45. K. W. Bruland, *Earth Planet. Sci. Lett.* **47**, 176 (1980).
46. M. K. Chan, J. S. Kim, D. C. Rees, *Science* **260**, 792 (1993).
47. J. W. Peters *et al.*, *Biochemistry* **36**, 1181 (1997).
48. T. Tsukihara *et al.*, *Science* **269**, 1069 (1995); figure is from S. Yoshikawa *et al.*, *Science* **280**, 1723 (1998).
49. H. Beinert, R. H. Holm, E. Munck, *ibid.* **277**, 653 (1997).
50. H. W. Rich, F. M. M. Morel, *Limnol. Oceanogr.* **35**, 652 (1990).
51. N. M. Price, B. A. Ahner, F. M. M. Morel, *ibid.* **39**, 520 (1994).

52. I thank K. W. Bruland, M. G. Haygood, G. W. Luther, III, and F. M. M. Morel for valuable discussions and M. T. Simpson for assistance with graphics. Supported by grants from the National Science Foundation (CHE 9529374), the National Institutes of Health (GM38130) and the AP Sloan Foundation. Partial support for my work on marine haloperoxidases and siderophores is also sponsored by NOAA, U.S. Department of Commerce under grant number NA66RG0447, project number R/MP-76 through the California Sea Grant College System and in part by the California State Resources Agency.

Climate-Ocean Variability and Ecosystem Response in the Northeast Pacific

John A. McGowan,*† Daniel R. Cayan,* LeRoy M. Dorman*

REVIEW

The role of climatic variation in regulating marine populations and communities is not well understood. To improve our knowledge, the sign, amplitude, and frequency of climatic and biotic variations should be compared as a necessary first step. It is shown that there have been large interannual and interdecadal sea-surface temperature changes off the West Coast of North America during the past 80 years. Interannual anomalies appear and disappear rather suddenly and synchronously along the entire coastline. The frequency of warm events has increased since 1977. Although extensive, serial, biological observations are often incomplete, it is clear that climate-ocean variations have disturbed and changed our coastal ecosystems.

The biological consequences of climatic variability of the atmosphere and ocean are largely unknown. This is probably because of the mismatch between the scales of important atmospheric and oceanographic processes and the spatial and temporal dimensions of biological research programs (*1*). However, there is a widespread consensus that marine populations respond to climatic events and that major changes have taken place in the past 20 years in the marine ecosystems of the Pacific (*2*). Much of the biological, observational evidence is disconnected spatially and often discontinuous temporally, but because the potential consequences of large-scale ecosystem disturbance and disruption are uncertain and possibly detrimental, we must accept less than ideal data in our attempt to understand what is happening. Atmospheric and certain hydrographic properties are much better sampled, especially sea-level pressure (SLP) and sea-surface temperature (SST). By using these two measures, we are learning that the relation between large-scale, low-frequency climatic variability (*3*) and that of ecosystem and population biology is close.

Temperature variations not only affect an organism's metabolic rates directly but also influence other equally important variables such as sea level and therefore exposure of intertidal organisms, local currents and the movement of planktonic larvae, erosional regimes and therefore substrate structure, photosynthetic light intensity (cloudiness), and water-column stratification and nutrient cycling and therefore production. These environmental variables affect population and community dynamics strongly and, over time, community structure and function. The use of departures of temperature from long-term daily or monthly means (nonseasonal anomalies) can indicate physical perturbations of the kind that act as ecosystem disturbances.

Disturbance theory is well developed and is central to our understanding of the maintenance of community structure and patterns of diversity (*4*). But what types of hydrographic perturbations disturb marine ecosystems and what types do not? For example, does a single large, brief warm (cold) event have greater effects than, say, a decadal trend? We cannot answer this question because many of our concepts of the biological consequences of physical perturbations are based on brief, process-oriented studies. Large, low-frequency changes are simply not well detected by short, small-scale studies (*1*, *5*).

There are long-term daily (since 1916) coastal SST time-series measurements over much of the Pacific coast of North America (*6*) and a shorter (since 1947) oceanic SST series and good, but interrupted, biological measurements of zooplankton, fish catch, and kelp forest communities for two to six decades. Departures from nonseasonal, long-term average SSTs (anomalies) have varied considerably between years and over decades (*7*). Thus, ecosystem disturbances as indexed by SST changes can be inferred back some 80 years, and their relation to basin-wide patterns of SST and SLP can be studied. Some of these low-frequency coastal temperature anomalies are connected to warm El Niños and cool La Niñas. Particularly strong tropical events during 1957 to 1958 and 1982 to 1983 had noticeable effects on Pacific coast marine populations (*8*–*10*). Here, we used anomalies from long-term coastal SSTs to describe environmental perturbations and what is known of the biological consequences. Such knowledge will be necessary for the further development of conceptual models of marine ecosystem dynamics and of fisheries management.

Physical Changes

Interannual scales. Daily SST has been measured for decades at 17 stations along the Pacific coast (*6*) (Fig. 1). SSTs episodically varied from monthly, nonseasonal means over large areas by up to 3°C (Fig. 2). Large-scale heating and cooling occurred rapidly and apparently synchronously in many instances along the entire 1130 km of coastline. Many of the warm episodes lasted only a couple of months, sometimes less. Remarkable warm events associated with the 1957 to 1958 and 1982 to 1983 tropical El Niños stand out. In both of these cases, the warming off California persisted long after the tropical signal had died out.

Conventional wisdom and a well-established theory of coastally trapped Kelvin waves (*11*) would lead us to expect that warming episodes should propagate poleward along the West Coast. This signal should be especially pronounced during large equatorial El Niños. Sea-level changes do apparently progress from south to north (*12*), but there is no consistent evidence in the data (Fig. 2) of south to north movement of warm anomalies. Because monthly averages of SST anomalies might not resolve a south-to-north signal if Kelvin waves pass along the coast in less than 1 month, we plotted daily anomalies from long-term daily means for each station, for segments of our record during which there was a large-scale warm period (the tropical

---

J. A. McGowan and L. M. Dorman are at Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA. D. R. Cayan is at Scripps Institution of Oceanography and the U.S. Geological Survey, University of California, San Diego, La Jolla, CA 92093, USA.

*These authors contributed equally to this study.
†To whom correspondence should be addressed.

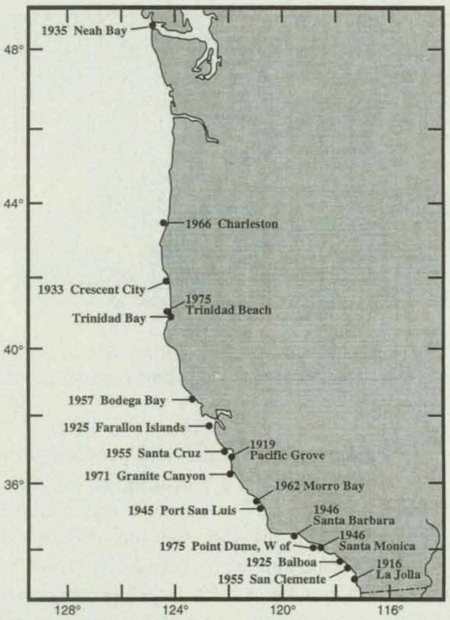


Fig. 1. Locales where daily SSTs and, at some, surface salinities have been taken since the years shown.

Table 1. Correlations of the monthly coastal time series of temperature anomaly averaged over seasons (wn, winter; sp, spring; sm, summer; fl, fall) with the Southern Oscillation Index (SOI) for La Jolla, Pacific Grove and Neah Bay. These correlations were calculated at lags out to four seasons in advance (SIO leading SST) for each season. The record length is shown.

SOI season	wn	sp	sm	SST season		sp÷1	sm÷1	fl÷1
				fl	wn÷1			
				La Jolla 1916–1993				
wn	−59*	−48	−7	−8	−3	−8	−18	−12
sp	−44	−40*	−1	−12	−25	−24	−16	−11
sm	−27	−35	−17*	−40	−51	−33	−5	10
fl	−18	−26	−11	−38*	−55	−35	5	8
				Pacific Grove 1919–1993				
wn	−57*	−56	−36	−22*	−14	−4	−9	−9
sp	−34	−36*	−30	−24	−32	−30	−15	−1
sm	−13	−25	−27*	−32	−44	−32	−10	5
fl	−5	−20	−29	−37*	−52	−40	−16	−5
				Neah Bay 1955–1993				
wn	−47*	−68	−43	−14	−4	−18	−17	−8
sp	−38	−53*	−25	−17	−38	−51	−34	−22
sm	−7	−26	−24*	−17	−44	−56	−36	−5
fl	−9	−27	−29	−31*	−54	−61	−30	−11

*Concurrent SO1 and SST.

El Niño of 1982 to 1983) and one segment during which there was a large-scale cool period (Fig. 3, A and B). There are no regularly appearing northward progressions of anomalies. To examine these data in a more quantitative fashion, we calculated two statistics from each pair of daily time series for all combinations of pairs. First, we calculated the mean squared coherence, which is the fraction of the variance in one predictable from the other (Fig. 4A), for a warm period for all stations south of Pacific Grove with respect to Port San Luis (*13*). The coherences are significantly different from zero for most frequencies below 20 cycles per year. The coherences are particularly high in bands around two and six cycles per year. The analysis shows that the phase relative to Port San Luis is not significantly (at 95%) different from zero (Fig. 4B).

Spatial scales. To further investigate the structure of the shore station monthly SST anomalies, we conducted an empirical orthogonal function (EOF) analysis. EOFs provide an efficient means of condensing coherent variability within several individual time series into a few "modes," each consisting of a spatial pattern that is modulated by a time-varying set of temporal coefficients.

The first two EOFs of the winter and summer analyses account for 80 and 60%, respectively, of the variance of monthly anomalies along the West Coast. These results imply that the regional coastal temperature signal is quite well represented by a single station (for example, La Jolla or Pacific Grove). This is consistent with results from a shorter study (*6*) and our visual (Fig. 2) and correlative study of the data.

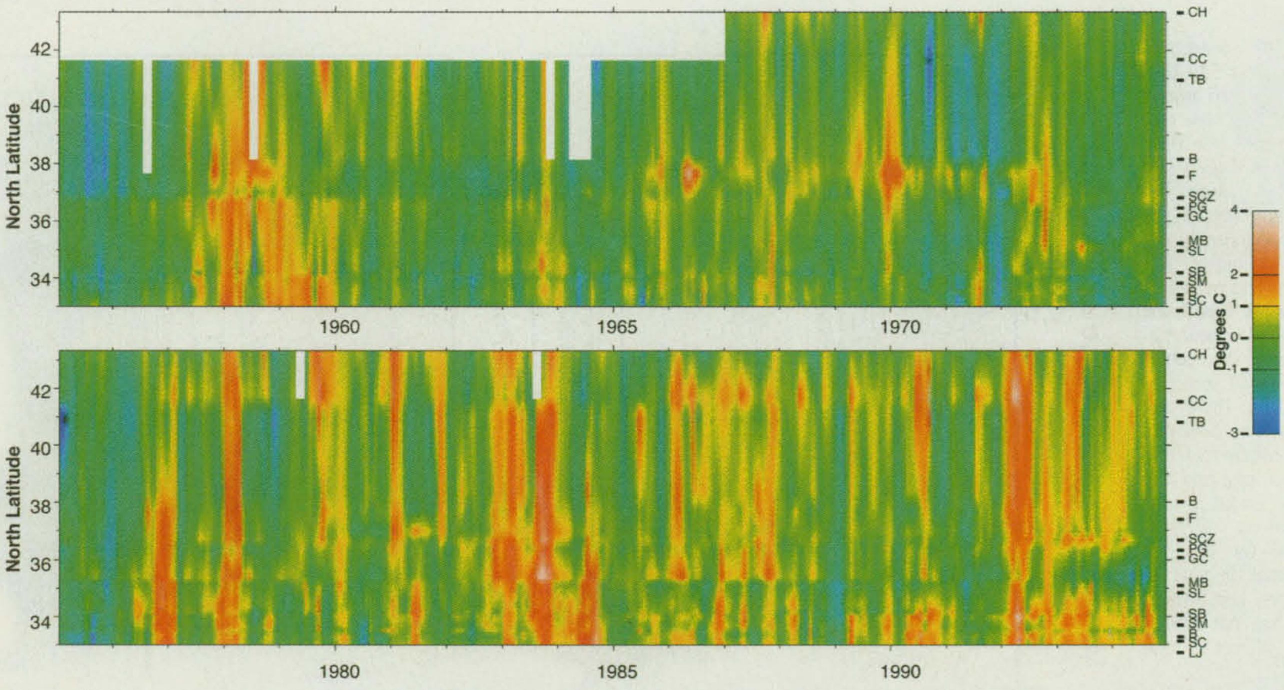


Fig. 2. The nonseasonal, monthly SST anomalies by latitude since 1955. The notations on the right are station locales. CH, Charleston; CC, Crescent City; TB, Trinidad Bay; B, Bodega Bay; F, Farallon Islands; SCZ, Santa Cruz; PG, Pacific Grove; GC, Granite Canyon; MB, Morro Bay; SL, Port San Luis; SB, Santa Barbara; SM, Santa Monica; SC, San Clemente; LJ, La Jolla.

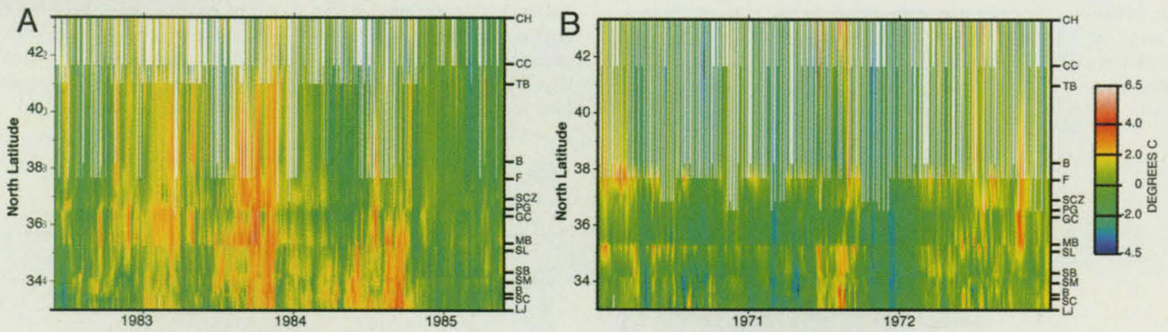
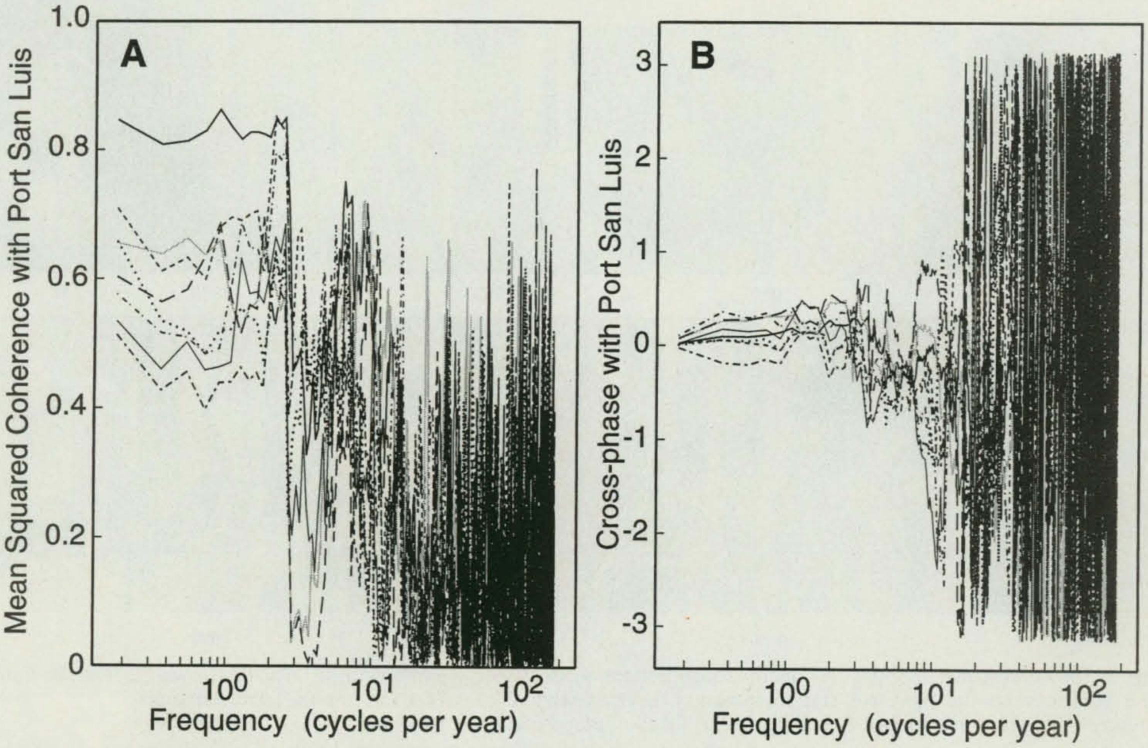


Fig. 3. (**A**) Daily SST anomalies from long-term daily means for stations La Jolla to Crescent City, before, during, and after the warm period of 1983 to 1984. (**B**) Daily anomalies for stations La Jolla to the Farallons before, during, and after a cool period. Abbreviations are defined in the legend to Fig. 2.

To examine the link between the coastal temperature fluctuations and tropical El Niños, we correlated the coastal station time series with the Southern Oscillation Index (SOI) (*14*). Because El Niño–Southern Oscillation (ENSO) events persist over several months, the month-to-month noise was smoothed out by averaging the monthly data over 3-month seasons. Correlations over the length of record (1916 to 1993) were calculated at lags out to four seasons in advance (SOI leading SST) for each season (Table 1). These correlations exhibit a connection to ENSO that appears quite uniformly along the coast, as La Jolla, Pacific Grove, and Neah Bay all display correlations of −0.5 to −0.6. Significant correlations appear in each season, but the links to winter and spring temperatures are strongest. There is a time lead (changes in the tropical Pacific precede those along the West Coast), in that summer SOI correlates almost as strongly to winter coastal temperature as winter SOI does to winter coastal temperature.

To address whether both tropical El Niños and La Niñas influence coastal SST anomalies, we examined the evolution of the anomalous SST at La Jolla during eight strong tropical El Niño events and eight strong La Niña events (Fig. 5). These anomaly traces begin in the year ("year 0") in which an ENSO event is acknowledged to have developed in the tropical Pacific and proceed through the next 2 years ("year +1 and year +2"). Strong El Niños usually produce warm coastal California SST anomalies, and strong La Niñas usually produce cool SST anomalies, but the envelope of the individual SST traces at La Jolla indicates a broadly varying association. The changes during El Niños have been larger (average anomaly reaches almost 1.5°C) than those during La Niñas (average anomaly reaches almost −1°C). The timing of the anomaly development is consistent with the lag correlations seen for the SOI (Table 1). During El Niños, La Jolla SST anomalies began to rise at the end of year 0 and peaked in spring of the following year (year +1); thereafter, the anomalies diverged widely; in some instances, anomalies remained quite high and in other instances they fell. In some remarkable cases, such as the 1957 to 1958 and the 1982 to 1983 tropical El Niños, anomalously warm SSTs persisted into year +2 off California. In composite, anomalous SSTs associated with El Niños and La Niñas persisted for about 6 to 12 months, which is only slightly longer than the persistence of anomalies that would be typical of the entire record. During La Niñas, La Jolla SST anomalies began to show significant negative values in spring of year 0 and in most events persisted through spring of the following year (year +1); for about half of these cases, SSTs reversed

Fig. 4. (**A**) Coherences between Port San Luis, centrally located among stations that have reasonably complete daily time series, show a plateau at frequencies below 2 cpy (cycles per year) and generally decrease at higher frequencies. This pattern is common for broadband propagation phenomena, where the coherence distance scales as wavelength. There are, however, two bands of higher coherence, one around 2 cpy and the other at about 6 cpy. We have no ready explanation for this. (**B**) The phases relative to Port San Luis. These phases are not significantly different than zero.



to warm conditions by fall of year +1. Thus, these warm and cool anomalies persist for nearly 1 year, and the amplitudes are approximately symmetric; that is, the California coastal regime has experienced a response to tropical cool events that are nearly equal and opposite. From the relatively small sample of cases on hand, there does appear to be a modest link between the strength of tropical El Niño conditions and the magnitude of warming along California.

Oceanic and atmospheric relations. All of the SST variations shown in Figs. 2 through 5 were obtained very nearshore, usually within 100 m of the beach. Although most measurement stations are at sites exposed to the open ocean, some are not (Morro Bay, Pacific Grove, Santa Cruz, and Charleston). Even so, there is a remarkable low-frequency spatial coherence of the anomalies, as shown in Figs. 2 to 4 and in our EOF patterns. But to what degree do any of these stations represent the open ocean? Cross correlations of monthly anomalies at La Jolla with those of 5° squares from the entire North Pacific show high correlations with much of the California Current and Gulf of Alaska for every month of the year. There are also strong negative correlations with the Central Gyre of the North Pacific. Similar patterns of correlations held for our other shore stations as well (Fig. 6).

Taking a larger, nearly global perspective, we correlated monthly SST anomalies at La Jolla with an array of SST and SLP anomalies (1951 to 1991) over a near-global domain (*15*), and there is an impressive coherence (Fig. 7). Thus, measurements at this single locale contain a significant component of global climate variability.

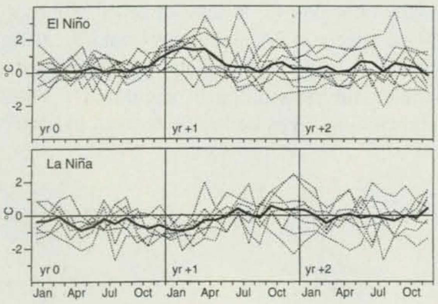


Fig. 5. Temperature anomalies from eight strong El Niño years and eight strong La Niña years, at La Jolla and their composites. These traces begin in the year (year 0) in which an ENSO event is acknowledged to have developed in the tropical Pacific. The traces proceed through the following 2 years.

Interdecadal climate-ocean changes. Among the least understood aspects of climate variability are the changes that occur on decadal time scales. These regime shifts can be gradual over many years or dramatic in less than a year (*3*). Such regime shifts are seen in marine populations and communities as well (*2, 5, 16*).

Such a rapid shift occurred in the North Pacific during 1976 to 1977 (*17*). There was a deepening of the Aleutian Low, a drop in SST in the central Pacific, and a rise in SST in the California Current and the Gulf of Alaska. This shift can be seen in our coastal data as well (Fig. 2; also Fig. 9, which is discussed below). In a composite of 40 different environmental variables, an abrupt, steplike change took place (*17*). Models forced by the observed anomalies of total heat flux and wind stress are capable of generating a shift in midlatitude SST similar to those observed (*18*). This region experienced a shoaling of the mixed layer depth (MLD), whereas in the central North Pacific, there was a cooling and a deepening of the MLD due chiefly to wind mixing. The fact that SST anomalies in the eastern North Pacific and the central North Pacific are out of phase is well known (*19*) and may be clearly seen in Fig. 6.

Another suggested mechanism for the interdecadal change depends on the observed, quasi-permanent, west-to-east transport of the West Wind Drift, a major current of the North Pacific. This current bifurcates as it nears North America (at about 45°N), with part of the transport directed equatorward and part poleward. Nearshore measurements of sea-level heights suggest that when poleward transport increases, equatorward transport decreases, and vice versa (*20*). Thus, it has been suggested that the two systems, the cyclonic gyre of the Gulf of Alaska and the eastern boundary current of the central anticyclonic gyre (the California Current), fluctuate out of phase. Because sea-level height is largely an integrated measure of upper ocean heat content, this too should be out of phase. But other than near-coastal (tide gauge) data of sea level, there seems to be no observational evidence for such a phase difference in transport. However, mass transport from the north, in the California Current, does vary on an interannual scale, and this transport is correlated with

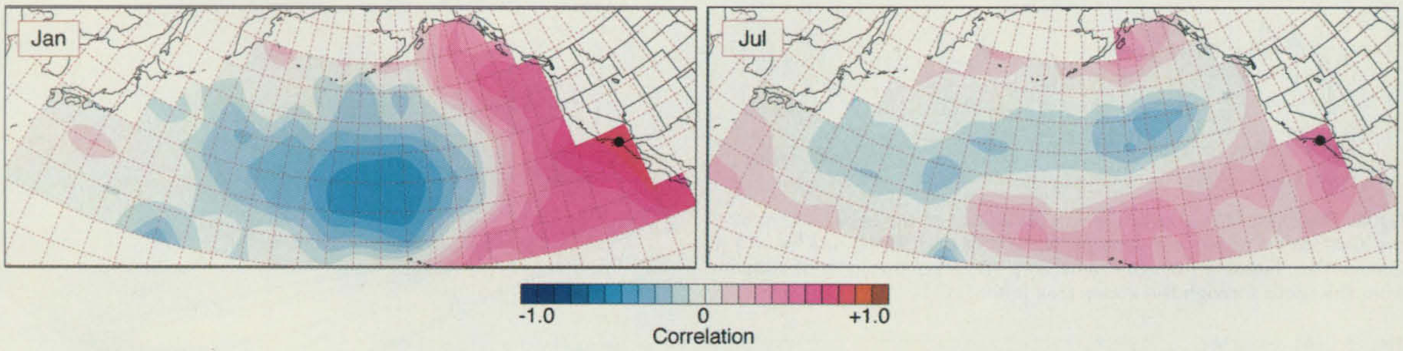


Fig. 6. Spatial correlations of monthly La Jolla SST anomalies and those of the North Pacific Basin during Januarys and Julys (1942 to 1996).

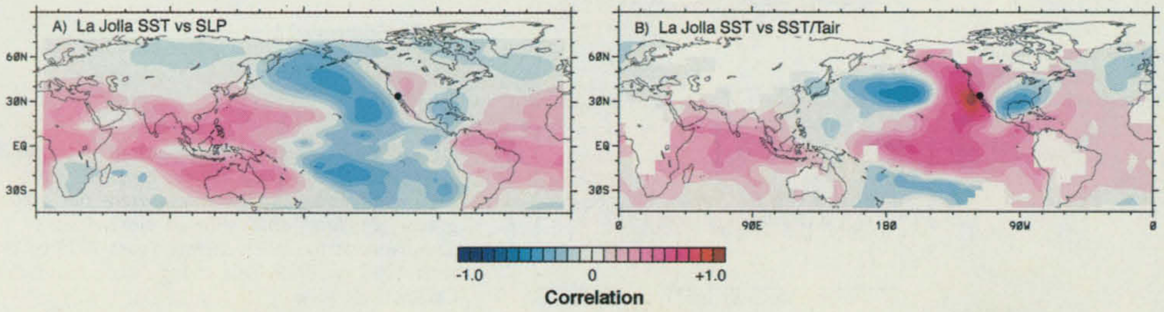


Fig. 7. **(A)** Spatial correlations of monthly La Jolla SSTs with global SLPs (1951 to 1991). **(B)** Spatial correlation of monthly La Jolla SSTs with global sea-surface and air temperatures.

mixed layer temperature, salinity, and biology of the system (*21*). Although there are clear interannual signals here, no interdecadal regime shift is evident in the mass transport from the north in the California Current (*22*) (Fig. 8D). Although there is much evidence for an interdecadal regime shift in both the California Current and the Gulf of Alaska, this proposed mechanism of north-south alternating allocation of water seems to have little supporting physical evidence.

The Biological Response

Interannual variations. Hubbs (*23*) reported that many fish and invertebrates in coastal California were found well north of their usual range in the summer of 1926. He noted an increase in SST but that there was "a regrettable lack of serial observations." We now know that SSTs were high in 1925 to 1926 at La Jolla (Fig. 9). There appear to be no reports of the biological effects of the 1931 to 1932 large warm event, but in 1958 to 1960 warming of the California Current was related to an equatorial El Niño (*8*, *9*). At that time, the thermocline was depressed in the California Current, and zooplankton biomass and the abundance of larval fish declined throughout the region (*8*, *9*, *21*, *22*). The harvest of coastal pelagic fish dropped from 114,000 metric tons in 1956 to 79,000 in 1960. Southern pelagic forms such as red crabs (*Pleuroncodes planipes*), jumbo squid (*Dosidicus gigas*), and many fish species were found well north of their normal range (*24*). This El Niño (1958 to 1960) is one of the largest in the past 80 years and was preceded by an extensive cool period (Fig. 9). The sudden transition from cool to warm SSTs disturbed the structure of the plankton community (Fig. 10). In addition to the substantial decline in plankton biomass and larval fish abundance, there was a large rearrangement of the dominance structure of functional groups of macrozooplankton. The rank order of abundance for 18 groups, containing an estimated 546 species, changed from 1955 to 1959 (*25*). Plankton community structure was similar in 1955 to 1957 but shifted in 1958 to 1959. That is, onset of the 1958 to 1959 El Niño caused an abrupt change in the structure of the community (Fig. 10). The large nearshore kelp forest near San Diego declined, and others in the Southern California Bight were affected as well (*26*). These biological changes are nearly coincident with variations in the strength of the California Current. Over the period 1950 to 1980, plankton varied positively with periods of increased transport of cool, relatively fresh water from the north (*21*).

The biological consequences of the 1983 to 1984 West Coast El Niño were extensive, but reports were scattered over taxa (*9*, *27*). Again, the zooplankton and kelp forests declined greatly, as did many individual populations of fish and invertebrates. The thermocline and nutricline in the California Current deepened by some 50 m, and the phytoplankton biomass was largely redistributed from the upper layers to a deep chlorophyll maximum. The upper 200 m of the system was strongly density-stratified. The range of many entire fish populations and invertebrates shifted to the north in 1983 (*9*, *27*). The 1982 to 1983 season was disastrous for commercial salmon fishing off California, Oregon, and Washington. The average weight of Coho salmon in the Oregon fishery was the lowest on record, and a large shift in the rank order of abundance of major prey species of juvenile salmon off Oregon occurred. There were substantial changes in the spawning ranges of commercial pelagic fish during this period (*28*). The 1983 breeding season was an exceptionally poor one for at least three of Oregon's most important nesting seabird species (*29*), and other seabirds along the entire coast were affected as well. That year the pup counts for California sea lions and Northern fur seals dropped precipitously; either they or their mothers were starving. Even harbor seals seem to have been affected (*30*).

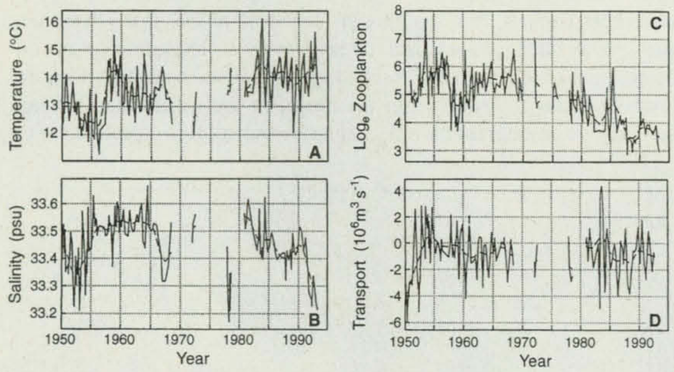
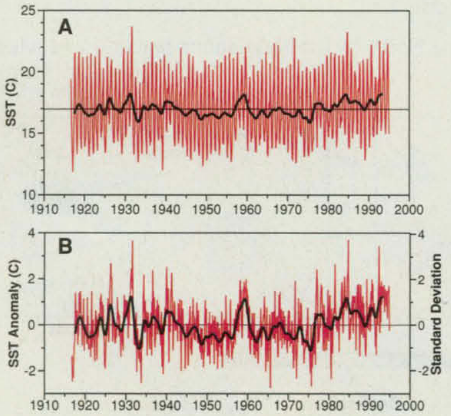


Fig. 8. The mean (**A**) temperature and (**B**) salinity of the upper 100 m of the California Current between 30°N, 124°W and 35°N, 124°W. (**C**) Zooplankton biomass from the same area. (**D**) Mass transport of water from the north through the above area [after (*22*)].

Fig. 9. (**A**) Monthly SSTs at La Jolla (red line) and a 37-month running mean (black line). (**B**) Monthly SD of SST anomalies at La Jolla (red line) and a 37-month running mean (black line).



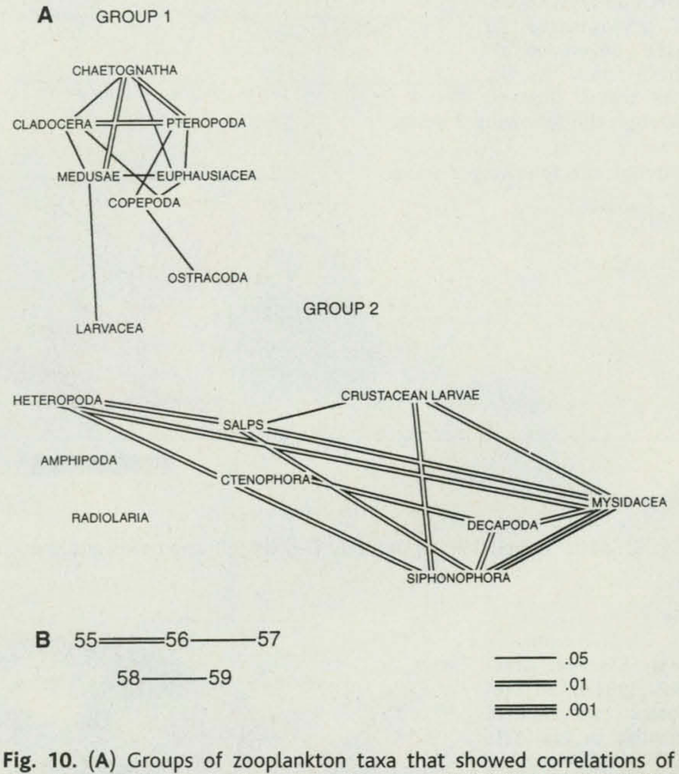


Fig. 10. (**A**) Groups of zooplankton taxa that showed correlations of abundance at the levels shown, over the years 1955 through 1959. The taxa amphipoda and radiolaria were not well correlated with either group. (**B**) Years that showed similarities of plankton rank order of abundance at the levels shown. Years 1955 to 1957 were not correlated with 1958 or 1959. This change occurred during the onset of a large California El Niño.

There have also been interannual variations in the abundance of zooplankton at weather station "P" (1956 to 1980) in the Gulf of Alaska, but the variations seem to be random (*16*). The biological consequences of the 1997 to 1998 El Niño are not fully known, but there are numerous scattered reports of large population declines, bird and mammal mortalities, and range shifts similar to those of 1983 to 1984.

Interdecadal regime shift variations. The regime shift in the entire North Pacific Basin greatly complicated our efforts to understand the biological consequences of the interannual warm and cold events. This interdecadal environmental change had accompanying biological changes of large magnitude and of similar spatial and temporal dimensions. Cause and effect are clearly implied. This shift (Figs. 2 and 9) was first detected by the discovery of the remarkable intensification of the deep chlorophyll maximum in the Central North Pacific Gyre, which took place sometime in 1977 (*31*). It was also found that the spatially averaged measurements of California Current zooplankton abundance declined by over 70% beginning about then (Fig. 8C) and have remained low ever since (*5*).

Beginning sometime in the late 1970s, the mean temperature and salinity shifted over a large area of the California Current (Fig. 8, A and B). Salinity and temperature anomalies, which had been positively correlated over the previous 20 years, now became negatively correlated. That is, this system was now not only warmer but also fresher. There was no evidence for a systematic trend in mass transport of water from the north (Fig. 8D). Systematic, spatially extensive, oceanic seabird counts in the Southern California Bight did not begin until 1987, but abundances have declined some 90% since then (*32*). Fisheries' data typically are highly variable, but although there may have been some "compensatory" shifts in the species mix of the commercial catch, there has been a long-term decline in total commercial, pelagic catch since well before the regime shift, but this decline accelerated after its onset. Other aspects of coastal biology have also changed. Kelp forests that suffered great damage during the interannual warm events but often seem to recover (*33*) are now systematically smaller and depauperate, a trend that began in the late 1970s. Three species of abalones have all but disappeared, and a 60% reduction of the allowable catch of previously abundant groundfish has been imposed by the Pacific Fisheries Management Council. A large change attributed to climate variation occurred in the intertidal flora and fauna in central California, with many southern species now dominating the community (*34*). Thus, the evidence, although spatially scattered and in many cases temporarily discontinuous, all points to a large-scale persistent biological response to the climatic regime shift in the California Current. There has been a general increased frequency of southern species moving north, a substantial lowering of secondary productivity and fish landings, and a major decline in seabirds and changes in species proportions in most sectors of the ecosystem.

Although it suffers even greater data gaps and fragmentation, the populations in the Gulf of Alaska seem also to have responded to the climatic regime shift. For example, some of the primary evidence for a general response here is the large increase of spring zooplankton in the Gulf of Alaska between the years 1956 to 1962 and 1980 to 1989 (*35*). But, in addition to an 18-year gap in the data, the comparison is between composite maps with different spatial sample distributions both from year to year within each period and between them (*36*). Interdecadal frequencies of variation cannot be statistically resolved by these data. Additional plankton data come from the continuous monthly Canadian time series at the old Weather Station "P" at 45°N, 150°W (1956 to 1980), in the center of the Gulf of Alaska. Here, however, there is no visually apparent interdecadal, regime shift signal (*16*). Of course, this single local may or may not be very representative of variability over the entire Gulf of Alaska, because spatial correlation length scales of plankton variability here are unknown.

Long-term continuous annual data from commercial fisheries in the Gulf of Alaska indicate that, although some species have decreased, there have been large increases in yield of several of the more important stocks of fish, so that the total catch went from some 2.64×10^6 megatons in 1970 to 3.38×10^6 megatons in 1990 (*37*). The most spectacular shifts upward were those of the sockeye and pink salmon (*2*). Although these species make up only about 5.5 and 4.5%, respectively, of the total, their catch increased markedly beginning in 1976, close to the onset of the regime shift. Catches of other species including pollock, hake, and Pacific cod also rose in the early to mid-1980s, but some of these have declined since. Ocean perch, herring, and slope rockfish, all of which were reasonably large fisheries (>100,000 megatons per year), have decreased, as have catches of shrimp, king crab, and other crustaceans. These decreases began well before the onset of the regime shift. Catches of Coho and Chinook salmon along the southern coast of British Columbia, Washington, and Oregon, areas in the bifurcation zone of the West Wind Drift, have decreased markedly since about 1978. These sharp declines have been attributed to changes in the survivorship of young and juveniles in the open ocean after the regime shift (*38*).

Mechanisms. The biological changes in the California Current and the Gulf of Alaska Gyre have, in both cases, been attributed to changes in the physical mechanisms controlling primary production, chiefly those that influence the depth and rate of vertical mixing. But the two areas operate quite differently and are claimed to have responses to climatic forcing that are 180° out of phase with each other. Interannual variations in plankton abundance in the California Current are associated with the climatically driven variations in mass transport of water from the north (*21*). The source of this water is at the bifurcation of the West Wind Drift, and waters here are high in nutrients. As this water moves south, the nutrients are utilized and recycled, resulting in high standing crops of zooplankton. When this horizontal circulation is vigorous, there are large positive anomalies of zooplankton abundance, and when the horizontal circulation is weak, there are lower ones. These large, low-frequency changes in biomass are uncorrelated with local coastal upwelling indices, thus supporting the idea that forcing external to the system is responsible for the large interannual biological changes.

The interdecadal regime shift in the California Current system differs from that of the interannual changes. The persistent increase in mean SST has reduced the density of the upper layer. This density reduction has resulted in a shoaling of the depths from which waters are mixed, stirred, or upwelled and therefore a reduction in the rate of supply of plant nutrients (*5*). Because the deeper, nutrient-rich water is also more saline, this reduction of upwelling should result in negative salinity anomalies throughout the system, as observed (*22*) (Fig. 8B). In those large parts of this system where appropriate serial measurements have been made, there is now warmer and fresher water, and there is no known, outside source for such. Our daily shore station data show that the trend for negative salinity anomaly and positive temperature anomalies occurred abruptly during the same few months of 1977. Thus, this interdecadal varying nutrient supply mechanism acts within the California Current. This mechanism differs greatly from the interannual nutrient supply mechanism behind the interannual biological response.

The biological response to the interdecadal regime shift in the Gulf of Alaska is thought to have been in the opposite direction to that of the California Current (*2*). This concept is based on three observations: (i) Zooplankton abundance has decreased in the California Current System and increased in the Gulf of Alaska at about the same time, the onset of the regime shift. (ii) There has been an abrupt increase in the landings of two species of salmon and a much more gradual increase in the landings of some other species since the onset. (iii) There is bifurcation in the West Wind Drift, where during "type A" atmospheric circulation the mass transport of water to the south (California Current System) is strong and to the north (Gulf of Alaska) is weak, but during type B conditions transport to the south is weak and that to the north is strong. The proponents of this concept suggest that type B atmospheric circulations became predominant during 1976 to 1977 and are responsible for the biological regime shift in the Gulf of Alaska. Speed-up of the Subarctic and Alaska Current (type B) might result in increased upwelling and divergence in the center of the Gulf of Alaska and a transport of nutrients along the periphery of the gyre (*35*). Others propose that the MLD shoaled and, therefore, exposure of phytoplankton cells to light increased (*39*). Because phytoplankton growth in the Gulf of Alaska is thought to be chiefly light limited, primary productivity should be enhanced. The proposed increase in primary productivity resulted in more zooplankton and eventually in species of salmon, pollock, Pacific cod, hake, and other fish but not apparently other formerly important members of the Gulf of Alaska fauna, such as Pacific Ocean perch, herring, king crab, shrimp, sea lions, fur seals, murres, and kittiwakes, all of which have declined. This differs greatly from the California Current regime shift mechanism, whereby increased stratification has resulted in a lessening of plankton production (*5*) and total yields of almost all resident species of commercial fish and squid.

Discussion

It seems that there are large-scale biological responses in the ocean to low-frequency climatic variations in the atmosphere acting through changes in the horizontal and vertical movements of water. These responses result in changes in geographical ranges and spatial patterns of species, in easily detected anomalies in secondary productivity, and in community structure. However, the mechanisms by which climate exerts its influence vary by domain. In the California Current System, large warming episodes are linked to equatorial El Niños. These Californian El Niños result in episodic lowerings of the nutricline, the development of a deep chlorophyll maximum layer, and a decrease in secondary productivity of zooplankton. A longer term interdecadal regime shift has also occurred and has been associated with a southward shift and intensification of the Aleutian Low and prevailing westerlies over the midlatitude central and eastern Pacific. It is not clear if the climatic forcing here is closely related to El Niño, but this shift has resulted in a long-term increase in sea-surface and upper water-column temperatures and physical stratification in the eastern North Pacific. Because of this stratification, the depth of mixing of nutrient-rich water has shoaled off, resulting in a lower rate of supply of nutrients to the euphotic zone; a decrease in productivity and a general decline of zooplankton, sea birds, and kelp production; and a shift in benthic, intertidal community structure.

In the Gulf of Alaska, interannual variations in SST and zooplankton have been detected but have not been related to El Niño episodes, either those on the equator or in the California Current. But large interdecadal increases in SST, zooplankton abundance, and the landings of some commercial fish species have been reported. This interdecadal signal has been attributed to the shift of the Aleutian Low pressure system, the consequent regime shift intensification of Gulf of Alaska circulation (type B pattern), and a presumed interdecadal weakening of the California Current. A model of this speed-up has shown it to be accompanied by a shoaling of the MLD, and an additional model indicates that this shoaling should result in increased exposure of phytoplankton cells to light, in this light-limited system, and therefore an increase in primary production and, eventually, zooplankton (*39*). Thus, the out-of-phase fluctuation of the strength of the California and Alaska currents and the interdecadal decreased biological production in California Current and increase in Gulf of Alaska have been explained in terms of a large-scale shift in the Aleutian Low pressure system. However, the physical evidence for A and B type circulation changes at the West Wind Drift bifurcation does not appear to exist, and there is no evidence for an interdecadal decrease in transport into the California Current. The biological variations in plankton abundance in the two systems cannot convincingly be shown to be out of phase on either the interannual or interdecadal time scales, and the data on total fish production in the Gulf of Alaska present a mixed picture. Although the evidence for the proposed mechanism of change in the Gulf of Alaska and even the magnitude and extent of the change is murky, something important may have happened to populations on the regime (interdecadal) scale, and this is likely associated with a climatic variation on a similar scale. Spatially fragmented, temporally discontinuous, and ecologically narrow sampling is in large part responsible for this uncertainty. After all, fisheries' stock assessments are not made for the purpose of studying the role of climate in the management of fisheries (*40*), and much of the evidence for a biological regime shift in the Gulf of Alaska comes from such data. A more inclusive approach to studies in support of fisheries management has been proposed (*40*).

The situation in the California Current is more clear, chiefly because of the existence of a longer term, spatially extensive physical and biological monitoring system, with far fewer data gaps. There have been frequent, large, interannual zooplankton and temperature anomalies, and these anomalies are well correlated with climatically driven, observed changes in the strength of the California Current. The consequent variations in both horizontal and vertical input of nutrient-rich water have affected zooplankton and larval fish productivity. These El Niño–correlated, interannual variations also lessen the canopy cover and stipe density of kelp forests and almost always are accompanied by numerous reports of southern species of fish and invertebrates occurring far north of their normal range. They are, then, climatically driven ecosystem disturbances. Larval fish abundance anomalies observed over a 20-year period are only weakly correlated with zooplankton abundance anomalies, and the total landings of commercial pelagic fish have been highly variable but mostly declining over the past few decades, so the relation of fish populations and yield to interannual variations is not clear. But there was an abrupt drop of landings after the 1958 to 1960 El Niño, a small recovery, then another drop after the regime shift in 1977, and another drop after the 1983 to 1984 El Niño.

The California Current ecosystem showed a large, interdecadal regime shift change in its physical structure and presumably its dynamics, especially that of vertical mixing, starting about 1977. The biological response was large, of a similar temporal scale, and could be seen in zooplankton abundance, sea birds, kelp forests, and intertidal benthic community structure. But it is more difficult to attribute the currently very low commercial fish harvest directly to these climatic events because harvesting itself affects fish population dynamics in, as yet, not quite predictable ways. This is especially true when there are large environmental variations also occurring in, as yet, not quite predictable ways. The development of models for achieving the sustained yield of fish will depend on our ability to predict the direction, magnitude, and frequency of these ecosystem disturbances, that is, the role of climate variability in the regulation of fish populations (*40*). It may be that the entire concept of sustained yield is misdirected.

If we use the criterion of ±2 SD, there have been 12 warm episodes in the California Current since 1916, and another one is now in progress. There have been 10 cold periods of that magnitude as well. But the temperature anomalies during these episodes were only about ±2.5°C or 3°C. These relatively small physical changes resulted in large biological consequences.

There is now no question that interannual and interdecadal climatic variations strongly affect the structure and function of marine ecosystems. Not only is it evident from these California Current, Gulf of Alaska, and Central Gyre studies, but similar results have been obtained in the North Atlantic (*41*) and off Chile (*42*). These perturbations and resulting ecosystem disturbances may be chiefly responsible for the state of high-diversity coastal ecosystems. But the time-series studies used to detect them have been rather crude and few in number. If, as we think, the frequency of disturbances may be increasing, then more sophisticated programs are needed to achieve better understanding of how harvested populations or entire ecosystems respond to climate variations.

References and Notes

1. W. S. Wooster, in *From Year to Year*, W. S. Wooster, Ed. (Washington Sea Grant Publication, University of Washington, Seattle, WA, 1983), pp. 1–16; C. M. Duarte, J. Cebrían, N. Marbá, *Nature* **356**, 190 (1992); J. A. McGowan, in *Natural Climate Variability on Decade-to-Century Time Scales*, D. G. Martinson *et al.*, Eds. (National Academy Press, Washington, DC, 1995), pp. 555–570.
2. R. C. Francis and S. R. Hare, *Fish. Oceanogr.* **3**, 279 (1994); A. B. Hollowed and W. S. Wooster, in *Climate Change and Northern Fish Populations*, R. J. Beamish, Ed., *Can. Spec. Publ. Fish. Aquatic Sci.* **121**, 373 (1995); T. L. Hayward *et al.*, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 22 (1996); R. C. Francis, S. R. Hare, A. B. Hollowed, W. S. Wooster, *Fish. Oceanogr.*, in press.
3. A. J. Miller, D. R. Cayan, T. P. Barnett, N. E. Graham, J. M. Oberhuber, *Clim. Dyn.* **9**, 287 (1994); K. E. Trenberth and J. W. Hurell, *ibid.*, p. 303; N. E. Graham, *ibid.* **10**, 135 (1994).
4. R. T. Paine and S. A. Levin, *Ecol. Monogr.* **51**, 145 (1981); S. T. A. Pickett and P. S. White, Eds., *The Ecology of Natural Disturbance and Patch Dynamics* (Academic Press, New York, 1985).
5. D. Roemmich and J. A. McGowan, *Science* **267**, 1324 (1995).
6. Surface Water Temperature, Salinity and Densities at Shore Stations, U.S. West Coast (Data Report, University of California, San Diego, CA, 1916–1997).
7. R. S. Arthur, *Deep Sea Res.* **2**, 107 (1954); J. L. Reid, *Calif. Coop. Oceanic Fish. Invest. Rep.* **7**, 77 (1960); G. I. Roden, *ibid.* **8**, 95 (1961); E. J. List and R. C. Y. Koh, *J. Geophys. Res.* **81**, 1971 (1976).
8. O. E. Sette and J. D. Isaacs, Eds., *Symposium on the Changing Pacific Ocean in 1957 and 1958*, *Calif. Coop. Oceanic Fish. Invest. Rep.* **7**, 14 (1960).
9. W. S. Wooster and D. L. Fluharty, Eds., *El Niño: North Effects in the Eastern Subarctic Pacific Ocean* (Washington Sea Grant Program, Seattle, WA, 1985).
10. J. Radovich, in *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*, M. H. Glantz and J. D. Thomson, Eds. (Wiley-Interscience, New York, 1981), pp. 107–136.
11. L. A. Mysak, in *Climate Change and Northern Fish Populations*, R. J. Beamish, Ed., *Can. Spec. Publ. Fish. Aquat. Sci.* **121**, 464 (1995).
12. D. B. Enfield and J. S. Allen, *J. Phys. Oceanogr.* **10**, 557 (1980).
13. D. J. Thomson and A. D. Chave, in *Advances in Spectrum Analysis and Array Processing*, S. Haykin, Ed. (Prentice-Hall, Englewood, NJ, 1991), pp. 58–113.
14. C. W. Ropelewski and P. D. Jones, *Mon. Weather Rev.* **115**, 2161 (1987).
15. D. E. Parker, M. Jackson, E. B. Horton, *Climate Research Technical Note 63* (Hadley Centre, Meteorological Office, London, 1995).
16. B. W. Frost, in *From Year to Year: Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and the Eastern Bering Sea*, W. S. Wooster, Ed. (Washington Sea Grant Publication, University of Washington, Seattle, WA, 1983), pp. 146–157.
17. C. C. Ebbesmeyer *et al.*, in *Proceedings of the 7th Annual PACLIM Workshop* (Interagency Ecological Studies Progress Technical Report 26, California Department of Water Resources, Sacramento, CA, 1990), pp. 115–126.
18. D. R. Cayan *et al.*, in *Natural Climate Variability on Decade to Century Time Scales*, D. G. Martinson *et al.*, Eds. (National Academy Press, Washington, DC, 1995), pp. 133–150; A. J. Miller, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 69 (1996).
19. J. Namias and R. M. Born, *J. Geophys. Res.* **79**, 797 (1974); J. Namias, X. Yuan, D. C. Cayan, *J. Clim.* **1**, 682 (1988).
20. D. B. Chelton and R. E. Davis, *J. Phys. Oceanogr.* **12**, 757 (1982).
21. D. B. Chelton, P. A. Bernal, J. A. McGowan, *J. Mar. Res.* **40**, 1095 (1982).
22. J. A. McGowan, D. B. Chelton, A. Conversi, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 45 (1996).
23. C. L. Hubbs and L. P. Shultz, *Calif. Fish Game* **15**, 234 (1929).
24. J. Radovich, *Calif. Coop. Oceanic Fish. Invest. Rep.* **7**, 163 (1960).
25. The method used to obtain these results is described by M. H. Williamson [*Bull. Mar. Ecol.* **5**, 207 (1961)] and was designed to study changes in the community composition of zooplankton. The object is to find out which groups of species have shown similar variations from year to year. It uses Spearman's rank correlations. Monthly maps of these California Current zooplankton data are given by J. D. Isaacs, A. Fleminger, and J. K. Miller [*California Cooperative Oceanic Fisheries Investigation Atlas 10* (State of California Marine Research Committee, 1969), pp. 1–122; graphs and more maps are given by A. Fleminger, J. D. Isaacs, and J. G. Wyllie [*California Cooperative Oceanic Fisheries Investigation Atlas 21* (State of California Marine Research Committee, 1974), pp. 1–118].
26. M. J. Tegner, P. K. Dayton, P. B. Edwards, K. Riser, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 111 (1996).
27. P. K. Dayton and M. J. Tegner, in *Global Consequences of the 1982–1983 El Niño–Southern Oscillation*, P. Glynn, Ed. (Elsevier, Amsterdam, 1990), pp. 433–472.
28. P. E. Smith, in (9), pp. 121–142.
29. M. R. Graybill and J. Hodder, in (9), pp. 205–210.
30. J. Barlow *et al.*, in *Pinnipeds and El Niño: Responses to Environmental Stress*, F. Trillmich and K. A. Ono, Eds. (Springer-Verlag, New York, 1998), pp. 1–33.
31. E. L. Venrick, J. A. McGowan, D. R. Cayan, T. L. Hayward, *Science* **238**, 70 (1987).
32. R. R. Veit, P. Pyle, J. A. McGowan, *Mar. Ecol. Prog. Ser.* **139**, 11 (1996); R. R. Veit, J. A. McGowan, D. G. Ainley, T. R. Wahls, P. Pyle, *Global Change Biol.* **3**, 23 (1997).
33. M. J. Tegner, P. K. Dayton, P. B. Edwards, K. L. Riser, *Mar. Ecol. Prog. Ser.* **146**, 117 (1997); M. J. Tegner and P. K. Dayton, *ibid.* **77**, 49 (1991); P. K. Dayton, M. J. Tegner, P. E. Parnell, P. B. Edwards, *Ecol. Monogr.* **62**, 421 (1992).
34. J. P. Barry, C. H. Baxter, R. D. Sagarin, S. E. Gilman, *Science* **267**, 672 (1995).
35. R. D. Brodeur and D. M. Ware, *Fish. Oceanogr.* **1**, 32 (1992); R. D. Brodeur, B. W. Frost, S. R. Hare, R. C. Francis, W. J. Ingraham, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 80 (1996).
36. R. Le Brasseur, *Limnology and Oceanography, Manuscript Report Series*, vol. 201 (Fisheries Research Board, Nanawno Canada, 1965), pp. 1–260; Data Record of Oceanographic Observations and Explorations Fisheries nos. 24 to 33 (Hokkaido University, Hakodate, Japan, 1981–1990).
37. C. Stamatopoulos, *FAO Fish. Circ.* **855**, 3 (1993).
38. R. J. Beamish *et al.*, *Fish. Oceanogr.* **4**, 243 (1995).
39. J. J. Polovina, G. T. Mitchum, G. T. Evans, *Deep Sea Res.* **42**, 1701 (1995).
40. L. W. Botsford, J. C. Castilla, C. H. Peterson, *Science* **277**, 509 (1997).
41. N. J. Aebisher, J. C. Coolson, J. M. Colebrook, *Nature* **347**, 753 (1990); A. H. Taylor, *ICES J. Mar. Sci. J. Conseil* **52**, 711 (1995).
42. T. L. Hayward, *Trends Ecol. Evol.* **12**, 150 (1997); P. Muck, in *The Peruvian Upwelling System: Dynamics and Interactions*, D. Pauly, P. Muck, J. Mendo, I. Tsukayama, Eds. (ICLARM Conference Proceedings 18, International Center for Living Aquatic Resources Management, Metro Manila, Philippines, 1989).
43. We are indebted to the many volunteers who have recorded daily SSTs along the Pacific coast for many decades. Our Fig. 2 was originally hand drawn by P. Walker, and both she and C. Fey have accessioned data from the field and prepared the subsequent data reports. A. Mantyla has seen to quality assurance. D. Judkins did analysis for Fig. 10. L. Riddle and J. Griffith prepared our illustrations, and M. Olivarria typed the manuscript. The shore station sea-surface measurement program was supported for decades by the State of California through Scripps Institution of Oceanography and the Marine Life Research Group. Three years' support came from the National Oceanic and Atmospheric Administration (NA47GP0188), the Vetlesen Foundation, and a small supplement from Office of Naval Research.

Nutrient Biogeochemistry of the Coastal Zone

T. D. Jickells

REVIEW

The coastal seas are one of the most valuable and vulnerable of Earth's habitats. Significant inputs of nutrients to the coastal zone arrive via rivers, groundwater, and the atmosphere. Nutrient fluxes through these routes have been increased by human activity. In addition, the N:P:Si ratios of these inputs have been perturbed, and many coastal management practices exacerbate these perturbations. There is evidence of impacts arising from these changes (in phytoplankton numbers and relative species abundance, and deep-water oxygen declines) in areas of restricted water exchange. Elsewhere, the nutrient fluxes through the coastal zone appear to be still dominated by large inputs from the open ocean, and there is little evidence of anthropogenic perturbations.

The coastal seas are one of the most important areas of the world oceans from a human perspective. We use these areas for food supplies via fishing, with almost all the world's fish catch coming from coastal waters and adjacent upwellings (*1*); as a source of nonrenewable (such as hydrocarbons and sand and gravel extraction) and renewable resources; and for power and transportation (*2*), as well as for waste disposal and for recreation. In a recent attempt to value the world's ecosytems (*3*), coastal seas were assigned a higher value than the whole terrestrial or open ocean system, despite their much smaller area. Almost all this value is associated with the storage and cycling of the nutrients N and P. The approach and conclusions of this study (*3*) are open to criticism, because it is not possible to value an

---

The author is in School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK. E-mail: t.jickells@uea.ac.uk