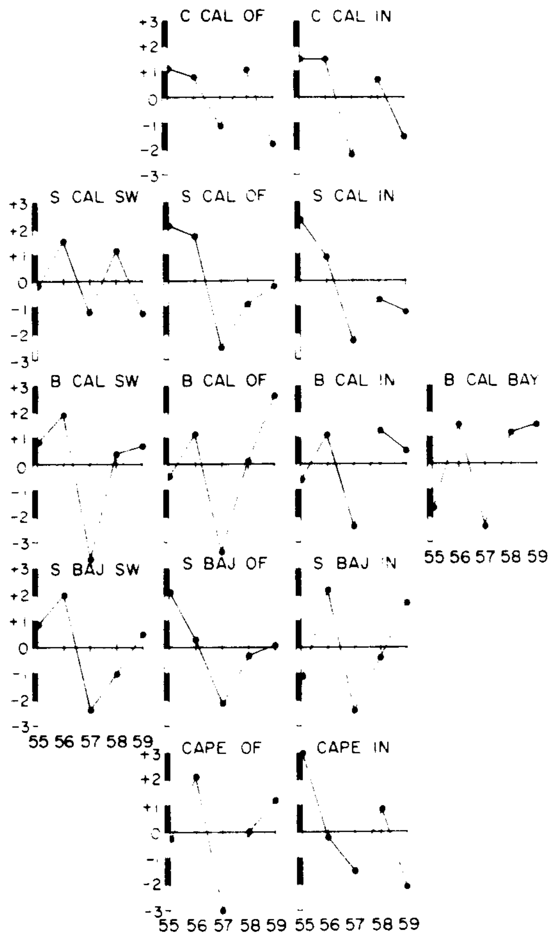


FIGURE 8.—Graphs, for each CalCOFI standard zone, of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 6.

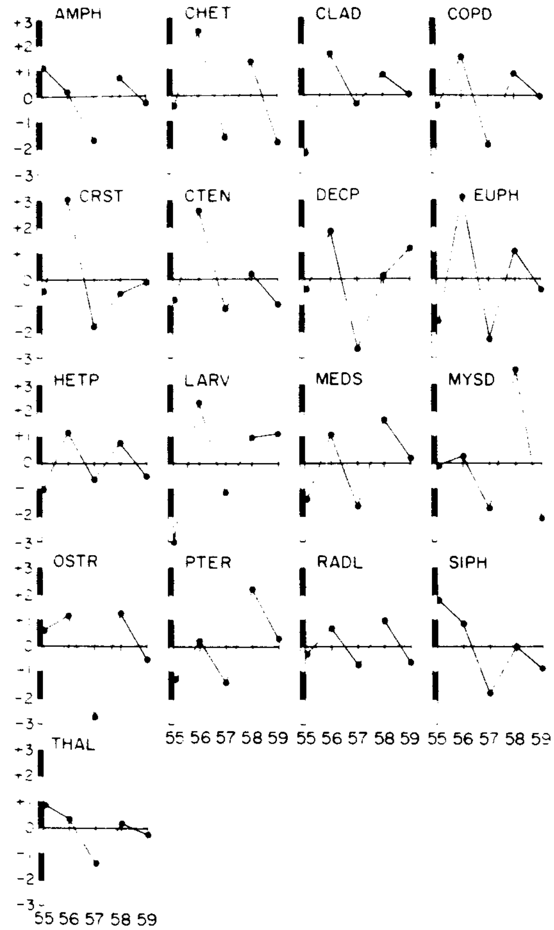


FIGURE 9.—Graphs, for each taxonomic group (Table 1), of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 7.

present within the components, and graphs of these are given in Figure 10. The pattern was found as the first component in all the months except March and April where it was found in the second component. Graphs of the first components for August to December are also given in Figure 10.

There is a marked similarity between the pattern of year-to-year fluctuations in upwelling as represented by the components for the first 7 mo of each year and the fluctuations in biomass of the zooplankton represented by the components shown in Figures 8 and 9, and it is reasonable to assume that some form of causal relationship is involved. As with the first component in relation to the temperature range, the precise mechanisms involved cannot be inferred from the information here. Upwelling has effects on the vertical temperature structure and particularly on the timing of the establishment of a clear thermocline. It can also be expected to have a considerable influence on the supply of nutrients. It is probable, therefore, that the effect on the zooplankton is an indirect one through the influence of vertical stability of the water column and the supply of nutrients on primary production processes. Peterson (1973) has established a relationship between year-to-year variation in upwelling

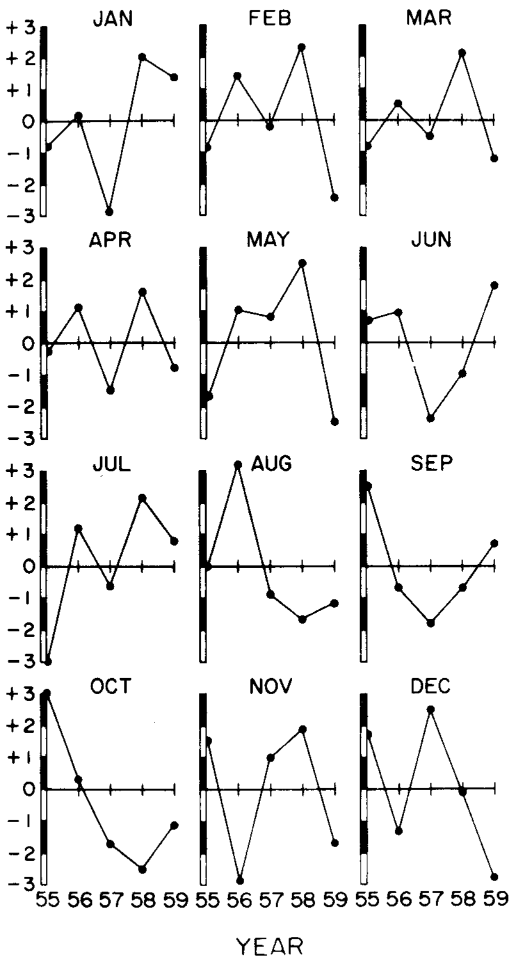


FIGURE 10.—Graphs of principal components of upwelling index for the CalCOFI survey area for each month for the years 1955-59. See text and Bakun (1973).

off the coast of Oregon and the catch of the Dungeness crab, *Cancer magister*, with a time lag of about 18 mo. He attributed this to an increased food supply in years with pronounced upwelling, implying a relationship between upwelling and plankton similar in sign to that found further south in the California Current.

CONCLUSIONS

At least during the period 1955-59, a considerable proportion of the variability from year to year in the biomass of zooplankton, as represented by estimates for the taxa listed in Table 1, can be associated with hydrographic events, variations in the strength of the California Current, and variations in the intensity of coastal upwelling. The precise mechanisms involved are not clear, but in relation to the California Current there is a similarity in the relationships within the taxa with respect to both geographical distribution and annual fluctuations in abundance which suggests that advection of stocks may be involved to a considerable extent. The influence of upwelling on primary production through effects on temperature stratification and the supply of nutrients probably accounts for the relationship with the zooplankton.

The only data that have been produced routinely from the whole series of CalCOFI cruises, which relate to plankton other than fish eggs and larvae, are in the form of displacement volumes of unsorted samples (Smith 1971). The marked coherence between the various taxonomic categories suggests that these data can be expected to produce estimates of long-term variations which indicate real changes in the abundance of the zooplankton. Such data cannot, however, reflect the geographical differentiation within the zooplankton, and this imposes a limit, to the extent to which they can be used, to provide the basis for the examination of the influences of a complex of environmental factors of the kind suggested by this study as playing an important role in determining the year-to-year fluctuations in the plankton.

The taxonomic categories used in this study were selected by Isaacs et al. (1969) to represent the plankton as food for fish. I have used them to represent fluctuations in the zooplankton as such for the 1955-59 period.

For future studies the only definitive method of selecting taxa to represent year-to-year changes in the zooplankton is by trial and error: there are, moreover, numerous possibilities, and the labor involved would be prohibitive if some compromise is not made. It is indicated above that there is a tendency for taxa which have similar geographical distributions also to show similar year-to-year fluctuations in abundance. As a first approximation, this fact might be used as a guide to the selection of representative categories. It is implicit that each selected category should be geographically homogeneous, and the set of categories should cover the full range of geographical distributions.

It is probable that the species is the highest taxon for which geographical homogeneity can be assumed, and even here there may be some species which have geographically differentiated races. Isaacs et al. (1969) gave an estimate of about 550 species found, or likely to be found, in the zooplankton of the CalCOFI survey area. Allowing for the fact that somewhere between one-half and three-quarters of these species will probably occur infrequently in samples, the labor involved in routinely analyzing for this number of species is very considerable. The geographical distributions of species belonging to many of the major taxa within the zooplankton have been studied and published in the CalCOFI Atlas series which could provide the basis for the selection of a limited number of species which will represent the range of geographical distributions in the survey area and, hopefully, will provide a good representation of the range of year-to-year fluctuations in abundance.

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