PLANKTON PATTERNS, CLIMATE, AND CHANGE IN THE CALIFORNIA CURRENT

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INTRODUCTION

The Problem

A serious problem facing oceanographers is evaluating the climate's role in the regulation of populations and communities. There can be no doubt that entire ecosystems respond to climate perturbations and that these responses can be large (Chelton et al. 1982; CPR survey team 1992; Frances and Hare 1994; Barry et al. 1995; and this symposium). While evidence for these effects has accumulated, no real theory has developed about the role of climate in population or community dynamics.

Recognizing that climate is important, most marine biologists have emphasized the role of seasonal changes in the regulation of populations. But species tend to adapt well to predictable seasonality. It is the unpredictable anomalies from seasonal norms that we do not understand and that seem to affect populations so strongly. Nor do we understand the driving forces behind such anomalies. It is in the study of climatic and biological anomalies and their interrelationships that a rich field awaits us. After all, we have pretty much known since Copernicus (in 1540) the cause of seasonality.

Our ability to define what is meant by the word *change* is at the root of the problem of understanding climate's role. Populations, communities, temperature, and water movement do vary on a seasonal basis, but they also vary on many other frequencies as well, both higher and lower. These other frequencies of change are of special interest now. Because humans have altered the mix of gases in the atmosphere, there are good reasons to believe that the heat budget of the earth may also be altered and that the consequences will be more variable atmospheric and oceanographic climates. It is expected that these changes will be evident and be felt by ecosystems sometime in the next 10 to 100 years (Martinson et al. 1995).

Defining such temporal changes and understanding their consequences to biological systems are important tasks. But such large environmental temporal changes involve large spatial dimensions as well, so large-scale spatial/temporal ecosystem studies will be necessary because effects due to local changes simply cannot be extrapolated outward to include large areas without evidence for doing so. We can also expect that some changes in time may well include range shifts, and this is a spatial problem as well.

The issue, then, is how will climate change affect marine biological systems? How and in what direction will they respond? There are two basic approaches: (1) local, short-term, process-oriented research, and (2) long-term time-series monitoring. These need not be mutually exclusive, but usually are.

Approaches to the Climate Problem

Process studies. All plants and animals constantly interact with other plants and animals of the same species and other species. Many of those others are competitors, predators, prey, symbionts, or degraders. Because of close spatial/temporal species associations, many biologists have come to believe that at least some of these groupings of species are recurrent and that over time a skein of interactions between species has evolved through natural selection so that there are persistent feedback loops which determine community structure, and regulate energy flow and population dynamics. The introduction of foreign species and the subsequent observed disruption of food webs and established species structure are taken as evidence for this, as are numerous case history studies of coevolved species-species interactions.

If this concept of community is even partially true, then to fully understand the population dynamics of a single species—say the anchovy (*Engraulis mordax*)—some reference to the entire system in which it lives is necessary. But the word *community* and its companion concept *stability* are used in ambiguous ways, and there are still no clear, generally accepted, meanings (Schrader-Frachette and McCoy 1993).

Because of this vagueness of concept and because of the great complexity of even simple communities (that is, many linkages and cross-linkages between co-occurring species populations) many ecologists have chosen to make simplifying assumptions in order to study them. The most common of these assumptions is that various species populations can be aggregated into functional groups. But even here the definition of a functional group is frequently elusive. Many functional designations are synonymous with trophic level. Here the definitions are clear even if the measurements in nature—of, say, the

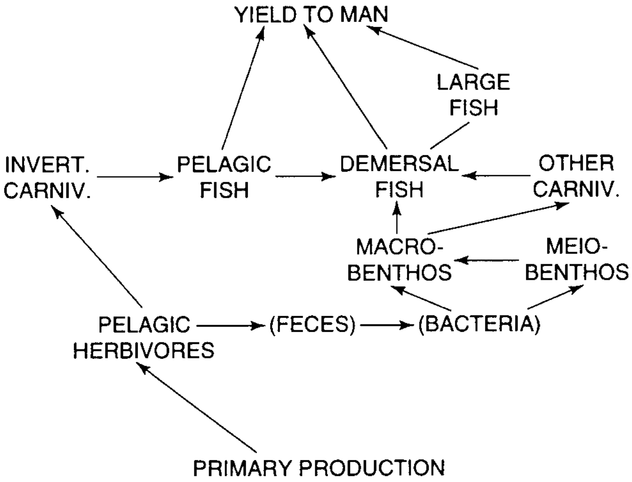

Figure 1. A typical box model of a pelagic food web in which the *arrows* indicate the transfer or "flux" of energy (usually as calories) or biomass or nitrogen or some other index. The emphasis in almost all studies based on this sort of concept is to measure one or more of the rates of transfer either directly or indirectly (as respiration, for example). Some box models are more complex, others are simpler, but very few measure all fluxes at once, so the assumption must be made that the system is in steady state (after Steele 1974).

energy flux through an entire trophic level—are at best dubious. This is especially true if the research objectives are to measure the flux through several or all the levels to some top predator, like the anchovy, in order to determine its potential yield (figure 1).

There are also practical considerations in measuring flux or even just the biomass of entire trophic levels. In order to apply the trophic-dynamic theory of Lindemann or Odum, one generally measures the flux of energy through "representative" species and assumes that the rest of that level is pretty much the same. Alternatively, the respiration of the biomass of what can be captured with a certain mesh-size net is used. But not all herbivores metabolize at the same rates even under identical conditions, and a zooplankton biomass sample may contain as many as three trophic levels.

Trophodynamic studies have not falsified many important hypotheses nor been useful in predictions nor helped us understand the role of climate. But we have learned much from the efforts to understand flux between components, the most important "fact" being the almost universal finding that these fluxes are nonlinear and density dependent. The systems are usually not known to be in steady state when measured. This, of course, makes modeling very difficult.

Ecosystem models are popular, but present models may or may not have much to do with nature. At their worst they are full of untested and untestable assumptions and preconceived ideas. At their best, they are simple quantitative approximations of what we believe we have observed about complex interactions. As such, they stimulate us to think about the potential consequences of such interactions and what might perturb them. Such models should have predictive value and lead to potentially disprovable hypotheses, although there is little evidence for this.

Many contemporary studies in biological oceanography seem to have the mostly unstated objective of providing data for filling in one or another functional role in flux models; i.e., the arrows between the boxes in ecosystem box model depictions (such as figure 1). But this rationale is often unclear. These studies are often referred to as "process oriented" or "case histories," and some of the most decipherable models are based on such observations (e.g., Ross et al. 1993). Many such process studies are reductionist in the extreme, and there are few attempts at true replication, or randomization or controls, and almost never any manipulation of the variables. The more successful of the ecosystem models, based on such studies, have managed to duplicate a seasonal biological signal, but not the sort of responses to anomalies in seasonality that are observed. Such case history or process studies have no doubt enhanced our understanding of some of the details of how the ocean functions and have clear advantages, some of which are:

1. They describe aspects of the dynamics of parts of larger systems and are therefore mechanistic.
2. They can test some specific hypotheses such as: The clearing rate of copepods is not a linear function of food concentrations.
3. They can sometimes provide advice to managers of single-species fish populations.
4. They can sometimes circumscribe or set limits on some rates of transfer of energy or material.
5. They can sometimes provide rough generalizations such as: The rate of growth of individuals is a positive function of temperature; or Phytoplankton growth is limited by nutrients.
6. They are compatible with short funding cycles.
7. They are simple conceptually and therefore popular.

Process studies also have shortcomings, which are:

1. In the context of ecosystem response to climate change, process studies cannot define the word *change* in any meaningful way because of the short duration of the data set.
2. There is no quantitative algorithm for scaling them up in space or forward in time.
3. They are often so highly focused that the relation to the rest of the system is problematical.
4. They are often not really experimental, in the sense that there are usually no replicates, randomization, controls, or manipulation.
5. The ecosystem from which the sample is drawn is seldom in steady state, and the fluxes between boxes are almost always nonlinear.

6. They are often tautological; as such, they are derivative, repetitious questions and add little to our understanding.
7. Conclusions drawn from a process study at one location are not always applicable to other locations; for example, *Calanus* life histories in the North Atlantic versus the North Pacific.
8. There are many untidy system effects. For example, predator switching is a common phenomenon. It has been observed that exogenous perturbations can make prominent players out of system components which were not response variables in the first place.

Time series. Time series are merely the repetitive measurement of some variable over time. The objective is to determine how it varies in magnitude with respect to time in order to define the temporal scales of variability—that is, the frequency spectrum.

Apart from selecting the variable to be measured and the location, time series are designed with few prior assumptions about the behavior of the variable or what may or may not influence its frequency spectrum of variability. Time series are, or should be, empirical. Because they assume little prior knowledge of rates, directions, amplitudes, or frequencies of variation, the sampling should be as frequent as possible for as long as possible. High-frequency changes are just as likely to be the "important" ones as low-frequency under this empiricism.

The main questions asked by a time-series study have been given by Wiebe et al. (1987). What are the temporal scales of variability of basic community ecosystem properties? Are there some frequencies that show the largest and therefore the most ecologically "important" changes? If various components of the biogeochemical system interact to influence each other's magnitude, there should be detectable statistical relationships between them, even in the presence of a large amount of noise. What are the cross-correlations or coherences between system components? We need to know more about what types of atmospheric or hydrographic perturbations affect biogeochemical systems and what types do not. How and in what direction is the response to different kinds of physical events? It seems likely that the mean state of ecosystems is set by the cumulative effects of variability on many space and time scales. But if there are multiple steady states, how are shifts between them brought about? Is it necessary for forcing to change on all frequencies for a shift from one system state to another?

Can a long time series of measurements of the products of nonlinear interactions help us understand the limits of predictability and modeling? Predictions based on models of complex systems about which we have only limited knowledge have not enjoyed great success. But the product of these flexible webs of functional rates, namely changes of the main components of community structure with respect to time, can be easily measured. Changes in structural state can be quantitatively described. Testable null hypotheses can be proposed. We can then construct a sort of inverse model, not based on "first principles" (whatever they are) but on empiricism: what kind of a structure and what kinds of dynamic interactions can result in the system we have observed?

As with the process study approach, there are advantages and shortcomings with the time-series approach. The advantages are:

1. The research is empirical.
2. This research can define what is meant by the word *change*.
3. Dominant frequencies of change can be determined. Frequency spectra can be examined.
4. Time series are on the correct scale for studying ecosystem change on interannual and decadal time scales.
5. If a number of properties at a number of locations have been measured, spatial coherence information can be determined.
6. With a number of well-spaced stations, spatial averaging can be done, thus allowing a smoothing of noisy, high-frequency spatial patchiness.
7. Such series can generate and test higher-order null hypotheses such as: Zooplankton productivity does not respond to changes in coastal upwelling index.
8. Empirical results obtained from time series provide important guidance for designing and developing process studies and ecosystem models. The data can also be used to validate or invalidate models.

The disadvantages of time series are:

1. The results of time series studies provide little information on the intermediary mechanisms of change.
2. Insight into cause and effect depends on correlations.
3. If correlations "fail" there are usually no explanations.
4. Time series are tricky; they can easily be done improperly and are often complicated by practical considerations. If there are frequent gaps or changes in frequency of sampling or if the frequency of sampling is much less than the frequency of variability, the data can be badly aliased, which can lead to misleading results. Single stations do not necessarily tell us about spatial extent of variability or change.
5. Time series require sustained effort over a long period of time.

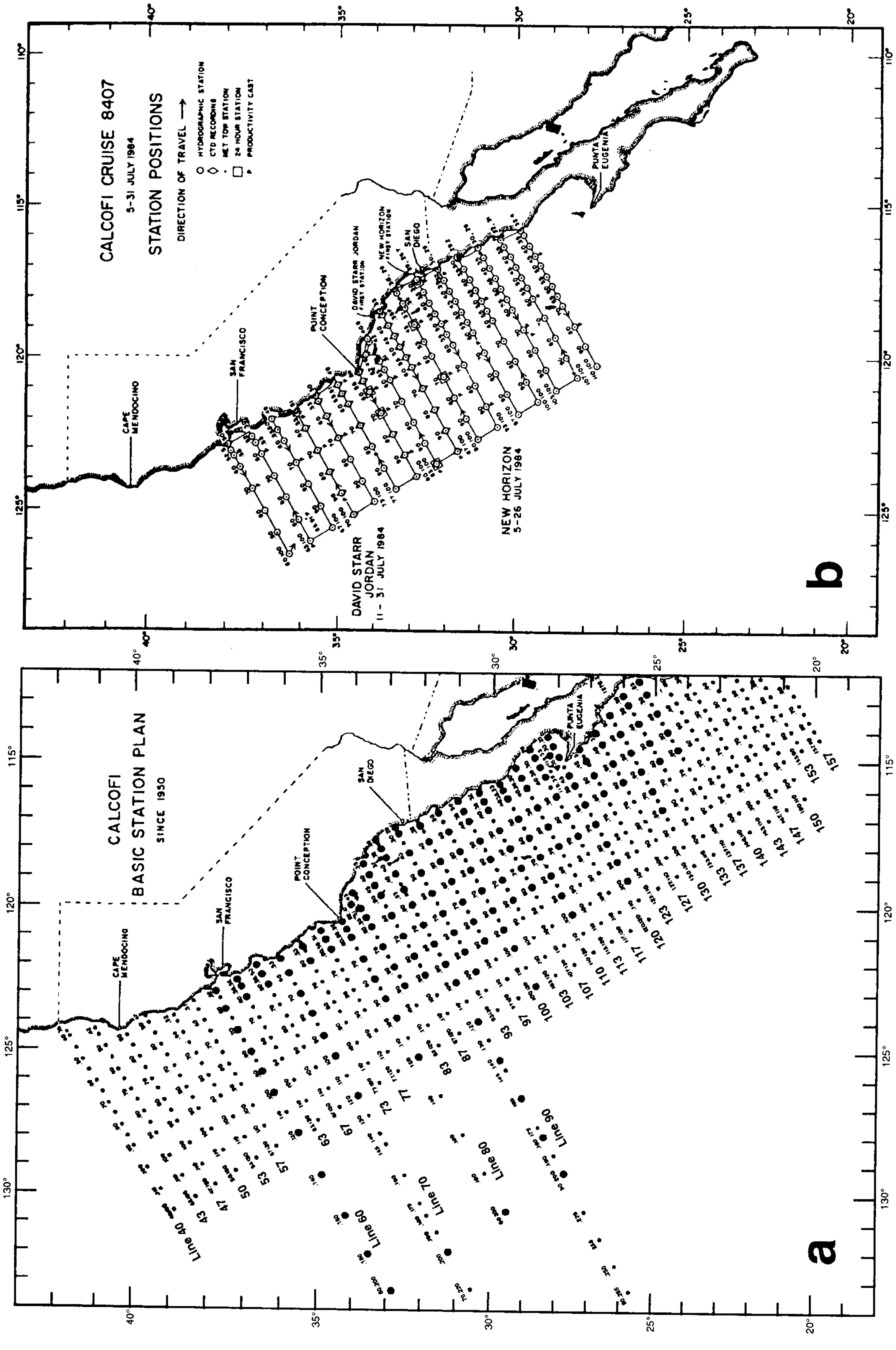

Figure 2. *a*, The basic CalCOFI plan. No one cruise covered this area (*small dots*). The most frequently sampled stations (1950–79) are shown also by *large dots* (after Lynn et al. 1982). *b*, A typical cruise pattern from the 1970s and early 1980s, showing the type of sampling done on each station (SIO Cruise Report).

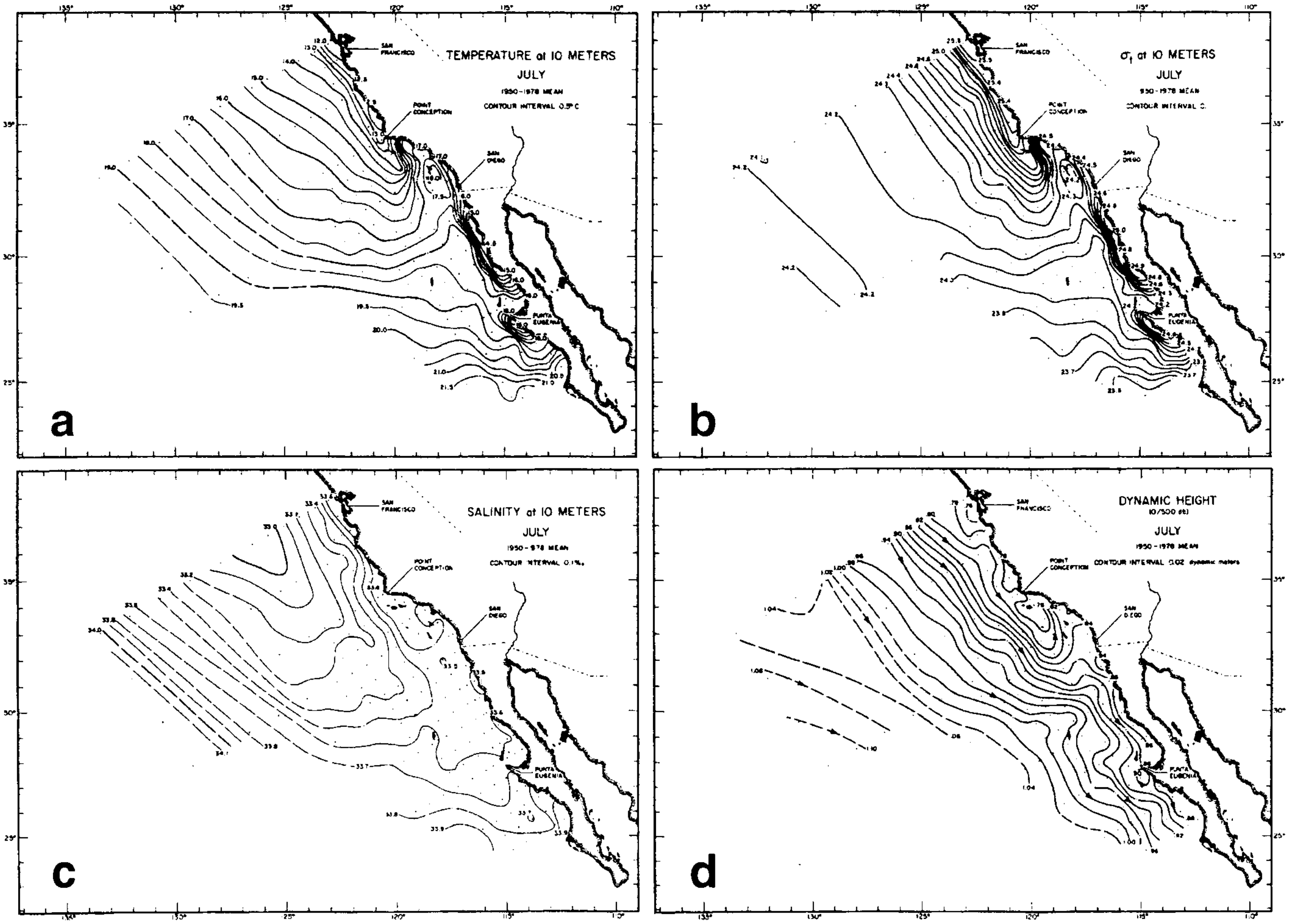

Figure 3. *a*, The 1950 to 1978 mean 10 m temperature for the summer season (July–Sept.). Longshore and onshore-offshore gradients are evident. After about 1977 the California Current warmed significantly. *b*, The 1950 to 1978 mean summer salinities at 10 m. *c*, The mean 10 m summer density patterns, 1950–78. *d*, The mean summer dynamic heights 10/500db for summer. Separation of isopleths indicates speed of current (close together, faster; widely separated, slower). There is a longshore jet in midstream (*a–d* from Lynn et al. 1982).

6. Collecting time series is routine and uninteresting until enough time has elapsed so that natural phenomena can be resolved.

In spite of these shortcomings, time series remain the only way to obtain information on ecosystem variability, and they almost always reveal important new and unexpected results.

THE CALIFORNIA CURRENT

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program was designed in the late 1940s as a time series, chiefly to study the Pacific sardine and its physical and biotic habitat. There were preconceived notions in the selection of variables to be measured and the time and space scale on which to measure them, but these had little or nothing to do with an assumed architecture or dynamics of the system. The program was driven mostly by practical considerations—the decline of the sardine, and what time-space resolution could be afforded that was consistent with understanding the habitat, i.e., the problem posed by Stommel (1965). A grid plan was selected and adhered to; methods, while changing somewhat over time, were intercalibrated and found to be reasonably consistent.

Several of the many advantages of the CalCOFI plan are that it covers a large area that includes most of the spawning area of the sardine and some other fish; important biogeographic and physical features can be seen; and large-sector spatial averaging of the time series can be used to generalize about real temporal changes.

This grid plan is well known (figure 2), as are the long-term spatial means of temperature, salinity, density, and dynamic heights (figure 3). These show considerable spatial variability and strongly imply that time series and spectral analyses are called for in order to investigate the temporal nature of this variability.

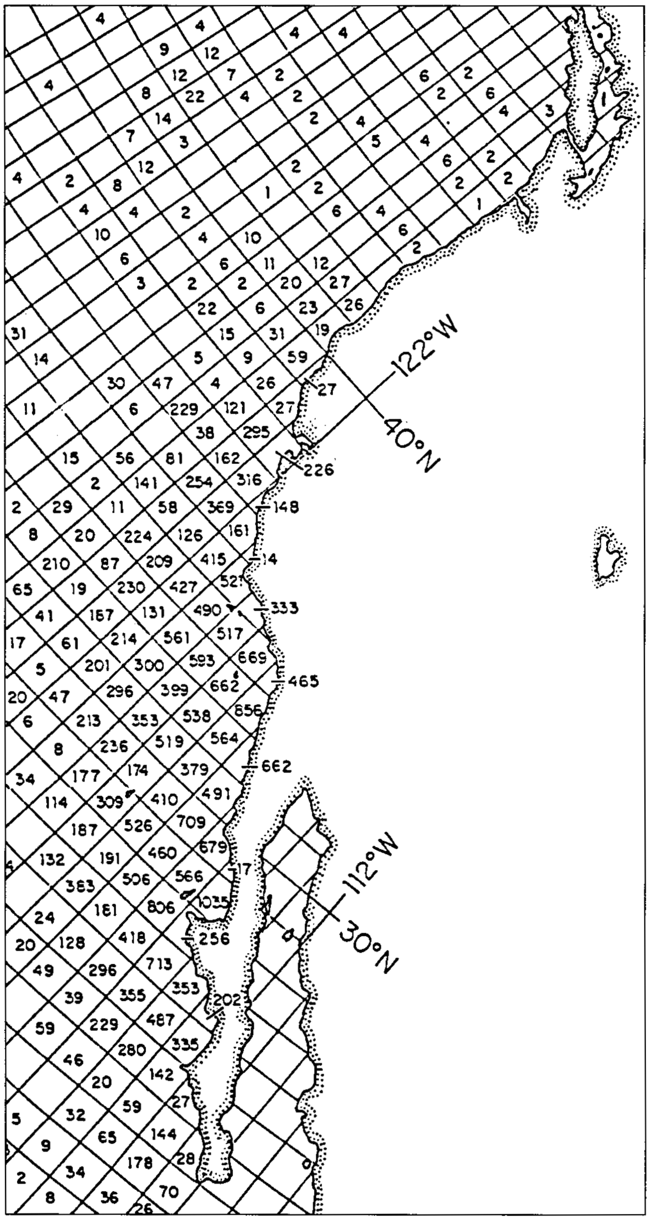

Figure 4. The number of large oblique zooplankton tows per 1° square 1950–88 (see Kramer et al. 1972 for methods).

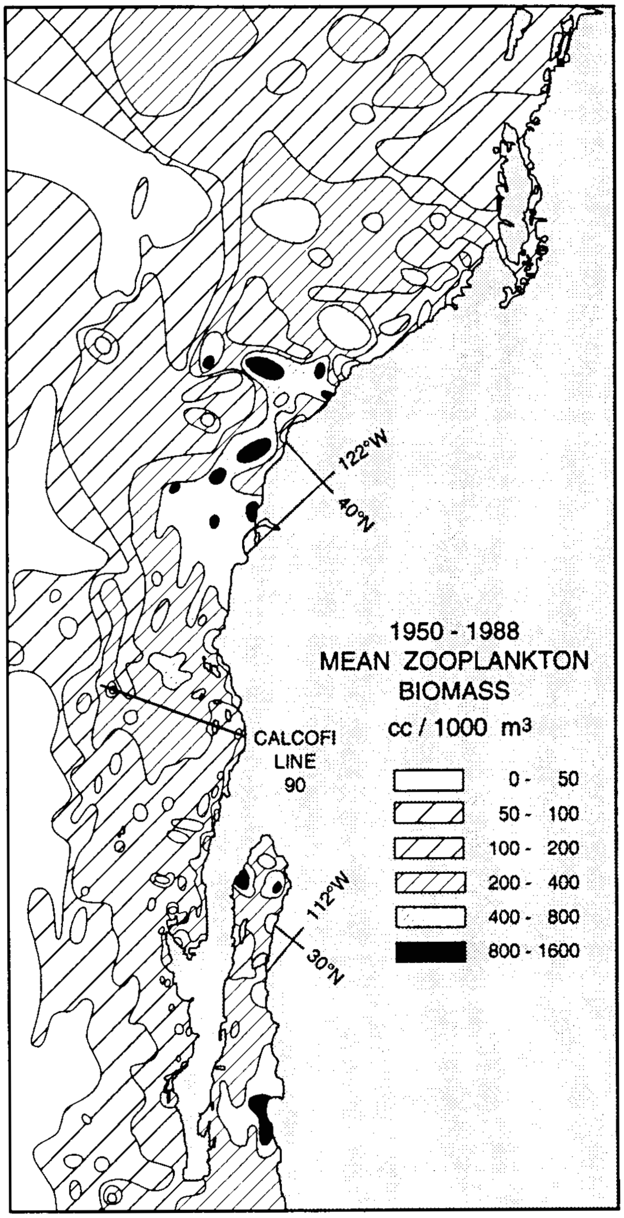

Figure 5. The long-term mean zooplankton biomass. There are onshore-offshore gradients and north-south gradients.

Spatial Patterns

The main purpose of the net tows conducted since 1949 by CalCOFI was to obtain samples for estimating the patterns of abundance of fish eggs and larvae. Since sampling zooplankton at the same time could hardly be avoided, a very large time series of zooplankton has accumulated. Figure 4 shows the number of plankton tows per 1° square over the period 1950–88. Each of these is accompanied by a hydrographic cast to at least 500 m, so that relations between biological and physical variables can be examined on the same frequencies. Although it is clear that there have been wide variations in the intensity of measurement per 1° square, a very large number of measurements do occur in the central sector (the main area of fish spawning), especially on lines 80 and 90.

The long-term spatial mean of zooplankton biomass (figure 5) shows an extraordinarily patchy field despite the long-term temporal averaging. This seems especially true where the sampling intensity is high. Further, most of the plankton is concentrated in a relatively small fraction of the time-spatial domain. But it is clear that there is a north-south gradient off most of California and a well-defined offshore maximum south of Point Conception. The low values off Oregon and Washington may be due to sparse sampling in that region.

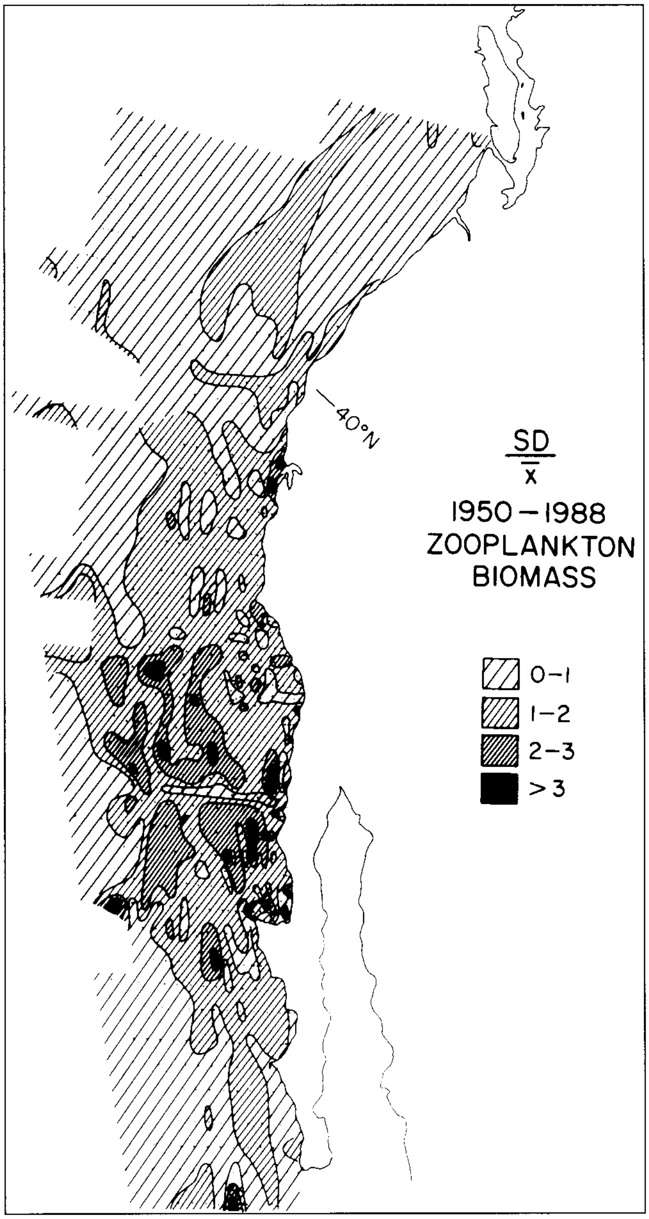

Figure 6. The index of variation (standard deviation divided by the mean) of the zooplankton biomass data in figure 5.

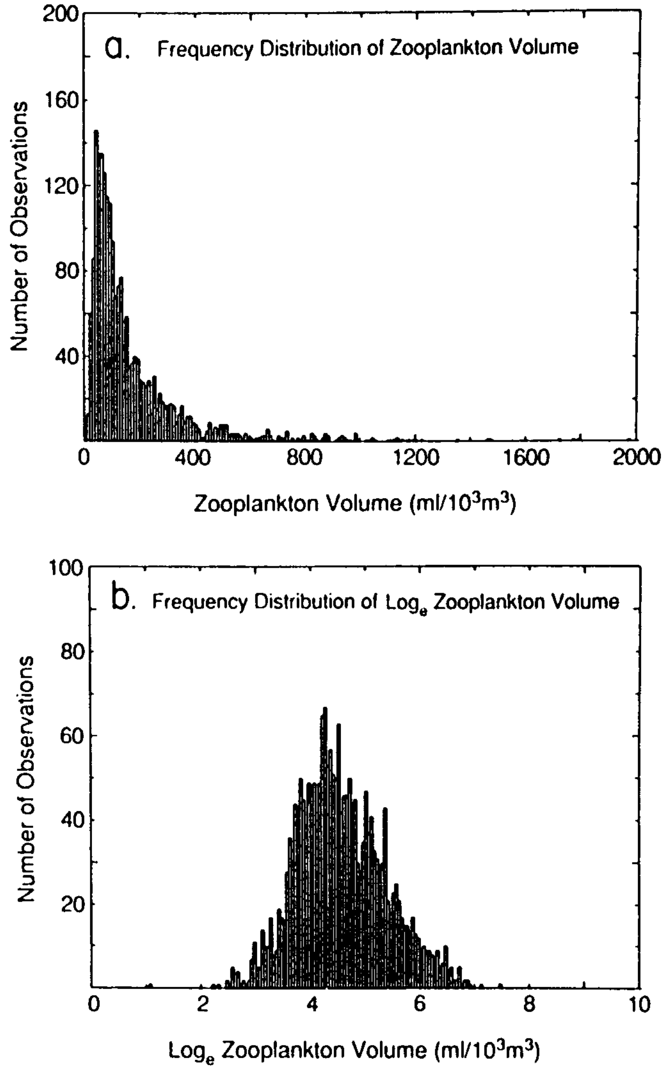

Figure 7. *a*, The frequency distribution of CalCOFI zooplankton biomass estimates; *b*, $\log_e$-transformed data.

In an effort to smooth the data further we used the coefficient of variation (SD/$\bar{X}$) since the magnitude of the variance is dependent on the mean in this case (figure 6). This did smooth the patchiness somewhat and also had the effect of shifting the main area of apparent high spatial variability farther south. The frequency distribution of zooplankton biomass (figure 7) shows many large outliers 4 to 10 times the overall mean. These must represent very dense patches which are episodic in space and time, thus the failure of our averaging and coefficient of variation to effectively smooth the long-term data. This seems clear evidence of the highly variable nature of zooplankton and strongly implies that large but episodic and spatially limited ecological events are features of the California Current System.

The area of high biomass variability is also one of highest species diversity (McGowan and Miller 1980). It is here that species whose populations are continuous with those of the Subarctic, the Transition Zone, and the Central Gyre, and with warm-water cosmopolites mix together (figures 8, 9, 10). This zone of high variability in biomass and diversity (figure 11) is almost certainly due to physical mixing of waters and their faunas from different source regions. Species dominance shifts in the plankton here occur very rapidly and over very short distances as compared to the Central Gyre (McGowan 1990). Such rapid and large shifts in rank order of abundance are unlikely if competitive displacements are the main cause. It seems much more likely

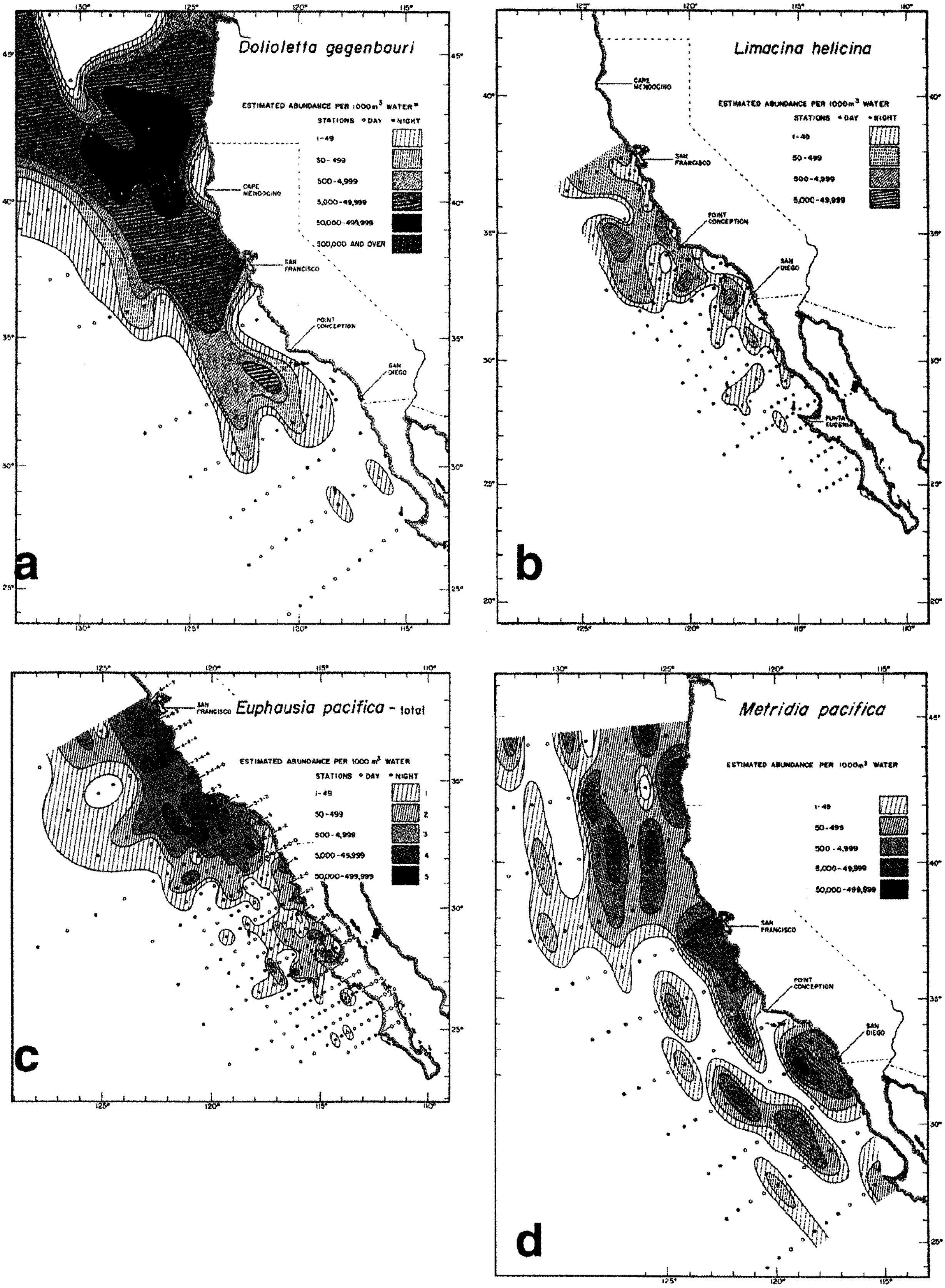

Figure 8. The distribution and abundance of four species of zooplankton that are common in the Gulf of Alaska and the Subarctic North Pacific. *a*, *Doliolletta gegenbouri* from cruise 4907 (from Berner 1967); *b*, *Limacina helicina*, a pteropod from cruise 5204 (from McGowan 1967); *c*, *Euphausia pacifica*, a euphausiid from cruise 4907 (from Brinton 1967); *d*, *Metridia pacifica* from cruise 4909 (from Bowman and Johnson 1973).

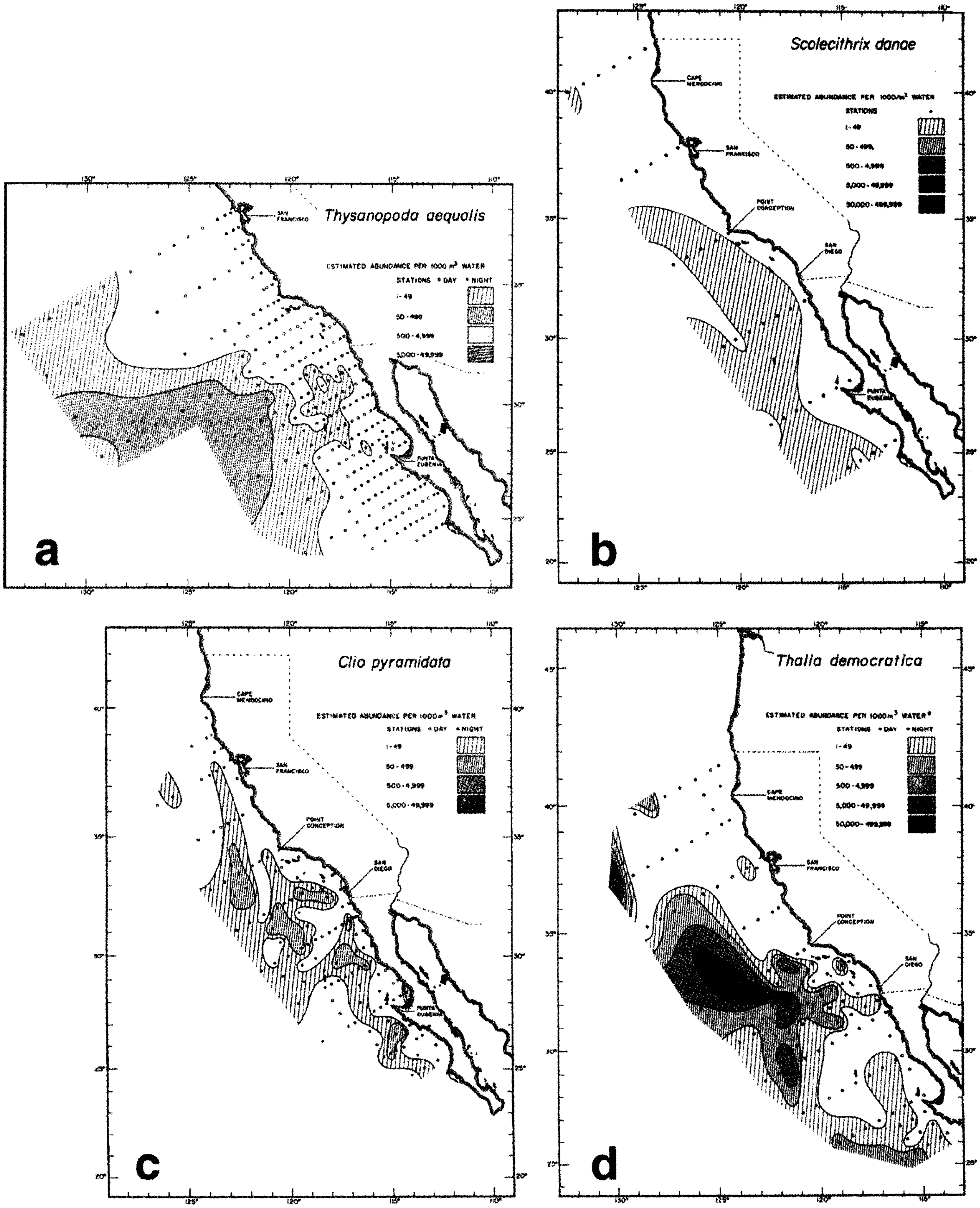

Figure 9. The distribution and abundance of four species that are common in the Central Gyre of the North Pacific and intrude into the California Current from the west. *a*, *Thysanopoda aequalis*, a euphausiid from cruise 6304 (after Brinton 1967); *b*, *Scolecithrix danae*, a copepod from cruise 5807 (after Fleminger 1964); *c*, *Clio pyramidata*, a pteropod from cruise 5206 (after McGowan 1967); *d*, *Thalia democratica*, a thaliacean from cruise 5005 (after Berner 1967).

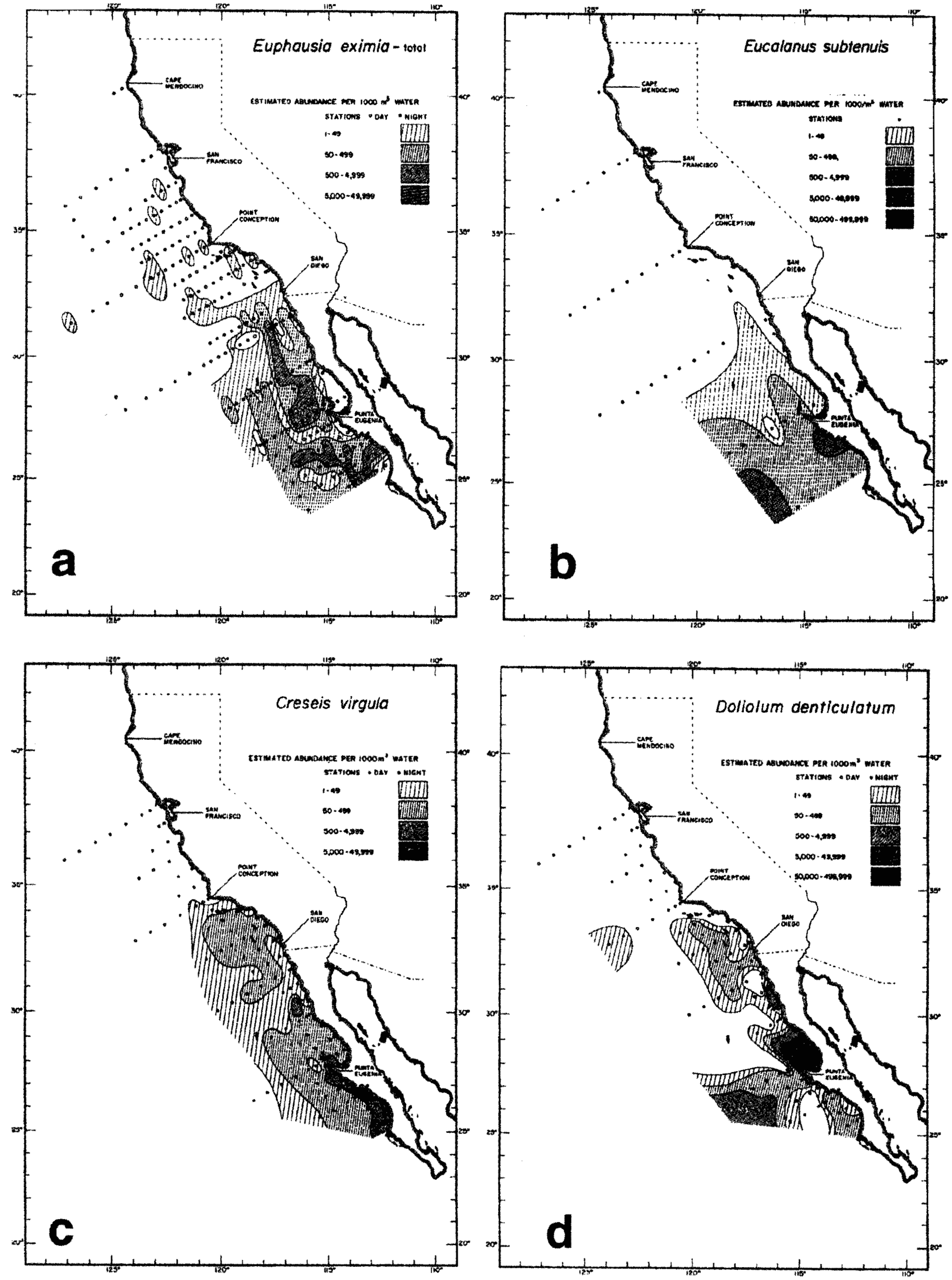

Figure 10. The distribution and abundance of four species of zooplankton that are common in the eastern tropical Pacific and intrude into the California Current from the south. *a, Euphausia eximia* from cruise 5804 (after Brinton 1967); *b, Eucalanus subtenuis* from cruise 5804 (after Fleminger 1964); *c, Creseis virgula* from cruise 5210 (after McGowan 1967); *d, Doliolum denticulatum* from cruise 5210 (after Berner 1967).

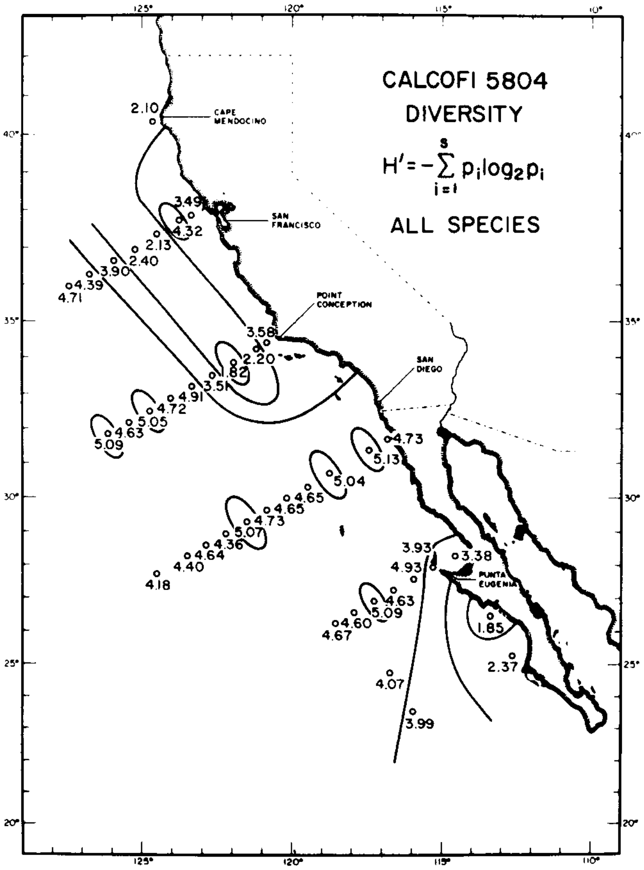

Figure 11. The spatial pattern of zooplankton species diversity in the California Current, from cruise 5804. Over 100 species were used in this study (from McGowan and Miller 1980).

that simple physical mixing of water parcels from different sources with different faunas is the cause behind the nonsignificant species-rank correlation coefficients between samples from this area (McGowan and Walker 1993).

Interannual Patterns

The mean spatial distribution of variables shows the California Current System to be very complex, especially the zooplankton biomass field. But there are reproducible patterns, especially on the large spatial scales. There are also patterns in temporal variations (Bernal 1979; Bernal and McGowan 1981; Brinton 1981; Chelton et al. 1982; Roesler and Chelton 1987; Roemmich 1992; Roemmich and McGowan 1995).

The seasonal temperature signal in the mixed layer was well resolved by the early period of the CalCOFI surveys, when cruises were at approximately monthly intervals (figure 12). It was, and still is, a strong and unambiguous signal. But as the time series progressed, it became evident that there were strong interannual variations as well. Standard deviations of 1.5°C in the monthly mean temperature were common (figure 13). A large El Niño occurred in 1958–59 (Sette and Isaacs 1960). As further low-frequency events occurred, these temperature standard deviations became larger. Eventually it became apparent that a long-term trend of increased temperature of the mixed layer had occurred, but this required about 40 years of data in order to be detected unambiguously (Roemmich 1992). The entire upper layer of the area surveyed up to 1992 had warmed by at least 0.8°C between 1950 and 1990.

Early in the program Reid et al. (1958) showed a negative relationship between zooplankton biomass and 10 m temperature over time. Perhaps because his data set was limited, this observation did not receive much attention, and ecosystem modelers continued to use temperature increase to drive higher production. With the much larger data set now available, we can confirm Reid's point (figure 14). Experimentalists have shown that the growth rate of individuals increases with temperature. This observation has led many to believe that somehow population growth also increases with temperature because larvae and juveniles pass through their vulnerable early stages more rapidly and therefore survivorship is enhanced. The CalCOFI temperature biomass data indicate that this hypothesized relationship is not the dominant mechanism controlling zooplankton abundance in the California Current.

Whereas zooplankton biomass and larval fish have seasonal variations of abundance (figure 15), Chelton et al. (1982) have shown that there are large interannual variations as well and that the magnitude of interannual variability is comparable to or larger than that of the seasonal variability. It is quite clear now that zooplankton biomass and larval fish abundance in the California Current System are both dominated by interannual variability (figure 16). The nonseasonal variations (anomalies from the seasonal signal) are of particular interest since (unlike the causes of the seasonal cycle) the causes of interannual variations are not yet well understood. These interannual variations are indicators of short-term climate changes in the California Current System.

Chelton et al. (1982) have examined lower-frequency changes in both hydrography and plankton. They found that interannual anomalies in temperature, salinity, zooplankton, and mass transport from the north rise and fall together throughout the entire system. The anomalously high zooplankton biomass episodes were correlated with colder, low-salinity episodes which occur during periods of anomalously high transport from the north (figure 17).

The high productivity of the California Current System is a well-known feature in reviews and textbooks, and this richness is almost routinely attributed to the fact that coastal upwelling of deeper water brings nutrients to the surface near shore, enhances primary production,

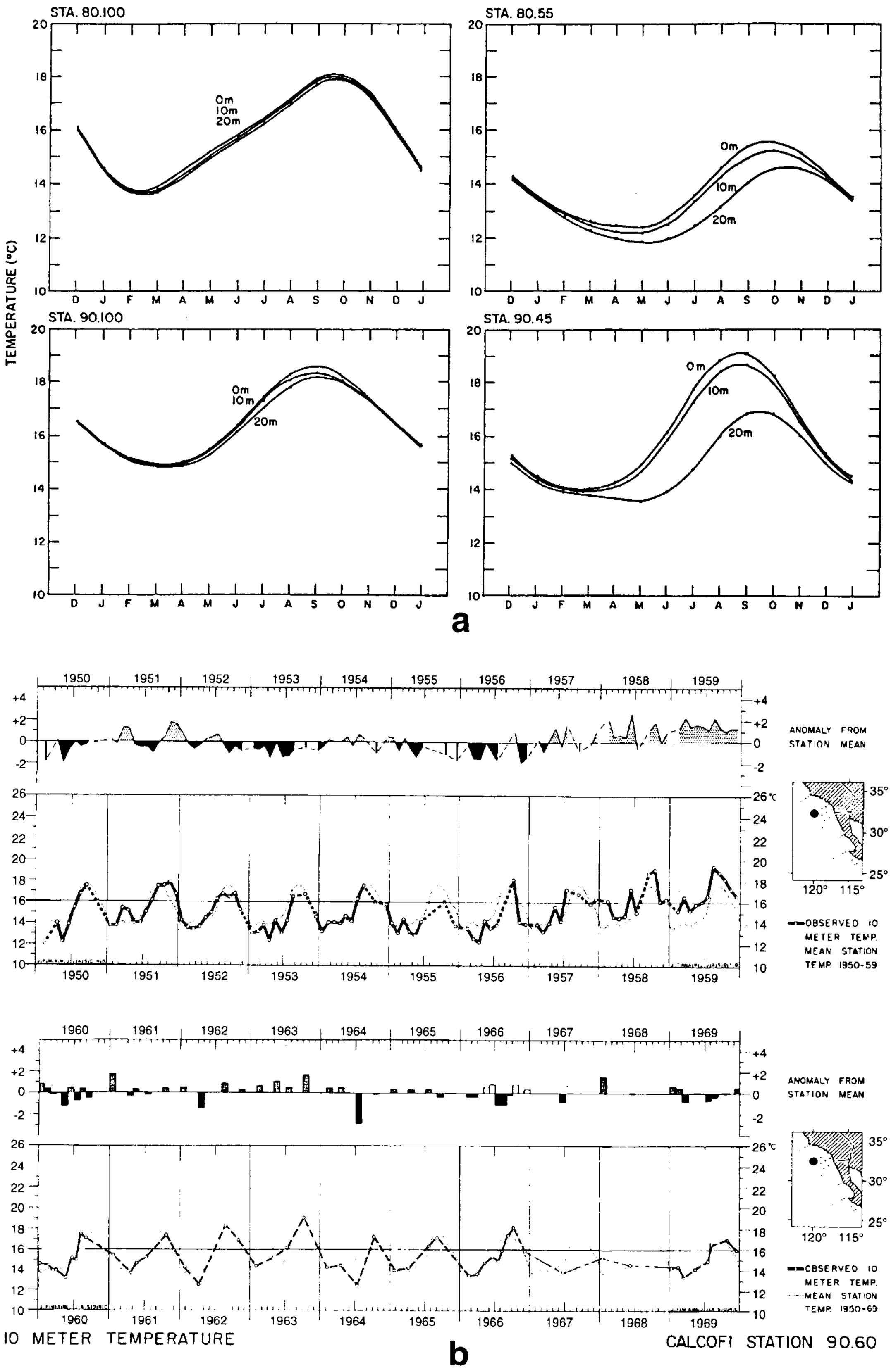

Figure 12. *a*, The seasonal temperature harmonics for four stations at four depths, 1950–80. Stations 80.55 and 90.45 are relatively nearshore; stations 80.100 and 90.100 are offshore. See figure 2 for locations. *b*, The 10 m temperature and temperature anomalies at station 90.60 in the Southern California Bight (see inset) for 1950–69 (after Anonymous 1963 and Wyllie and Lynn 1971).

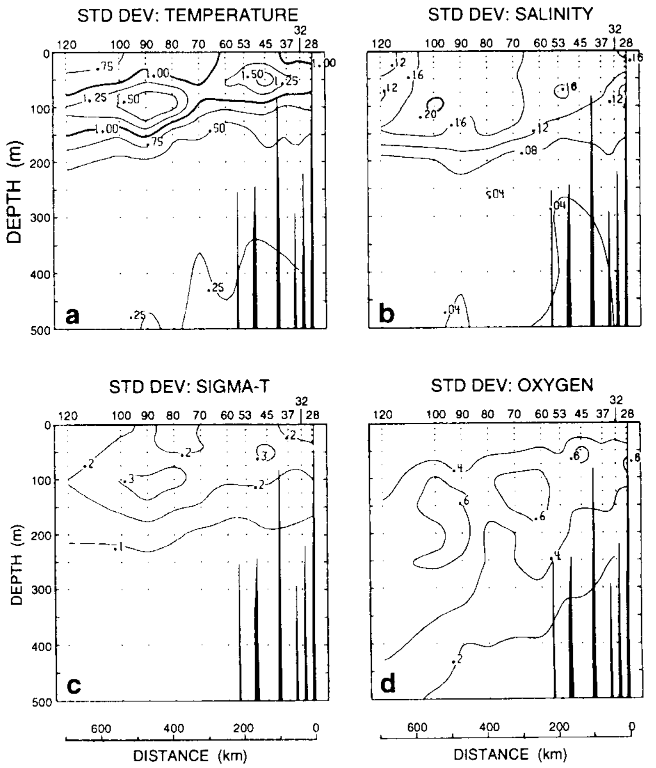

Figure 13. The standard deviation of temperature, salinity, density, and oxygen along line 90 (1950–76, after Eber 1977).

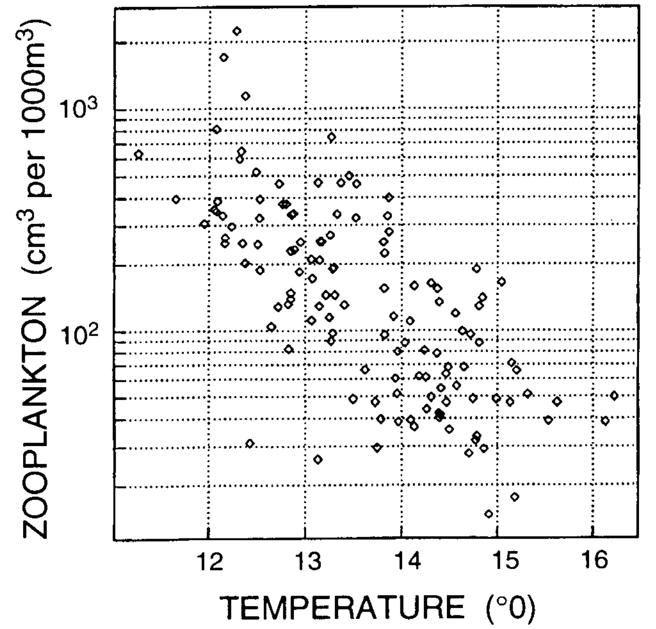

Figure 14. Average California Current zooplankton biomass per cruise, 1950–93, from stations 30 to 120 on line 90 (see figure 2) and the average temperature per cruise of the upper 100 m on that line. There were 10 or 11 stations on this line per cruise.

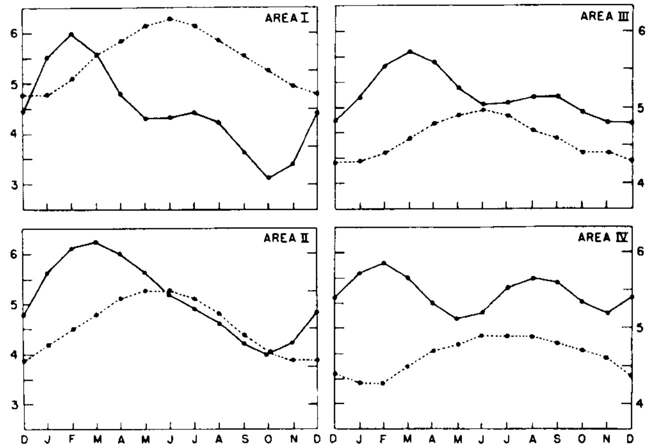

Figure 15. Seasonal cycles of zooplankton displacement volumes in 10^{-3} ml/m^3 (*dashed lines*) and larval fish in units of 10^{-3} individuals/m^3 (*solid lines*) 1950–70. The seasonal cycle is defined here to be the sum of an annual and a semiannual harmonic and a constant offset. The amplitude and phases of these three constituents have been determined by least squares regression.

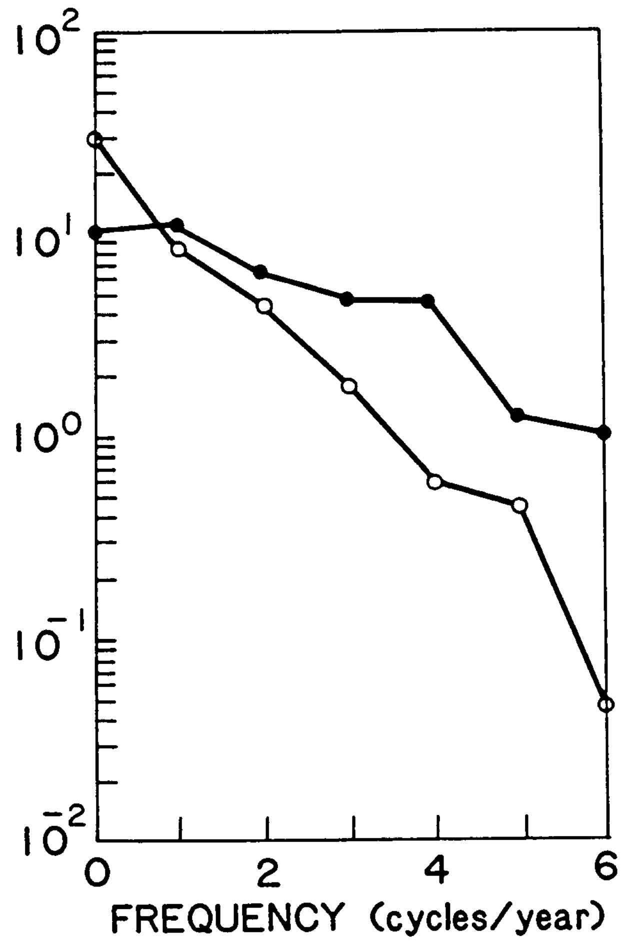

Figure 16. Normalized power spectrum, showing the average, nonseasonal log$_e$-transformed zooplankton biomass (*open circles*) and the nonseasonal log$_e$-transformed larval fish abundance (*solid circles*). The fish power spectrum is much more regular than the zooplankton spectrum, and there seems to be a residual broad-bandedness. The small peak of one cycle per year in seasonally corrected fish data may be due to fish having a sharply peaked spawning period but one that varies from year to year.

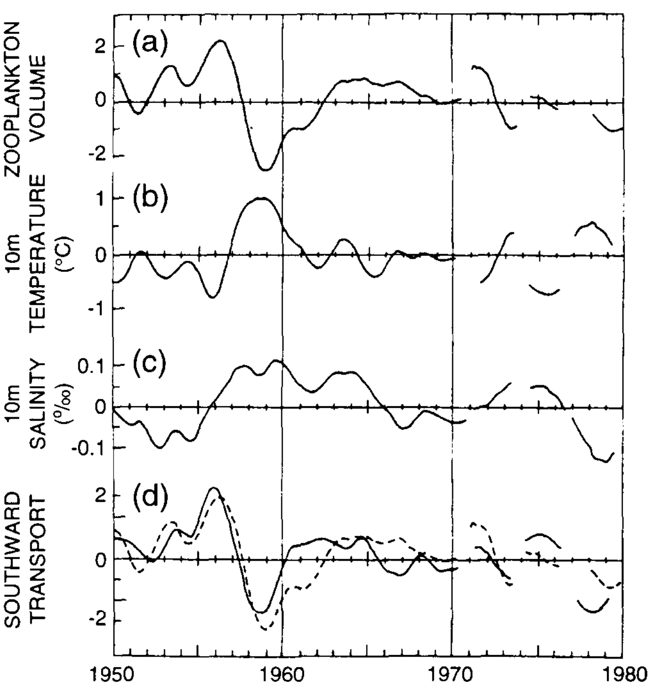

Figure 17. Time series of nonseasonal values of four variables averaged over the entire area: *a*, zooplankton in $\log_e$ were standardized; *b*, average 10 m temperature over the area; *c*, average 10 m salinity; *d*, the amplitude time series of the principal EOF of 0/500 steric height. The raw time series were filtered with a double 13-month running mean. *Dashed line* in *d* represents the zooplankton time series shown in *a* (from Chelton et al. 1982).

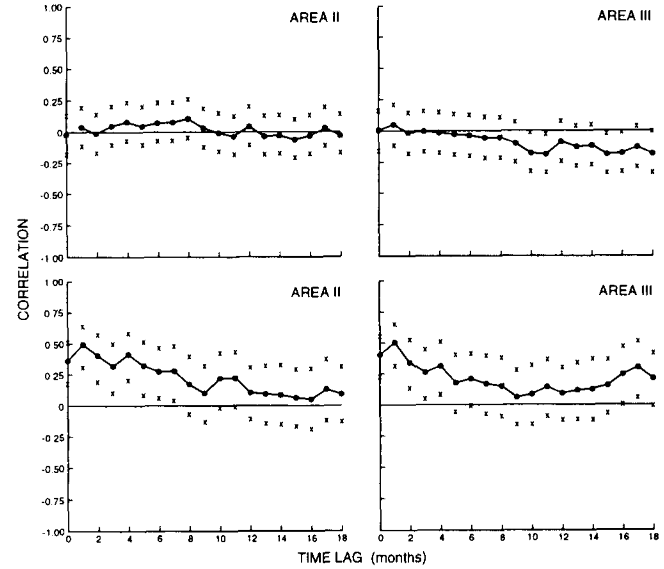

Figure 18. Time-lagged cross-correlations from 0 to 18 months. *a*, Nonseasonal Bakun's upwelling index in Area I leads nonseasonal zooplankton biomass in Area II. *b*, Nonseasonal upwelling index in Area II leads zooplankton biomass in Area III. *c*, Nonseasonal transport from the north (across line 80) leads zooplankton in Area II. *d*, Transport across line 80 leads zooplankton in Area III. *X*s are 95% confidence limits (after Bernal and McGowan 1981).

and thus enriches the rest of the food web. But direct measures of nutrient upwelling have proven elusive, and the surrogate often used by biologists is the Bakun index of coastal upwelling (Bakun 1973). This index, based on Ekman volume transport dynamics, is reported in both absolute terms of "metric tons per second per 100 m of coastline" and in anomalies. Thus the null hypothesis can be stated: H_0: "Nonseasonal zooplankton biomass anomalies are driven by coastal upwelling." This hypothesis was disproved from time-lagged cross-correlations (figure 18; Bernal and McGowan 1981). This correlation failure is largely due to the fact that the time scales associated with the physical and biological fluctuations are much longer than those of the local wind stress used in calculating the upwelling index.

An alternative null hypothesis is: H_0: "Zooplankton biomass anomalies are driven by mass transport from the north." This hypothesis could not be disproven, because the cross-correlations between transport anomaly and zooplankton are positive and significant (figure 18). Whatever the climatic forcing responsible for interannual changes in the mass transport from the north (otherwise known as the strength of the California Current), they clearly are associated with interannual zooplankton biomass variations off central and southern California. Some of these variations are associated with episodic El Niño events, but some are not.

The nature of the underlying causal mechanisms of the changes in advection are probably quite complex and are not yet understood, but they seem clearly related to climatic changes. Roesler and Chelton (1987) have more closely examined this biological response to physical forcing. They suggest that the timing of the biomass variations relative to variations in southward advection indicates that they are controlled by two processes: (1) the response of local zooplankton to advection of biomass—the dominant process in the north—and (2) the response of local populations to changes in local conditions caused by changes in advection. This latter process becomes increasingly dominant from north to south. Biogeographic species boundary shifts also indicate that these mechanisms control the interannual variability of zooplankton biomass.

The CalCOFI zooplankton samples were taken for the main purpose of capturing fish eggs and larvae. There is thus a 45-year record of variations in larval fish abundance accompanied by a zooplankton biomass volume for each sample. It is possible now to compare temporal variations in larval fish to temporal variations in zooplankton.

Theilacker (1987) and Theilacker and Shen (1993) have documented that sea-caught larval fish may often be badly undernourished, and Houde (1987), Lo et al. (1995), Kendall et al. (1996), and others have shown that the feeding larval and early juvenile stages of many—perhaps most—species of pelagic fish have larger rates of, and variations in, mortality than any other life-history stage. This variability is thought to be one of the important contributions to variations in recruitment. Since larval fish are about the same size as zooplankton, occur together with zooplankton, and frequently have similar diets, it is not unreasonable to assume that they compete with or are preyed upon by members of the macrozooplankton community. This is especially true in view of the fact that many individual species of macrozooplankton, as caught by CalCOFI, are far more abundant than the co-occurring larval fish (McGowan and Miller 1980). But those same macrozooplankton are the diet of the adults that gave rise to the fish larvae. Further, the crustacean zooplankton (at least) give rise to naupliar larvae, which are the food for many fish larvae. The interactions between trophic levels are clearly very complex and nonlinear.

MacCall and Prager (1988) have estimated "Historical changes in abundance of six fish species off Southern California, based on CalCOFI egg and larva samples" by "developing annual indices of larval abundances of the northern anchovy, Pacific sardine, Pacific mackerel, jack mackerel, and Pacific whiting (hake)." These are the most abundant pelagic species in the California Current System. Three of these five (the sardine, anchovy, and Pacific mackerel) had larval abundance indices that agreed well with other estimates of variations in adult population size. The other two species have apparently shifted their spawning range to the north because of the warming trend that began in the mid-1970s. But Hollowed (1992), in an extensive study of hake abundance, has concluded that "production of strong year classes of Pacific hake was regulated by factors influencing survival during early and late larval periods."

Thus there are good reasons to suspect that variations in macrozooplankton abundance can affect larval fish populations in several ways: (1) Adult fish fecundity may vary because of changes in the food supply; (2) Macrozooplankton provide food for larval fish through their own larvae, especially crustacean nauplii; (3) Macrozooplankton may compete for food with fish larvae; and (4) Some species of macrozooplankton are known to prey on larval fish. In cases 1 and 2 we expect macrozooplankton and larval fish abundance to be positively correlated, perhaps with some time lag. In cases 3 and 4 larval abundance changes should be negatively correlated with zooplankton. Large variations in larval abundance should result in variations in recruitment. Therefore large-scale interaction between trophic levels should be occurring. But it is well known that variations in the abundance of different species of harvested fish are not highly cross-correlated. That is, peak abundances occur at different times, and there appears to be a succession of species abundance over time (MacCall and Prager 1988; Sund and Norton 1990; MacCall 1996). It has been suggested several times that interspecific competition for food is a possible explanation of these results. As a consequence, repeated shifts of species dominance occur (Skud 1982), although the standing crop of total "fish" might remain fairly constant.

An important question to be addressed is whether variations in the trophic level represented by larval fish are somehow associated with variations of the trophic level represented by macrozooplankton. It is quite clear that selecting an individual fish species for the test may not yield interpretable results. The same is true if we wish to test whether or not larval abundances are affected by climate. Although variations of one or several species may be correlated with zooplankton or SST or wind-speed variations, these relationships cannot be generalized. If most pelagic fish do replace one another in some sort of competitive succession, then "total larval fish" is likely to be a more appropriate variable to consider.

In view of the evidence that mortality rates are highest during larval stages, that variations in the abundance of larval fish agree with estimates of adult fish, that recruitment depends on survivorship during larval periods, and that fish larvae may often be found to be malnourished, the assumption is made here that "total larval fish" is an index of the status of the next higher trophic level above macrozooplankton. Since the abundance of total fish larvae has been measured over time (figure 19), we can now test two more hypotheses.

Of these two, perhaps the most interesting is the null hypothesis: H_0: "Fish larvae variations in abundance over time are not related to macrozooplankton variations over time in the California Current System." Here we are asking whether both fish and their larvae are food-limited . . . and whether variations in the amount of food available to adults affect the rate of production and/or survivorship of larvae and juveniles. We may test this by asking if temporal variations in larval fish abundance are correlated at any time lag with macrozooplankton over the period 1950 to 1970, when sampling was frequent and before the warming trend to be described. The time lagging is important here because, if larval fish abundance declines occur well after zooplankton, it may mean that poor nutrition of adults in the preceding months has affected their fecundity. If, on the other hand, larval declines are virtually synchronous with zooplankton declines, it is likely that the availability of nauplii is important. Note that this latter result does not really distinguish between an instantaneous response of the adult fish to poor nutrition, and food limitation of fish larvae. If the correlation tends to be negative, then perhaps competition or predation are responsible.

Since nonseasonal, total larval fish variations throughout all four sectors of the California Current System are intercorrelated at low frequencies, we can space-average

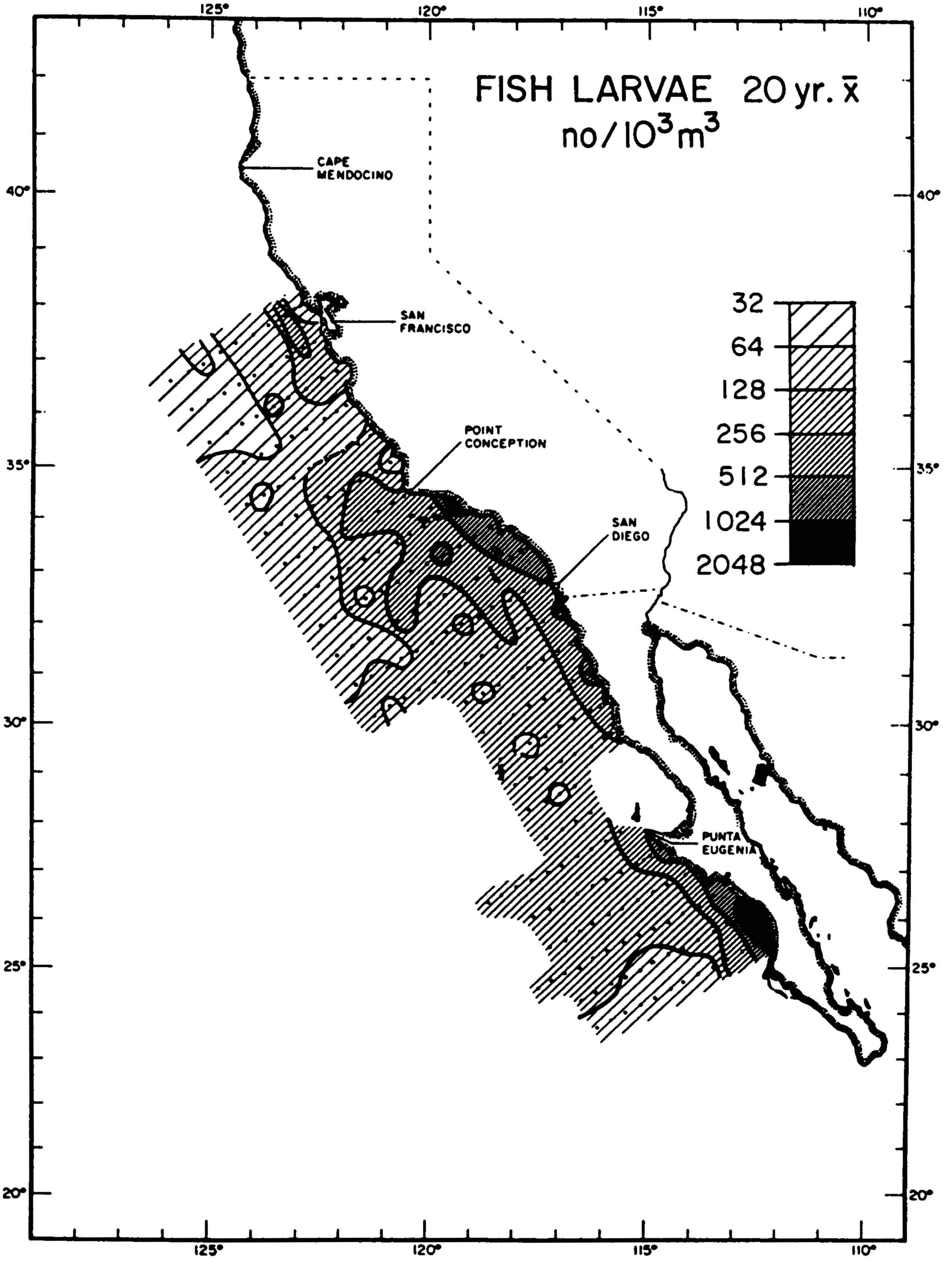

Figure 19. The spatial distribution of estimated number of larval fish of all species averaged per station 1950–70.

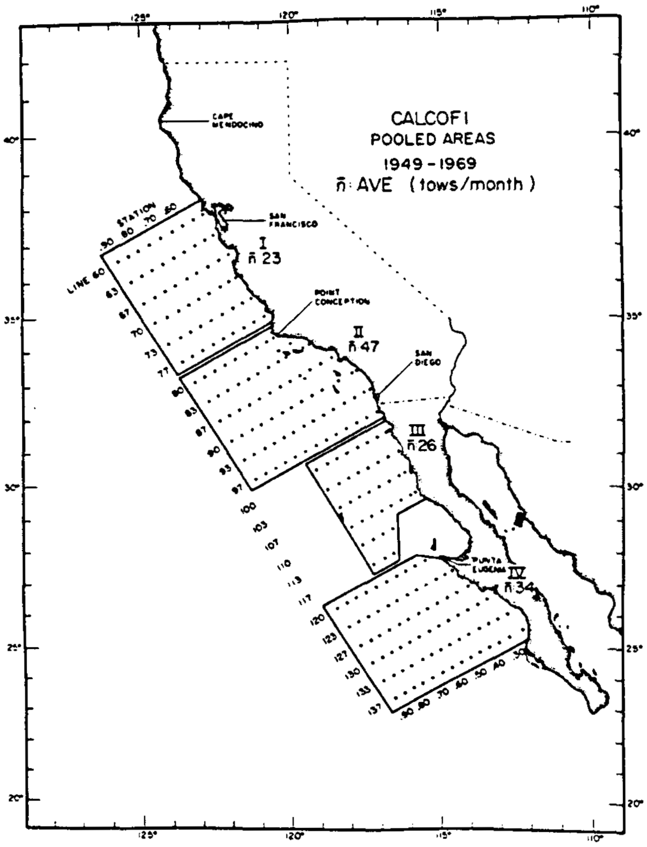

Figure 20. The stations used in the time-series analysis in figures 21, 23, 24, 25. The breaks between areas are not entirely arbitrary but are based on biogeographic and hydrographic patterns (after Bernal and McGowan 1981).

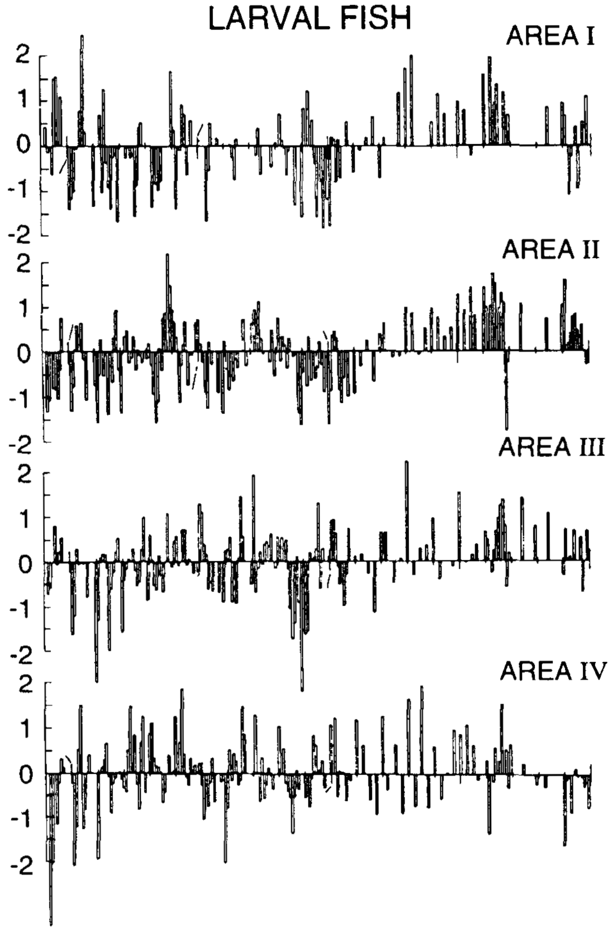

Figure 21. Time series of nonseasonal, $\log_e$-transformed, larval fish data abundance for each of the four areas. Seasonal cycles have been removed, and the time series for each area has been normalized to have a standard deviation of one. *Tic marks* are centered on January of each year.

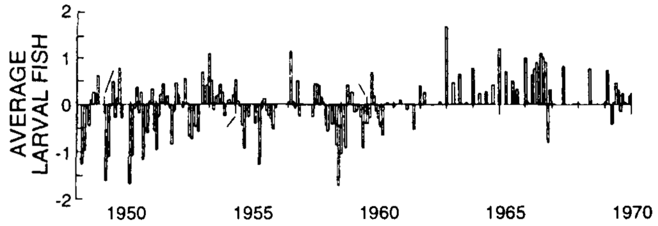

Figure 22. Time series of nonseasonal, transformed, larval fish as in figure 21, but with all four areas averaged.

the estimates throughout the entire system (figures 20–22 and table 1). Although fish and zooplankton abundance both exhibit energetic interannual variability (figure 23), there is little consistent relation between the two time series. This observation is illustrated by time-lagged correlations of the two data sets (figure 24). The maximum correlation between fish and zooplankton occurs when zooplankton leads fish by 4 to 5 months in all sectors but IV. These correlations are small (about 0.3 to 0.4) but are statistically significant even when the statistical significance is adjusted to account for the effective degrees of freedom using the method described by Chelton (1983). Autocorrelations of fish and zooplankton show very different decorrelation time scales (figure 25). That is, fish have a much shorter "memory" of past states than do zooplankton. Although the cross-correlations are weak and the autocorrelations are very different, we have been unable to formally disprove the null hypothesis of no relation between larval fish abundance and that of zooplankton. Further, it appears that the correlation does lag in the direction to be expected if poor nutrition of adult fish has affected their fecundity. But a visual examination of the overall, smoothed fish-zooplankton data shows just how weak this relationship is (figure 26).

Since zooplankton is well correlated, in general, with temperature, salinity, and transport, it seems unlikely that fish will be also, since they are poorly correlated with zooplankton. But we may ask if they are somehow influenced by some more general climate indicator. We may now propose the null hypothesis: H_0: "There is no difference between the time series larval fish and the time series longshore winds." Longshore wind anom-

TABLE 1

A. Cross-correlations of the Nonseasonal, $\log_e$-Transformed Time Series of Larval Fish Abundance in Areas I–IV (see figure 20)[a]

	Area I	Area II	Area III	Area IV
Area I		0.46 (0.25)	0.31 (0.27)	0.10 (0.30)
Area II	0.69 (0.63)		0.50 (0.27)	0.24 (0.26)
Area III	0.41 (0.47)	0.74 (0.40)		0.44 (0.25)
Area IV	−0.20 (0.73)	0.29 (0.50)	0.51 (0.21)	

B. Cross-correlations between the Nonseasonal, $\log_e$-Transformed Zooplankton Biomass Data in Areas I–IV[a]

	Area I	Area II	Area III	Area IV
Area I		0.57 (0.43)	0.42 (0.43)	0.19 (0.41)
Area II	0.75 (0.54)		0.74 (0.31)	0.31 (0.36)
Area III	0.69 (0.47)	0.91 (0.25)		0.55 (0.40)
Area IV	−0.23 (0.57)	0.49 (0.47)	0.71 (0.50)	

C. Correlations between the Large, Spatial-Scale Average, Nonseasonal $\log_e$-Transformed Larval Fish Time Series with Those of Each of the Four Areas

	Unfiltered[b]	Interannual[b]
Area I	0.71 (0.27)	0.72 (0.54)
Area II	0.77 (0.23)	0.93 (0.35)
Area III	0.80 (0.28)	0.87 (0.36)
Area IV	0.65 (0.23)	0.43 (0.29)

D. Correlations between the Large, Spatial-Scale Average, Nonseasonal $\log_e$-Transformed Zooplankton Biomass Time Series with Those of Each of the Four Areas

	Unfiltered[b]	Interannual[b]
Area I	0.75 (0.45)	0.72 (0.46)
Area II	0.85 (0.31)	0.90 (0.36)
Area III	0.88 (0.27)	0.98 (0.35)
Area IV	0.68 (0.44)	0.75 (0.51)

[a] Values above the diagonal are for the unfiltered data; those below are correlations of data filtered with a low-pass double 13-month running mean to emphasize the interannual signal. Parentheses show values required for 95% significance levels with the method described by Chelton (1983).
[b] Values in parentheses are 95% significance levels.

alies are used here because they form the basis for the coastal upwelling model. The reasoning behind this test is that there is a general consensus that coastal upwelling brings nutrients to the euphotic zone, thus stimulating new production and enhancing production in the entire food web. If this mechanism is important, larval fish survival should benefit from upwelling events. On the other hand, Lasker (1975) has proposed that windiness and upwelling may disturb and disperse the layers of food that some larval fish depend on, in which case their survivorship should be reduced. In the first case larval fish abundance should, at some time lag, be positively correlated with longshore winds. In the second case they should, at some time lag, be negatively correlated. Figure 27 shows the time-lagged correlations between local longshore wind and fish larvae. The two are uncorrelated, and both of the hypotheses are there-

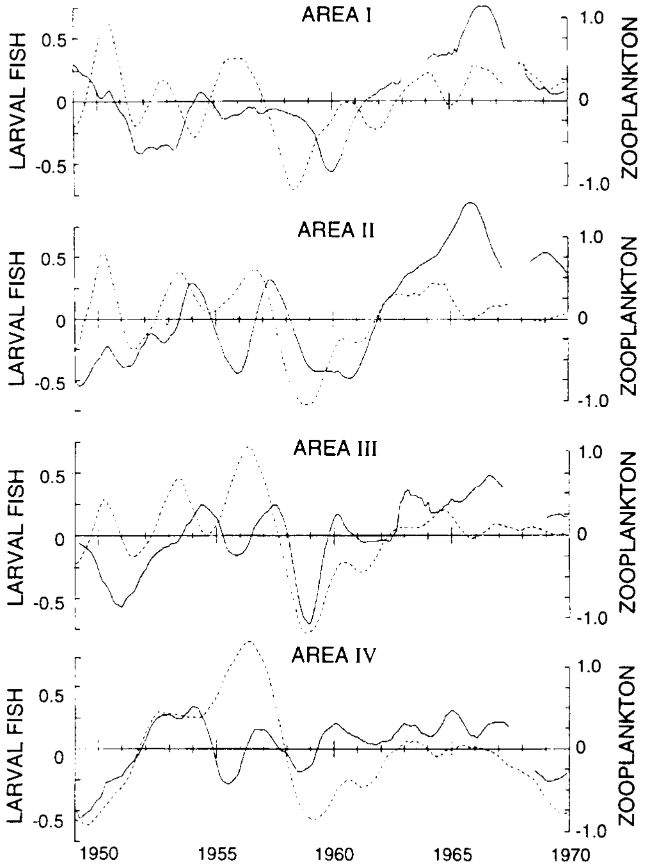

Figure 23. Low-passed filtered, time series of nonseasonal, $\log_e$-transformed larval fish (*solid line*) and zooplankton (*dashed line*) for each of the four areas. The raw, nonseasonal, time series were filtered with a double 13-month, objective, running mean, which effectively extracts the interannual variability.

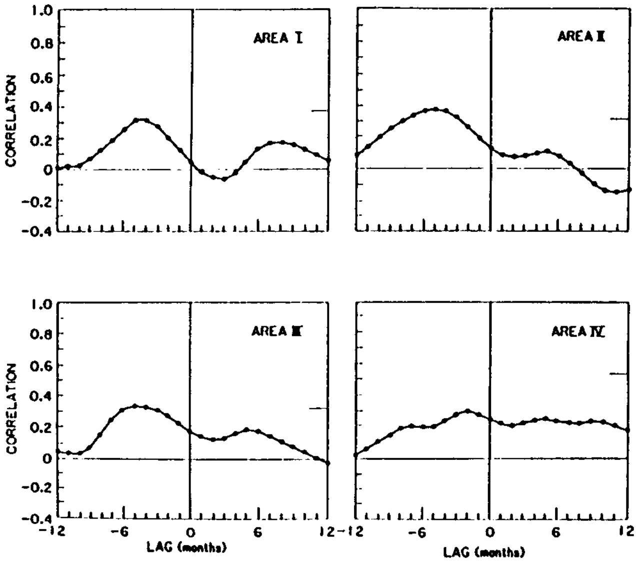

Figure 24. Time-lagged cross correlations between nonseasonal $\log_e$-transformed larval fish at time t, and nonseasonal $\log_e$-transformed zooplankton at time (t + lag). Negative lags indicate zooplankton leads larval fish. *Tic marks* on right axis represent 95% significance levels.

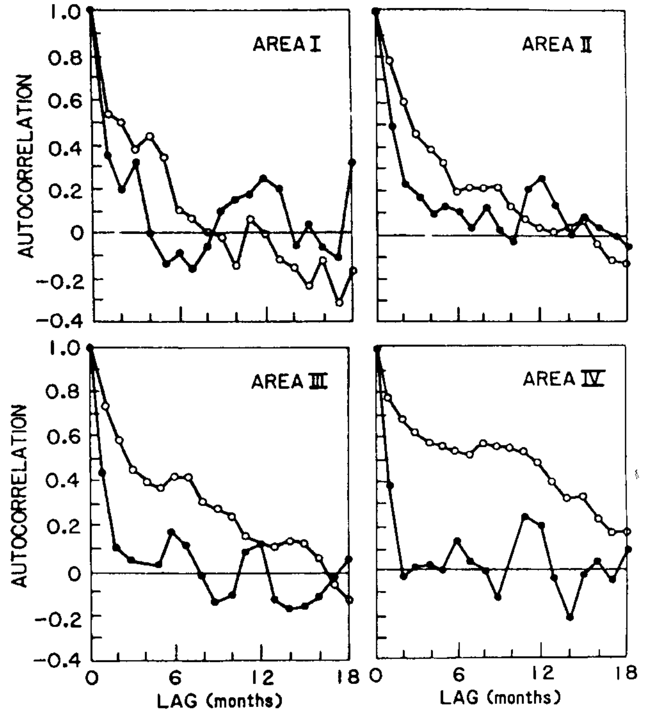

Figure 25. Time-lagged autocorrelations of nonseasonal, $\log_e$-transformed, larval fish (*solid circles*) and nonseasonal, $\log_e$-transformed, zooplankton (*open circles*) data. The secondary peak by fish at 12 months indicates strongly seasonal abundance anomalies.

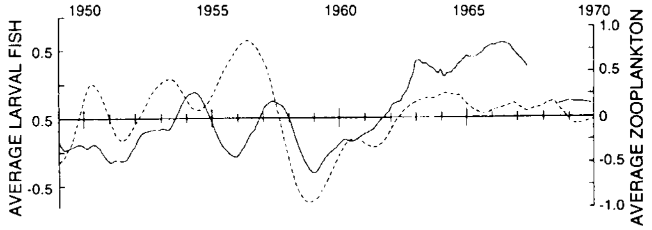

Figure 26. Low-passed filtered time series of nonseasonal $\log_e$-transformed larval fish numbers (*solid line*) and zooplankton displacement volume (*dashed line*) averaged over the four areas shown in figure 20. The nonseasonal time series were filtered with a double, objective running mean. The 1958–59 El Niño effects can be seen clearly. The decline of larval fish abundance tended to lag the decline of zooplankton.

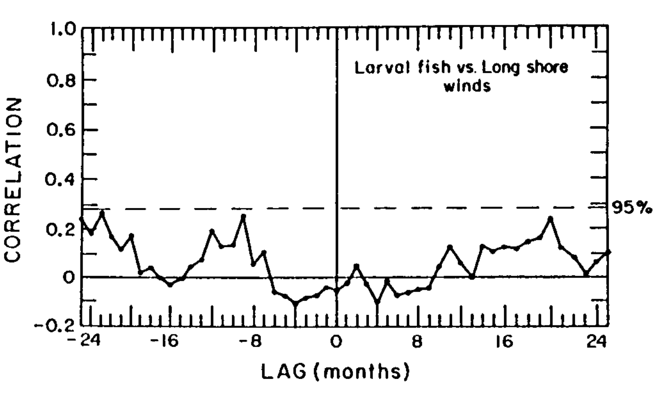

Figure 27. Time-lagged cross-correlation of mean larval fish abundance and longshore winds in Area II, 1950–69. Negative values indicate that winds lag fish. The upper 95% confidence limits are shown.

fore disproved. We thus conclude that the variations in the abundance of zooplankton do not strongly affect adult fish population fecundity or larval mortality. Nor does coastal upwelling affect larval fish survivorship in any simple manner.

The most abundant larvae in the CalCOFI samples are those of the harvested species. Harvesting of adults is an unusual intervention in the normal life histories of pelagic fish, where most natural population regulation seems to come from mortality of larvae. Intensive predation of adults (harvesting) at this point in the life history may so alter normal population dynamics that food limitation or climate-driven perturbations are simply not unambiguously resolvable in a time-series test unless they are large signals. But two further tests of hypotheses are suggested: do the larvae of nonharvested fish respond to plankton changes or weather? A third and unlikely possibility is that larval fish abundance shifts are normally uncoupled from adult population variability.

Interdecadal Patterns

It has become clear that large, spatial-scale environmental changes occur on an interannual (year-to-year) basis and that these variations are often larger than seasonal, monthly, or weekly changes. We are now learning that longer-period variations are also important—the interdecadal. Of course, paleontologists have long known that the thousand- or ten-thousand-year periods or Pleistocene epochs are important ecological and evolutionary milestones. But paleontologists cannot usually resolve any marine fossil frequency of change of much less than a thousand years except in the special circumstances of varved cores. The interdecadal-to-century frequencies of climate change are important in that the magnitudes can be large and there are demonstrable consequences to many environmental variables (Ebbesmeyer et al. 1991).

The 45-year data set of CalCOFI's physical-biological program can, however, be used to investigate interdecadal variability. Roemmich (1992) has shown that over the 42-year period 1950–91 temperature increased by 0.8°C in the upper 100 m of the California Current. An increase is clearly detectable even to depths of 300 m. Concurrently, steric sea level rose by 0.9 ±0.2 mm per year. The fact that the entire upper layer has warmed is of particular significance to marine life, for here is where all the primary productivity takes place and where the greatest fraction of the biomass resides. Roemmich compared the period 1950–56 to the period 1985–91 for changes in steric height. The onshore-offshore steric heights were spatially uniform between the two time periods, but differed systematically from one another by about 3 cm. This spatial uniformity indicates that the

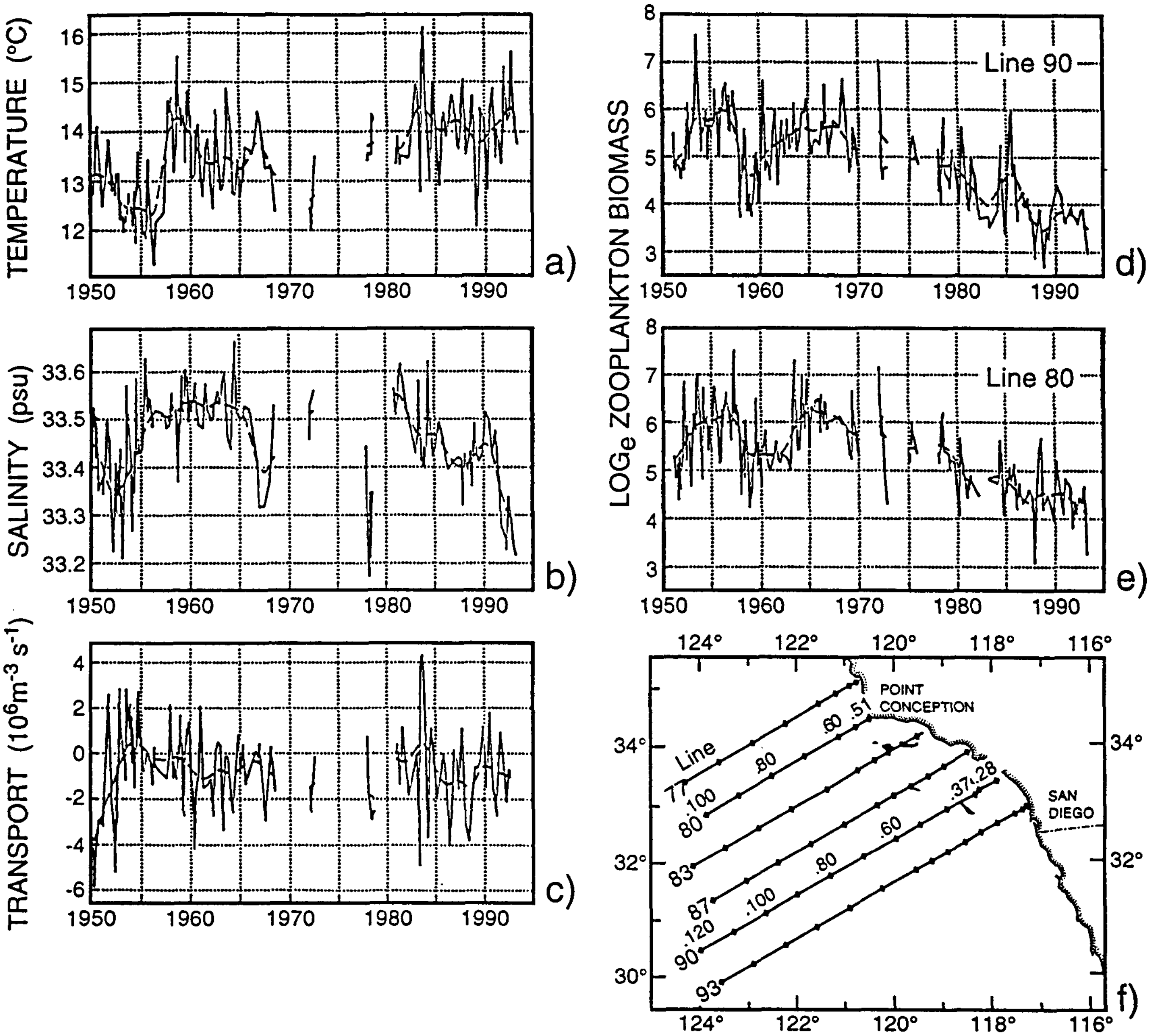

Figure 28. *Left,* Time series of the upper 100 m (*a*) temperature, (*b*) salinity, and (*c*) transport from the north. *Right,* time series of $\log_e$-transformed zooplankton volume per 1,000 m^3 of water filtered by the net on CalCOFI line 90 (*d*) and line 80 (*e*). (After Roemmich and McGowan 1995).

large-scale warming and sea-level rise were not accompanied by significant changes in the strength of the surface geostrophic circulation.

Nearshore, daily surface temperature records from Scripps Pier have been taken since 1916. These show a similar warming trend between 1950 and 1991 (Roemmich 1992), but there was no significant trend between 1916 and 1950. The decade of the 1980s was the warmest on record.

Roemmich and McGowan (1995) have reported that the warming of the California Current did affect the plankton populations (and no doubt others) of the upper 200 m. Since 1951, the biomass of macrozooplankton in southern California waters has decreased by over 70% during the same period that the surface layer warmed (figure 28). The temperature difference across the thermocline increased, and this increased stratification resulted in less lifting of the thermocline by wind-driven upwelling. A shallower source of upwelled waters would provide fewer inorganic nutrients for new production and hence support a smaller zooplankton population.

Because of the high energetic interannual variability, it is uncertain whether the zooplankton decline occurred gradually over the entire time series or more rapidly since the 1970s. At both the northern (line 80) and southern (line 90) zones, the onshore-offshore plankton gradients

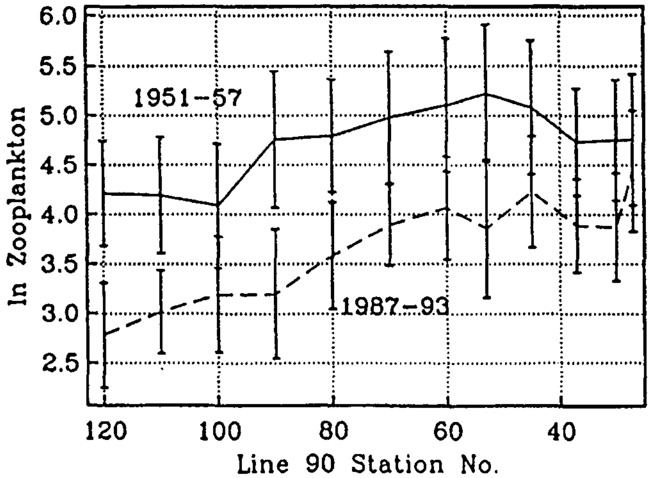

Figure 29. Temporal average and standard deviation (*vertical bars*) of $\log_e$-transformed zooplankton volumes for all cruises in 1951–57 and 1987–93 along line 90. Stations are numbered from nearshore (40) to offshore (120) (from Roemmich and McGowan 1995).

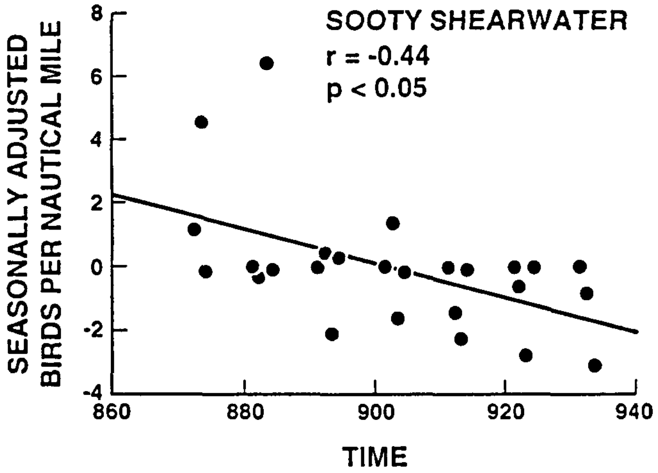

Figure 30. The seasonally adjusted counts of sooty shearwater abundance per cruise from 1987 to 1993. Counts were made during all daylight hours while the ships were underway. Each cruise lasted about two weeks; cruises were made approximately quarterly (from Veit et al., in press).

were approximately constant (figure 2a), as was the north-south gradient (figure 29; Roemmich and McGowan 1995). Geostrophic velocity at line 90 showed an increase in the wind-driven recirculation—greater northward flow nearshore and greater southward flow offshore—but no change in net transport. Bakun (1990), analyzing a combination of directly estimated winds and onshore-offshore barometric pressure differences, concluded that coastal winds off California favorable to upwelling increased substantially from 1946 to 1988. Although his reported increase in alongshore wind is consistent with the increase in recirculation noted above, his predicted consequences—SST cooling and increased production—are the opposite of the observed increased temperature and decreased zooplankton biomass.

The observed rate of decrease in zooplankton biomass is more than $5 \times 10^{-10}\ s^{-1}$ over 43 years. On long time scales, biomass is controlled by the net effect of decreases due to excess mortality over births versus increases through advection from the north. But advective input by currents is estimated to be $\sim 5 \times 10^{-8}\ s^{-1}$ (Roemmich and McGowan 1995), far larger than the observed trend. Thus the long-term trend is a small residual of much larger terms. It cannot be isolated by studies of advection or by process-oriented studies of reproductive rates or mortality. Nevertheless, it is a dramatically large signal when accumulated over 43 years.

These observed trends in the California Current may be related to basin-scale changes in wind forcing. A strengthening of North Pacific winter atmospheric circulation began in the late 1970s (Trenberth 1990; Graham 1994), near the time when the temperature increase and zooplankton decline began to be clearly seen. A number of other effects have been observed in relation to this basin-scale climate shift (Venrick et al. 1987; Miller et al. 1994).

In addition to the plankton decline, there has been a 90% decline in an apex marine predator—the sooty shearwater (*Puffinus griseus*), once the most abundant pelagic seabird in the California Current. Other seabirds have declined as well (figure 30; Veit, Pyle, and McGowan, in press), although not so dramatically (Veit et al., in press).

CONCLUSIONS

Determining the ecological consequences of climate change, whether it is natural or anthropogenic, is one of the most serious problems facing oceanographers today. At the heart of this problem is our limited ability to quantitatively define the word *change*. Because of the paucity of long time series of ecosystem variables, what does this word mean in terms of ecosystem structure and function?

Two Approaches

The departure from some expectation or norm, its sign, amplitude, spatial extent, and temporal persistence are surely essential aspects of the concept of change. A common practice of studying change is to extrapolate from relatively short-term, local, "process-oriented" studies with the expressed goal of providing values for "fluxes" of energy or materials between aggregated categories (sometimes called functional groups) of community ecosystems. These fluxes are assembled in the familiar ecosystem box model. Such inductive models have been used for many years in marine ecology but have not proven useful for understanding variability in system structure and function. In particular, they have provided little insight into the effects of climatic perturbations on system behavior or on the state of its populations. Pelagic community-ecosystem structure is complex, enigmatic, and vacillatory. There are many unknowns, and it has been necessary, therefore, to include untested and often untestable assumptions in such models. But such process-oriented, model-driven research has given us some valuable information. These studies have shown that most, if not all, of the rates of interaction between structural entities are nonlinear and density dependent. The studies have also provided many engaging details about the maze of intermediary mechanics in community function.

It is clear that time series, if they are long enough, can define the word *change*, its sign, amplitude, and persistence. They can also determine the spatial dimensions of change if the correlation length scales are adequately sampled. Anomalies from the baseline seasonal cycle can be calculated and compared with climatic signals by means of the classical methods of null hypothesis testing. However, correlations between climatic anomalies and biological anomalies cannot provide information on the innumerable intermediary mechanisms that link community response to climate change. Although time series, of themselves, do not provide predictive capability, they do offer a wealth of information for testing and validation of ecosystem models. Unless the models can reproduce the observed time series, they cannot be used for predictive purposes.

The California Current Example

The CalCOFI time series has been used to construct long time series over a large portion of the California Current. In spite of highly variable and patchy data, these maps show persistent onshore, offshore gradients and north-south gradients of virtually all physical, chemical, and biological properties. Subarctic and Transition Zone species intrude from the north, along with cool, low-salinity waters. Warm-water cosmopolites come in from the west with warm, high-salinity Central Gyre waters. Equatorial species intrude from the south. These species are mixed together in the central sector of the California Current. It is here that plankton species diversity is the highest of any sector of this current. It seems reasonable to infer that the spatial maximum in diversity is due to simple physical mixing rather than to ecological processes such as resource allocation or disturbance.

The 45-year monitoring study has also allowed time-series and spectral analyses, even though gaps exist in the data. All ecosystem variables show large, nonseasonal, low-frequency variations. Macrozooplankton biomass changes are clearly correlated with interannual, climate-driven changes in mass transport of water from the north. Larval fish are also highly variable in time, but these variations are seldom clearly related to changes in zooplankton (the diet of the adult fish) and, in our data, never to anomalies in longshore winds, the basis of coastal upwelling indices.

Zooplankton also responded to another lower frequency of climate change, the interdecadal. This is manifested as a long-term warming of the entire upper 300 m water column and a coincident decline in zooplankton production. The very large decline in zooplankton (over 70%) with such a "small" temperature signal (~0.8°C) indicates that the organisms were not responding directly to temperature with, say, a change in their thermally regulated metabolism, but rather that the warming is a surrogate index for some greater environmental change. A candidate mechanism is an increase in water column stratification due to the warming (Roemmich and McGowan 1995). This would lead to a decrease in vertical eddy diffusivity, mixing, and upwelling and therefore a lesser input of inorganic nutrients from the deep water. The overall effect would be less primary and secondary productivity, consistent with the observations.

There are several steps in this proposed mechanism as yet to be verified by analyses of the existing observations. But if it is substantially correct, it differs greatly from the mechanism proposed for interannual changes. This mechanism had to do with horizontal advective input to the system proposed for interannual changes (Bernal and McGowan 1981; Chelton et al. 1982). The interdecadal trend in upper-layer temperature may be related to basin-scale wind forcing. A strengthening of the North Pacific winter atmospheric circulation began in the late 1970s (Graham 1994), near the time when the CalCOFI trends began to be clearly seen (figure 28). A number of other effects have been observed in relation to this basin-scale change (Venrick et al. 1987). If the interdecadal decline in zooplankton is part of a natural climatic cycle that reverses itself in coming years, then the impact will be similarly transient. But if the decline is anthropogenic or a natural trend of longer duration, then the magnitude of the decline is a cause for concern (Roemmich and McGowan 1995). For example, if large-amplitude physical perturbations work the way we suggest and if fish populations generally become food limited during such periods, then we may anticipate large-scale declines in the populations that eat macrozooplankton or whose larvae depend upon their larvae.

Thus there are different forcings, amplitudes, and consequences depending on time scales (daily, weekly, monthly, seasonal, interannual, and interdecadal). This demonstrates the dangers of induction. Climate studies dominated by short-term, process-oriented work cannot simply be extrapolated to interannual or decadal time scales where the balance of terms is different from monthly or seasonal balances.

The continuous plankton recorder studies in the North Atlantic (CPR Survey Team 1992), other studies in this volume, and the CalCOFI time series have all shown that the most energetic biotic changes in space and time are of low frequency; that is, the frequency spectra of biological variables are dominated by low-frequency variability. These low-frequency variations in macrozooplankton are all closely associated with large-scale climatic trends in both the Pacific and Atlantic.

If large changes in biomass over time and over large areas are considered to be important ecological and evolutionary events, then the spectra dominated by low-frequency variability have great underlying meaning; there must also be structural and functional changes occurring, and they cannot be understood or predicted by short-term, process-oriented studies. If the consequences of climate and climatic change are of interest, then biotic measurements must be maintained over periods of many decades in order to detect, let alone understand, these consequences.

All of this argues for a new outlook to guide research on marine communities and populations. Apparently little can be inferred about kinematics and dynamics on scales much larger than the scales of measurement. This may be because density-independent forces extrinsic to the internal workings of communities are very important and yet essentially unpredictable from a knowledge of internal dynamics. Further, short-term perturbations such as weather often do not have large or lasting effects on ecosystems. The concepts of stability and resilience are based on this fact.

Since there is legitimate concern that large climate changes are possible in the near future, the time is now to direct more of our effort to defining, detecting, and understanding "change."

Many ecologists are not yet accustomed to thinking about larger scales or doing large-scale research. So the new challenge will require a different outlook and some new approaches. One such approach is to use time series to test some hoary old hypotheses such as zooplankton vs. upwelling index, larval fish vs. zooplankton, or larval fish vs. longshore winds.

It is very clear that there are large interannual changes in total larval fish abundance. This is a fact of considerable interest, for it appears that the entire complex of species is responding over a large area to some forcing other than seasonal. While microscale, fine-scale, or mesoscale studies can suggest some plausible scenarios for these large changes (see Mullin 1993 for a review) the number of potentially testable and falsifiable hypotheses derived from these works, relevant to the climate scale, is small, and the actual number of formal tests of hypotheses is practically nonexistent. Species populations exist on very large spatial scales, and their largest and therefore most energetic variations seem to be interannual or interdecadal. There is no evidence to support the notion that the results of micro- to mesoscale studies can be extrapolated upward and outward to the climate change scale. Time-series measurements can be made on the appropriate scales. They do, however, take time.

Some of the pragmatic details of this new research canon are not well formulated, and we are ill prepared to design a large-scale, long-term monitoring system, since most of our thinking and effort has been dominated by reductionism. But perceiving the problem of scale is necessarily the first step in formulating a new kind of marine ecology.

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