El Niño Effects on Southern California Kelp Forest Communities

MIA. J. TEGNER AND PAUL. K. DAYTON

I. INTRODUCTION

Coincident with the Christmas season in the Peruvian and Equadorian coastal areas, the normally cold water of the north-flowing Peru Current is displaced by a warm, southward current associated with a decrease in nutrients and a temporary reduction in fishing success. This is the generic "El Niño", a brief seasonal anomaly ending by March or April. Occasionally, however, the warm current strengthens and persists for a year or more, usually with a catastrophic effect on the important anchoveta population and the various populations which depend on it, including several species of higher-order fishes, guano birds, marine mammals and, more recently, human fishermen. The latter, much more severe event has become known as the El Niño (Ramage, 1986), which is how we will use the term. It is important to remember that there is a continuum of severity and, as no two events are the same, there are probably multiple causes of the El Niño phenomena.
While El Niños were defined in terms of events off South America, Jacob Bjerknes recognized the link with oceanic and atmospheric processes which extend across the Pacific and Indian Oceans in his study of the El Niño of 1957–1958 (Rasmussen, 1984). As early as the 1920s, Sir Gilbert Walker described the Southern Oscillation, a giant seesaw of atmospheric pressure and rainfall patterns between the Indian Ocean from Africa to Australia and the Pacific Ocean. This periodic disruption of climate is associated with severe droughts in some areas and massive floods in others, a redistribution of hurricane tracks, brush fires, crop failures and losses of livestock and human life. Changes in the Southern Oscillation index, calculated by Walker by subtracting pressure in the western Pacific from pressure in the eastern Pacific, correlate with many atmospheric and oceanic anomalies (see Wallace, 1985), and the relationship between El Niños and the Southern Oscillation is so accepted that it has acquired the acronym ENSO.

More difficult than creating a catchy acronym is understanding the mechanism. Over the years the models have focussed on the southeast trade winds driven by the pressure gradient between the South Pacific high-pressure system and the low-pressure system over Indonesia and Australia (reviewed by Ramage, 1986). A large pressure difference corresponds with a high Southern Oscillation index, strong trade winds, and high sea level in the western Pacific. A precipitous drop in the index and a corresponding collapse of the trade winds in the western Pacific signals the onset of an ENSO event. The water piled up in the western Pacific flows eastward near the Equator in subsurface waves known as Kelvin waves. The Kelvin waves generate anomalous eastward currents of warm water, raise sea level, and depress the thermocline in the eastern tropical Pacific. The deepened thermocline makes upwelling ineffectual and water temperatures soar. This results in the classical El Niño phenomenon. Unfortunately, the El Niños of 1976–1977 and especially 1982–1983 failed to follow this model based on a build-up of the trade winds (Ramage, 1986).

While the physical story of ENSO is far from complete, the effects of the El Niño on the Peruvian anchoveta system are reasonably well understood (Cushing, 1982; Arntz, 1986). The anchoveta was the largest fishery in the world, producing more than 12 million tons in 1970 (Cushing, 1982). During "normal" or non El Niño years, a coastal upwelling system feeds a short but highly productive food chain which, in addition to and largely dependent upon the anchoveta, includes other fishes such as different species of mackerel, hake, and rosefish and, offshore, various larger predators such as tunas. Also dependent on the anchoveta are several guano-producing birds such as cormorants, boobies and pelicans, and the guano they produced represented an important export industry once politically powerful enough to interfere with the development of the anchoveta fishery itself. Thus much of the ecosystem depends upon the anchoveta, and this population depends
upon the physical structure of the upwelling system. A major El Niño drastically reduces the productivity and greatly alters the spatial scales of the community. As El Niños are a normal part of the ecosystem, the component species have evolved buffers which allow rapid recovery. However, with the development of human overexploitation of the anchoveta, recoveries have been slower until the strong El Niño of 1972–1973, from which there has been little recovery (Cushing, 1982). The biological consequences of tropical El Niños have been reviewed by Cushing (1982), Barber and Chavez (1983, 1986), Oceanus 27(2) (1984), and Arntz (1986).

The 1982–1983 El Niño was the largest ever measured and reached into high latitudes of the eastern Pacific in both the Southern (Arntz, 1986) and Northern (Wooster and Fluharty, 1985; Mysak, 1986) Hemispheres. Wallace (1985) notes two possible mechanisms for transmitting the ENSO signal from the equatorial belt to higher latitudes. The first is the propagation of coastally trapped waves in the ocean. The second involves local forcing of coastal phenomena by anomalous surface winds associated with planetary-scale teleconnection patterns in the atmosphere. There is good evidence for the role of atmospheric teleconnections, but these are restricted to the winter half of the year for the hemisphere in question (Wallace, 1985). Whatever the mechanism, the most direct effects and the most thoroughly studied aspects are oceanic, especially planktonic food webs (see Chelton et al., 1982; McGowan, 1985). Here we review the effects of this massive oceanic phenomenon on the nearshore kelp communities of the southern California Bight.

II. SOUTHERN CALIFORNIA KELP FOREST COMMUNITIES

Shallow subtidal rocky habitats along most temperate coasts are dominated by large brown algae of the order Laminariales, commonly known as kelps. The kelp forests of southern California are rich and complex assemblages of many species of plants and animals, a number of which are important economically. These communities are organized around the giant kelp, *Macrocystis pyrifera*, and are characterized by large standing stocks and high rates of growth, production, and turnover. While subject to a number of small-scale disturbances, these communities exhibit considerable long-term stability (Dayton et al., 1984). However, in recent years it has become increasingly clear that the health of California kelp forests is linked to events thousands of kilometers away. The ENSO event which began in 1982, well known for its devastating effects in the tropical Pacific Ocean, was also associated with the largest disturbance of southern California kelp forests ever recorded (Dayton and Tegner, 1984a).
Fig. 1. Map of the coast of the Californias between central Alta California and central Baja California. While its range extends into Alaska (Abbott and Hollenberg, 1976), *Macrocystis pyrifera* forms significant forests only between Isla Asuncion and the coast south of San Francisco. The southern California Bight is the region between Point Conception and the Mexican border including the Channel Islands.

The timing of this event was opportune. The last massive El Niño to affect southern California kelp forests was 1957-1959, a time when biologists were faced with a major anomaly without understanding more typical conditions. Subsequent progress has led to the identification of specific physical parameters and biological processes important to the maintenance of kelp forest community structure. Here we use that knowledge and our 15 years of experience in the Point Loma kelp forest near San Diego to describe the effects of this massive El Niño on an extra-tropical community.

Like most natural communities, kelp forests are composed of distinct patches and are influenced by competition and various physical and biological disturbances (Dayton *et al.*, 1984). The algal patch types or guilds are composed of species of algae that can be categorized into vegetation layers distinguished by morphological adaptations. The layers and some southern California examples are: (1) a canopy supported at or near the surface by
Fig. 2. Sketch of the 15 m site at Point Loma, illustrating patches composed of algae with characteristic canopy guilds, including the floating canopy of *Macrocystis*, the stipitate canopy of *Pterygophora* and *Eisenia*, the prostrate canopy of *Laminaria*, and patches of turf and encrusting coralline algae (from Dayton et al., 1984).

floats (*Macrocystis*); (2) an erect understory in which the fronds are supported well above the substratum by stipes (*Pterygophora californica*, *Eisenia arborea*); (3) a prostrate canopy in which the fronds lie on or immediately above the substratum (*Laminaria farlowii*); (4) turf composed of many species of coralline, foliose, and filamentous red algae; and (5) a pavement of encrusting coralline algae (Fig. 2). At Point Loma, representatives of these patch types have been observed to persist for many years, which, for some species, is several generations. The mechanisms which enable patch types to resist invasion by other guilds include competition for light, limits to spore dispersal including the physical barrier of extant plants and distance, and spore swamping by patch members following small disturbances. The tallest perennial canopy guild dominates competition for light but is more susceptible to wave stress. Conversely, the lower standing guilds are much more tolerant of wave stress, and dominance hierarchies appear to be reversed in areas exposed to extensive wave stress (Dayton et al., 1984).

Important sources of disturbance for kelp forest communities are storms and grazing (Dayton and Tegner, 1984a; Dayton et al., 1984; Dayton, 1985; Ebeling et al., 1985). The effects of storms vary widely between kelp beds as a function of the frequency and magnitude of storms, degree of exposure to
waves, and stability of the substratum. The main source of mortality at Point Loma is storm-dislodged *Macrocystis* which subsequently entangle other plants. The area of the disturbance is a critical component of patch stability. The more common small disturbances are usually colonized by members of the existing patch type, both from preceding sporulations and by spore swamping by surrounding plants. Larger disturbances involve the relative dispersal abilities, physiological thresholds, and reproductive seasonality of the different species. A critical second-order result of large-scale disturbance of the kelps is the effect on the availability of detached, drifting algal material, the major food of sea urchins (Ebeling et al., 1985; Harrold and Reed, 1985).

Numerous animals feed on kelps but sea urchins are the most important herbivores in terms of the frequency and severity of destructive grazing (Leighton, 1971). Sea urchins are occasionally responsible for denuding large areas of algae, but predators such as spiny lobsters and fishes in southern California (Tegner and Dayton, 1981; Cowen, 1983; Tegner and Levin, 1983) seem to generally prevent urchins from devastating entire coastlines, as they have done in Nova Scotia (Mann, 1977; Chapman, 1981), or sea otter-free areas of the North Pacific (Estes and Palmisano, 1974). The scale of sea urchin disturbance varies from the small <1 m ambit from a refuge, to a few square meters in a boulder patch, to an entire kelp forest. A critical factor affecting the scale of disturbance is urchin recruitment, something clearly influenced by large-scale oceanographic processes (Dayton and Tegner, 1984b).

The health of *Macrocystis* forests in southern California is also strongly affected by the relationship between temperature and nutrients. Significant deterioration and occasional disappearance of the surface canopy is associated with warm temperatures during summer and fall; plants appear healthy below the thermocline. *Macrocystis* grows better in colder regimes but laboratory work has shown that the optimal temperature for photosynthesis is between 20 and 25°C, temperatures at which tissue damage has been observed in the field (reviewed by North and Zimmerman, 1984). Nutrient distributions in southern California coastal waters are affected by density stratification and uptake and release by plankton. As temperature is the dominant factor controlling seawater density in this area, there is a clear relationship between temperature and nutrient concentrations, and processes which affect density and temperature distributions, such as shoaling of isotherms near the coast, wind-driven upwelling or downwelling, and internal waves, also affect nutrient distributions (Eppley et al., 1979; Jackson, 1983). A strong negative correlation between temperature and nitrate, the nutrient most likely to limit growth (North et al., 1982), has been established for the southern California Bight; there are negligible amounts of nitrate above 15°C (Jackson 1977, 1983; Gerard, 1982; Zimmerman and Kremer,
Fig. 3. The daily Scripps Institution of Oceanography pier sea-surface temperature data for 1982–1985 in relation to the 63-year (1920–1982) mean daily temperature (courtesy of E. Stewart, SIO).

1984). The warmer water is generally surface water that has been there for some time; during this time the plankton have depleted it of nutrients. The importance of the correlation between temperature and nutrients for *Macrocystis* is supported by fertilization experiments; nutrient additions decreased summer canopy deterioration relative to controls (North and Zimmerman, 1984). *Macrocystis* growth rates are reduced whenever nitrate concentrations fall below 1 μm, a level reached at about 15.5°C (Zimmerman and Kremer, 1984). Surface temperatures are normally 16°C or warmer from May through November (Fig. 3). *Macrocystis* can build internal nitrogen reserves during periods when external nutrient availability is high, and then use these reserves to maintain relatively rapid growth for at least two weeks to a month in the absence of significant external nutrients (Gerard, 1982; Zimmerman and Kremer, 1986).
III. THE PHYSICAL ENVIRONMENT: RELATIONSHIP OF THE CALIFORNIA CURRENT TO ENSO EVENTS

The lesson of recent years is that kelp forests are not isolated systems responding only to local processes; they are also strongly influenced by much larger scale physical processes which, in this case, may involve all of the southern California Bight and the much larger California Current system. Oceanic and atmospheric processes in the Pacific cause large-scale, low-frequency changes in the California Current leading to highly significant interannual variability in physical and biological parameters (Bernal, 1981; Chelton et al., 1982). These and more local (mesoscale to hundreds of km) oceanic anomalies are probably responsible for the episodic recruitment events which characterize many populations of long-lived animals, including many important kelp forest species.

While El Niños were defined in terms of events off South America, it is now recognized that these changes are connected directly to changes across the entire tropical Pacific and indirectly to changes through much of the world's atmosphere and oceans (Cane, 1983; Rasmusson and Wallace, 1983). Chelton et al. (1982) have shown that the strength of the California Current is closely related to ENSO occurrences in the eastern tropical Pacific. The major El Niño events of 1957–1958, 1964, 1969 and 1972, as well as a number of minor events, are reflected in time series data from both areas. El Niños in the tropics are associated with positive California sea-level anomalies which correspond to anomalous poleward flow (Chelton et al., 1982). Negative (or anti) El Niños, which refer to anomalously low sea-surface temperatures and strong coastal upwelling off South America (Quinn et al., 1978), are associated with low sea level and anomalously strong equatorward flow in California (Chelton et al., 1982). For the purpose of this discussion, El Niño will refer to mid-latitude warming events or California “El Niños” (Simpson, 1983) associated with ENSO events in the tropical Pacific Ocean.

An example of a major California El Niño was 1957–1959 when the California Current system was marked by abnormally high water temperatures, salinity, and sea level, increased poleward flow, and decreased zooplankton volume (Chelton et al., 1982). Many species were observed far north of their usual range and some of these spawned successfully off southern California (Radovitch, 1961). Inshore, high temperatures persisted through much of the year. The southern coastal kelp forests from Newport Beach to San Diego apparently suffered to the greatest extent from the warm water. The annual harvest of the Point Loma bed relative to 1952, a year of high yield, was 48% in 1957, 21% in 1958, and 1% in 1959 (Clendenning, 1968). Sea urchins caused extensive grazing damage and effectively prevented kelp recruitment as many once luxuriant kelp beds all but disappeared (North and Pearse, 1970).
IV. THE 1982–1984 EL NIÑO IN CALIFORNIA

Anomalously high sea level, an indication of anomalous poleward flow, became apparent during the late spring of 1982 and was about three standard deviations above normal by fall and early winter (Fig. 4). The January 27, 1983 value was the highest sea level ever recorded off San Diego (Cayan and Flick, 1985). The sea-surface temperature was largely higher than the long-term mean in the latter half of 1982 and was 2°C above normal for the first three months of 1983 (Figs. 3 and 4). Satellite observations provided evidence of mesoscale changes in sea-surface temperatures in the southern California Bight by December 1982 (Fiedler, 1984).

![Graph showing monthly anomalies of surface temperature and sea level at the Scripps Institution of Oceanography pier, coastal upwelling index in a 3 × 3 degree square centered at 33°N, 119°W, and depth of the 14°C isotherm at 32.7°N, 118.2°W (adapted from Fiedler et al., 1986).]
The winter of 1982–1983 was the most severe storm season in many decades along the west coast of North America (Namias and Cayan, 1984; Seymour et al., 1984), and the extratropical atmospheric circulation was clearly linked to the warming of the east equatorial Pacific Ocean surface (Quiroz, 1983). The unusually deep Aleutian low-pressure center and the intensification of the westerlies resulted in an extraordinary number of severe storms making landfall along the west coast of the United States much further south than normal. There were six events with waves exceeding six meters during the winter of 1982–1983; there were only 18 such events during the period of 1900–1984 (Seymour et al., 1984). A wave monitoring station near Point Loma recorded the highest significant wave height in eight years of measurements (Seymour and Sonu, 1985). Eight storms from January through March had periods of peak energy between 17–22 seconds; only one storm reached 17 seconds in the previous three years. Thus there were more storms, with bigger waves and longer periods, and they devastated *Macrocystis* canopies.

Surface manifestations of the El Niño could not be seen during April and May of 1983; sea-surface temperatures were within the range of normal interannual variability in the California Current system, and coastal upwelling also increased to near normal levels (Fiedler, 1984). However, offshore subsurface temperature anomalies were as great as three standard deviations above normal during this period (Simpson, 1983). By July, large-scale surface warming was again evident with temperatures up to 4°C above normal along the coast (Fiedler, 1984). The temperature, salinity, and dissolved oxygen characteristics of the nearshore waters during this event were consistent with enhanced onshore transport of subarctic water induced by large-scale atmospheric forcing. Onshore transport leads to increases in coastal sea level and large-scale depression of the thermocline (Fig. 4); geostrophic readjustment to these changes causes enhanced poleward flow (Simpson 1983, 1984a). The 14°C isotherm marks the depth of the nutrient-depleted surface waters at this latitude (Fiedler et al., 1986). Depression of the thermocline rendered coastal upwelling ineffective and eliminated internal waves, critical sources of nutrients for kelps, from kelp forest depths.

The tropical ENSO event dissipated by early fall of 1983 (Kerr, 1983). However, the anomalous oceanographic conditions in the California Current system associated with this event persisted through 1984 (Simpson, unpubl. MS). The large-scale subsurface positive temperature and negative salinity anomalies (Simpson, 1984a) were very stable. In the absence of the major atmospheric events required to overturn the water column, these conditions persisted through the mild winter of 1983–1984 and became even warmer in 1984 with normal seasonal heating. Thus the temperature anomaly in 1984 was even greater than in 1983 (Figs. 3 and 4). Slow erosion
and storm mixing in the fall of 1984 led to near normal conditions by the end of 1984. The 1940–41 and 1957–59 El Niños also persisted longer off California than in the tropics (Simpson, unpubl. MS).

In the absence of a long-term record of in situ bottom temperatures in the kelp forest, the 66 years of sea-surface measurements collected from the Scripps Institution of Oceanography pier constitute the best available data set for evaluating temperature anomalies (North, 1985). List and Koh (1976) used digital filtering and covariance analysis to compare the pier and 10 m temperature records and found no correlation for high-frequency fluctuations (periods of two weeks and less). High-frequency fluctuations largely represent thermocline motion and are local phenomena. There was a very high degree of correlation for intermediate (two weeks to three months) and low-frequency (greater than three months) events, both between the pier and 10 m temperature records and between areas of the southern California Bight (List and Koh, 1976). Because ENSO events are clearly low-frequency, large-scale events, this temperature record is appropriate. The pier sea-surface temperature data for 1982–1985 in relation to the 63-year (1920–1982) mean are shown in Fig. 3.

V. STORM EFFECTS ON KELP FORESTS

The surface manifestations of the storms were dramatic. The Macrocystis canopy along the Palos Verdes Peninsula near Los Angeles declined from 196 ha on January 7, 1983 to 18 ha by January 31 (Wilson and Togstad, 1983). The Point Loma canopy was reduced from over 600 ha in fall of 1982 to less than 40 ha. Aerial surveys indicated similar results from Point Conception to Isla Asuncion, Baja California, the worst condition of the kelp resource in the 54-year history of the local kelp harvesting company (R. McPeak, Kelco, pers. comm.).

In addition to canopy loss, there were two major types of storm damage to Macrocystis: (1) holdfasts ripped off the substrate by large swells, and (2) entanglement of attached plants with drifting plants and holdfast bundles causing extensive to complete loss of stipes. The recovery of plants damaged but not killed by the storms appears to have been retarded or precluded by the warm, nutrient-poor water associated with the El Niño. The water column averaged 16°C during the stormy period of January through March of 1983, a critical elevation in terms of nitrate availability (Jackson, 1977, 1983; Zimmerman and Kremer, 1984).

Our studies of storm damage were designed to test predictions regarding relative severity of effects on surface canopies versus understory species and damage as a function of depth and location in the Point Loma forest. Diving surveys (see Fig. 5 for the location of our study sites) revealed that the
Mortality, indicated by densities of extant plants and recently killed holdfasts or holdfast scars in areas of 960 to 1440 m², was highest (66%) on the shallow, inner margin of the forest and decreased with depth (Fig. 5). Mortality at the northern and southern ends of the forest was considerably higher than at the central station of the same depth (Dayton and Tegner, 1984a). Two- and three-year-old *Macroystis* survive better than other ages at Point Loma (Dayton et al., 1984). In the winter of 1975–1976, mortality of two-year-old plants in a 400 m² area in the central part of the kelp forest was 6% (N = 84); during the following, more severe winter, mortality of the same cohort of now three-year-old plants was
21% \( (N = 38) \). In the winter of 1981–1982, mortality of two-year-old plants in the same area was 7% \( (N = 56) \), but the massive storms of 1982–1983 resulted in 44% \( (N = 48) \) mortality of the then three-year-olds (Dayton and Tegner, 1984a).

In contrast to the catastrophic effects on *Macrocystis*, storm effects on patches of understory species monitored since 1971 (Dayton et al., 1984) were moderate to nonexistent. Stipitate species were occasionally disturbed by drifting *Macrocystis* holdfast bundles, but there was no apparent damage to prostrate *Laminaria* or turf patches. In each case where an understory patch had bordered *Macrocystis*, the *Macrocystis* was gone or heavily disturbed and the lower standing guild patch had survived (Dayton and Tegner, 1984a).

In marked contrast to Point Loma, storm disturbances caused striking reversals of kelp forest community structure on Naples Reef, a small (2.2 ha), isolated reef near Santa Barbara (Ebeling et al., 1985). A severe storm in 1980 removed the *Macrocystis* canopy but spared most understory kelps. The supply of algal drift, which is largely *Macrocystis*, soon became limiting, causing sea urchins to leave their shelters and consume most living plants. The foraging urchins precluded algal recruitment and weakened the detritus-based food chain, especially the Embiotocid fishes. The storms of 1983 reversed the process because the exposed urchins were subject to the full force of the surge. With grazer populations greatly reduced and good conditions for recruitment and growth of kelps, normal community structure was soon re-established (Ebeling et al., 1985).

**VI. EVENTS SUBSEQUENT TO THE STORMS**

The spring of 1983 was a brief respite for the kelps at Point Loma. An increase in coastal upwelling to near normal levels (Fig. 4) dropped bottom temperatures in the kelp forest to about 13°C. *Macrocystis* plants which survived the storms formed a sparse surface canopy in late spring. The combination of large amounts of open space cleared by the storms, minimal canopy shading, and the appropriate temperature and light conditions (Dean and Deysher, 1983) led to massive recruitment of many species of algae in May.

There was some giant kelp recruitment at all five sites but we observed hundreds of juvenile *Macrocystis* per square meter at the shallower two sites where storm mortality (Fig. 5) had been highest. Another consequence of the storms was dispersal of algal reproductive material on scales far greater than observed from 1970 to 1982, when we collected dispersal data on the composition of recruits within patches and distance from presumed parent populations (Dayton et al., 1984). *Pterygophora* and *Laminaria* both
recruited heavily into areas formerly occupied by *Macrocystis*; however, the reverse was not observed. The most dramatic changes were seen in three species, *Desmarestia ligulata, Dictyopteris undulata,* and *Acrosorium uncinatum,* the first two of which had regularly been seen in low numbers around disturbed areas of our study sites in 1970–1982. A massive *Desmarestia* bloom dominated several hectares around our shallow site, *Dictyopteris* covered large areas of the two deeper central stations, and *Acrosorium* was abundant at the north and south stations. In past years, we had noted the relatively rare occurrences of these species as individual plants. However, McPeak (pers. comm.) reports that blooms of *Desmarestia* are common in barren areas after urchins have been removed. Thus El Niño effects on physical conditions, the structure of surviving *Macrocystis* populations, and scramble competition among competing species of algal recruits all appeared to affect the recovery of community structure at Point Loma.

Another facet of the storm damage at Naples Reef was extensive damage to the reef itself. Massive sections of the shale ridges were broken loose, exposing large areas of virgin rock. Harris *et al.* (1984) found more than ten times greater *Macrocystis* recruitment on these new surfaces than on old rock surfaces, where the presence of coralline algal crusts indicated that they had been in place before the storms. On the old surfaces, most foliage that developed was red algal turf, which apparently regenerated from basal fragments that survived the scouring. The new surfaces were covered with dense stands of filamentous browns. The longer filamentous browns facilitated the survival of *Macrocystis* recruits, apparently by hiding the small sporophytes from herbivorous fishes until the plants attained some refuge in size (Harris *et al.*, 1984).

In contrast to the benign spring, the warm El Niño summer and fall of 1983 had devastating consequences for the Point Loma kelp forest. Major upwelling events, defined as lasting more than six days with a maximum surface temperature reduction of more than 3°C from the long-term mean, usually occur twice a summer (Dorman and Palmer, 1981). Summer upwelling events are apparent in the temperature records for 1982 and 1985, but did not occur in 1983 or 1984 (Fig. 3). Bottom temperatures, measured above 16°C only on rare occasions in the past, were above 16°C from August through October of 1983 and went as high as 21.4°C. (We have had in situ recording thermographs at each site since 1983.) The normal thermocline was depressed to depths below the kelp forest (Dayton and Tegner, 1984a) eliminating nutrient input from internal waves. Surface temperatures were even warmer in 1984; with the exception of three brief excursions to the mean, surface temperatures were well above normal until November of 1984 (Fig. 3). Bottom temperatures were again anomalously high.

The *Macrocystis* canopy began to deteriorate during the summer of 1983 and by October, the tops of most plants were 6–8 m below the surface. Since
50% or more of the biomass of a healthy Macrocystis population is typically found in the upper 1 m of the water column (North et al., 1982), canopy deterioration could have a major impact on drift availability to herbivores. While Macrocystis tissue generally appeared healthier near the bottom, there was substantial mortality of adults which survived the storms. Mortality at Point Loma varied with depth and location (Fig. 6). The improved survival at the two end-of-the-forest stations may be a result of their positions; they face into longshore currents where they may be exposed to water not depleted of nutrients by the rest of the forest (Dayton and Tegner,
In 1975, a non El Niño year, summer mortality of two- and three-year-old *Macrocystis* at the 15 m site in the center of the forest was 14% \((N = 128)\) and 9% \((N = 45)\), respectively. In 1982, pre El Niño summer mortality of the two-year-old plants was 2% \((N = 52)\), and during the 1983 El Niño summer, mortality of the normally robust three-year-old plants was 59% \((N = 27)\) (Dayton and Tegner, 1984a).

Mean nitrogen content (measured as % dry weight), which typically ranges from 1 to 4% in southern California, can be used as an indicator of the nutritional status of *Macrocystis* (Gerard, 1982; North et al., 1982; North and Zimmerman, 1984). Gerard (1982) concluded that the critical level representing no nitrogen reserves for growth was an N content of 1.1% for laminar tissue. During a 20-month study of southern California kelp forests (1979–1980), North et al. (1982) found that the N content of canopy blades approached critical levels only once and basal blades not at all. *Macrocystis* at Point Loma had nitrogen reserves after the spring upwelling of 1983; basal blades (five blades averaged per determination) were 2.5 and 2.9% N and canopy blades 1.4 and 1.7% N at two sites in early July. By October 1983, major nitrogen depletion had taken place. Basal blades at the central and southern sites had dropped to 2% N but basal blades at the northern site had dropped to 1.1% N, Gerard's (1982) critical level. “Canopy” (collected as close to the surface as possible) blade averages, which dropped below critical level at all sites, ranged from 0.8 to 1.0% N.

Gerard (1984), working with an experimental population of adult *Macrocystis* at 11 m near Laguna Beach, reported other physiological changes during the summer of 1983. She attributed reductions in chlorophyll content and photosynthetic capacity of canopy blades to nitrogen starvation. Small fronds did not deplete their internal N reserves so their growth, normally dependent on the translocation of photosynthates from canopy fronds, was probably carbon limited. Finally, she suggested that slow growth before N or C content became limiting was due to temperature stress (Gerard, 1984).

There was poor survival of the massive spring *Macrocystis* recruitment at Point Loma, partly because of the heavy understory canopies which are known to interfere with giant kelp recruits (Dayton et al., 1984). The El Niño summer also affected the recruits because those *Macrocystis* which escaped the understory grew slowly, were discolored and often diseased, and by September, the fronds in many areas died 2 to 3 m above the bottom (Dayton and Tegner, 1984a). For example, recruitment at the shallow site was first observed in April but by September the mean plant size was only 137 cm (std. dev. = 61 cm, \(N = 60\)), poor growth for a species that can grow as much as 15 cm per day under optimal conditions (Neushul and Haxo, 1963). Some of these recruits survived to form canopy during the spring of 1984.

Growth of juvenile *Macrocystis* in coastal kelp forests of southern California is usually limited by irradiance (Dean and Jacobsen, 1984). Bottom
irradiance levels were significantly higher from 1982 through 1984 than in previous years (Dean and Jacobsen, 1986). Dean and Jacobsen (1986) used fertilizer experiments to demonstrate that low juvenile *Macrocystis* growth rates during the El Niño were due to nutrient limitation, not temperature stress. The clear water was apparently related to the southern California Bight-wide reduction in surface phytoplankton pigment concentrations as detected by satellite (Fiedler, 1984) and a deeper chlorophyll maximum layer (McGowan, 1985).

Water temperatures returned briefly to normal during November of 1983 (Fig. 3) and during the winter a *Macrocystis* canopy began to form. However, the surface warmed much faster in 1984 than 1983, and summer temperatures were higher than the year before. Deterioration began as early as June, when the per cent N of surface blades at three sites had dropped below Gerard’s critical value (including 0.5% at the shallowest site), and the canopy was largely gone by August. The effects of this El Niño on the *Macrocystis* canopy are apparent in the harvest records; in 1982, Kelco harvested 75% of its long-term average at Point Loma, but nothing was harvested in 1983, and only 9% in 1984, all at the beginning of the year (R. McPeak, pers. comm.).

Kelp forests in the lee of Santa Catalina Is. were protected from the storms but suffered perhaps the most severe effects of the warm summer and fall of 1983 in southern California (Zimmerman and Robertson, 1985). These forests depend upon vertical excursions of the thermocline for nutrient input. The depression of the 15°C isotherm to 50 m, more than twice as deep as 1981, effectively prevented the thermocline from reaching the lower limit of the kelp forest (20 m) on most excursions. Growth rates plummeted, the low rates of frond production were not able to keep up with frond losses at 7 and 10 m, plant sizes declined, and *Macrocystis* was extinct above 10 m by the beginning of November (Zimmerman and Robertson, 1985).

**VII. EFFECTS ON HIGHER TROPHIC LEVELS**

The decline and delayed recovery of many coastal kelp forests after the El Niño of 1957–1959 were associated with dense populations of sea urchins, especially red (*Strongylocentrotus franciscanus*) and purple (*S. purpuratus*) urchins (North and Pearse, 1970). These species normally feed on drift algae carried by water motion to their protected microhabitats in reefs and rock piles. When drift becomes limiting, hungry urchins leave their habitats to forage on attached plants (Dean *et al*., 1984; Harrold and Reed, 1985). Moving aggregations or fronts of urchins can denude large areas of kelp forest of all macro-algae, leaving only a pavement of encrusting coralline algae (the “barren areas” of Lawrence, 1975). Enough foraging urchins

There were three potential impacts of the storms and warm water on sea urchin populations, any of which could lead to further declines in kelp abundance: (1) substantial decrease in algal drift availability; (2) increase in sea urchin recruitment; or (3) decrease in sea urchin predation rates.

Gerard (1976) and Harrold and Reed (1985) demonstrated a seasonal cycle in drift availability; drift is more abundant in summer and fall when senescent fronds accumulate on the forest floor than in winter and spring when higher water movement increases export rates from the kelp forest. It is likely that most of the drift detached by the massive storms was washed out of the forest. We hypothesized that drift would be low during the rest of 1983 and during 1984 due to the reduction in algal standing stocks. Drift availability followed the seasonal cycle (Fig. 7). The quantity was about an order of magnitude less than Gerard (1976) observed at Monterey and similar to what Harrold and Reed (1985) found on San Nicolas Is. during non El Niño periods. No urchin fronts formed at any of our five sites. Much of the drift was decaying, heavily epiphytized *Macrocystis* suggesting that El Niño-induced canopy deterioration was making up for any potential decrease in drift production due to lower standing stock.
A second potential consequence of the storms was increased sea urchin recruitment. In previous years, red urchin recruitment (which we define as the proportion of the population in the zero-year age class) was highest at the outside edge of the *Macrocystis* canopy, or in the center of the forest after localized disruption of the canopy by storms (Tegner and Dayton, 1981). Elimination of the edge effect, after the storms devastated the canopy during the main period when urchins settle, created the potential for strong urchin recruitment throughout the bed. Instead, urchin recruitment was much lower than we have observed previously (Tegner and Dayton, 1981) and zero in some areas (Fig. 8). Complete canopy disappearance during the warm summers of 1983 and 1984 followed by partial recoveries the following winters continued to greatly minimize the edge effect compared to the pre El Niño canopy (Fig. 5) but urchin recruitment remained low in 1984 and only began to recover in 1985. Altered current patterns during these years may...
Fig. 9. Green abalone (*Haliotis fulgens*) gonad development during 1982–1983 from a site on the Palos Verdes Peninsula near Los Angeles. The gonad bulk index is a visual index developed by George Lockwood. The scale varies from 1, a spawned-out condition, to 6; spontaneous spawning has been observed at 3.5 or above. For consistency, all grading was done by one person. The curve for 1982 shows the two normal peaks of green abalone spawning. Variability is expressed as ± one standard error (Tegner, in press).

have been unfavorable for advection of these long-lived (30–50 days, Cameron and Schroeter, 1980) larvae. Furthermore, the extremely low nutrient concentrations, surface productivity, and zooplankton biomass in the waters of the southern California Bight during 1983 (McGowan, 1985) suggest that planktotrophic urchin larvae may have starved. With drift always available and no evidence of feeding fronts or a burst in urchin recruitment, it was not surprising that urchin abundances, as censused in 100 m² in each of our five sites, did not change significantly from spring 1983 to spring 1984.

The extended stormy period during the winter of 1983 also appears to have interfered with herbivore reproduction. Moderate surge conditions are optimal for the transport of drift algae to herbivores, but in very rough seas, drift may become impossible to catch (Shepherd, 1973). Abalones, like sea urchins, depend primarily on drift algae. We followed gonadal development of green abalones, *Haliotis fulgens*, living in a very shallow (4–6 m) kelp forest on the Palos Verdes Peninsula (Tegner, in press). The storms removed all attached *Macrocystis*; the abalones probably had little if any food from January until algal recruitment in May. Gonadal development in 1983 began later and remained low in comparison to the previous year (Fig. 9). While we did not monitor sea urchin gonadal development during this period, the roe yield of red urchins harvested by the commercial fishery was lower than normal, often to the point of making processing uneconomical, and many processors closed (Kato and Schroeter, 1985). Size-frequency distributions of red (*H. rufescens*) and pink (*H. corrugata*) abalones,
collected from a mid-depth (6–12 m) location at Palos Verdes in 1986, suggest that El Niño conditions affected the recruitment of these congenors differently (Fig. 10). There was a near absence of sizes corresponding to two- and three-year-old red abalones, animals which would have been spawned during 1983 and 1984; virtually all pink abalones were in these size categories. We speculate that these data reflect altered current patterns during the El Niño.

One of the most dramatic effects of the warm water was on starfish populations, especially the batstar, *Patiria miniata*. Apparent disease led to several episodes of mass mortality of *Patiria* in recent years. Dixon and Schroeter (unpubl. MS) interviewed researchers working at sites from San Diego to Carmel in order to determine the spatial and temporal pattern of the epizootics. The outbreaks began in shallow (<10 m) water in the southern part of the southern California Bight in 1978, a warm water year. (Water temperatures were warmer than normal from 1976 to 1984; Norton et al., 1985.) In 1981, a second outbreak devastated populations in deeper water and as far north as Santa Barbara. The disease reappeared during the El Niño, affecting populations as deep as 18 m and north to Diablo Canyon in central California (Dixon and Schroeter, unpubl. MS). Davis (1985) reports that *Patiria* numbers dropped an order of magnitude in three years.

**Fig. 10.** Size–frequency distributions of red (*Haliotis rufescens*) and pink (*H. corrugata*) abalones collected from Abalone Cove on the Palos Verdes Peninsula in 1986. The nearly inverse relationship of these data suggests that the El Niño affected recruitment of these species in opposing ways.
from over 1.43 per m² in 1982 to 0.86 in 1983 and 0.14 in 1984 in the Channel Islands National Park. Data from 1972 at Point Loma suggest a similar long-term decline of three asteroid species (Table 1). *Patiria* were present in very low numbers at 15 m in early 1983, disappeared by September and have not been re-observed on our transects. (Recruitment began with the onset of cooler temperature in 1985 but juveniles, found only under rocks, are not sampled by our transects.) At two deeper water (18 m) sites, where diseased *Patiria* were noted during the summer of 1983, densities subsequently decreased by 55 and 98%. Adult *Patiria* remain abundant in water deeper than 30 m. *Pisaster giganteus*, predators of molluscs, barnacles, and polychaetes (Morris *et al.*, 1980), declined at Point Loma (Table 1) and on the Channel Is. (Davis, 1985). *Dermasterias imbricata*, predators of purple sea urchins (Rosenthal and Chess, 1972), have also disappeared from mid-depths at Point Loma and are quite rare in deeper water.

Dixon and Schroeter's (unpubl. MS) laboratory experiments strongly suggest a relationship between the disease and temperature. During periods of disease, healthy *Patiria* will sicken and die in a few days at 18°C but animals in 15°C water remain healthy. Sick individuals will heal if placed in cold water. Disease also appeared to be implicated in a sea urchin die-off in shallow water at Santa Catalina Is. and some of the other warm water Channel Is. in the fall of 1984 (Dixon and Schroeter, unpubl. data; Tegner, pers. obs.). Mass mortality of diseased urchins off Nova Scotia, Canada was reported during years of record high sea-surface temperatures (Scheibling and Stephenson, 1984).

*Patiria* appear to control the distribution of the white sea urchin, *Lytechinus anamesus*, generally restricting this small echinoid to areas outside of kelp forests (Schroeter *et al.*, 1983). Concurrent with the *Patiria* die-offs, the Channel Islands monitoring program found that *Lytechinus* numbers increased from 0.97 per m² in 1984 to 8.27 per m² in 1985 (Davis, 1985). Destructive grazing by *Lytechinus* in 1985 has been reported from Channel Is. (Davis, pers. comm.), Palos Verdes (Wilson, pers. comm.), and San Onofre (Dixon and Schroeter, unpubl. MS) kelp forests of southern California. Before the effective loss of *Patiria* (densities declined from 1–2 per m² in 1981 to near zero in 1983) in the San Onofre kelp forests of

### Table 1

Asteroid densities from central Point Loma (15 m), 1971–1985. Data represent number per square meter from a sample of 400 m².

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td><em>Patiria miniata</em></td>
<td>0.23</td>
<td>0.005</td>
<td>0.005</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Pisaster giganteus</em></td>
<td>0.22</td>
<td>0.11</td>
<td>0.04</td>
<td>0.05</td>
<td>0.09</td>
<td>0.06</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td><em>Dermasterias imbricata</em></td>
<td>0.08</td>
<td>0.03</td>
<td>0.01</td>
<td>0.02</td>
<td>0.01</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
northern San Diego County, the community role of *Lytechinus* was to limit kelps by grazing on small stages, thereby reducing successful recruitment (Dean *et al.*, 1984). After a combination of recruitment and migration increased the *Lytechinus* abundance within the kelp forest, their community role changed. Grazing on adult *Macrocystis* led to giant kelp mortality and created a spatial refuge for competitively inferior understory species. These changes may be long lasting if *Lytechinus* continues to prevent *Macrocystis* recruitment (Dixon and Schroeter, unpubl. MS). To date, *Lytechinus* are rare at our Point Loma study sites but have been observed in high numbers at other areas near the south end of the bed (McPeak, pers. comm.).

The most important predators of red and purple sea urchins in southern California are spiny lobsters, *Panulirus interruptus*, and the labrid fish *Semicossyphus pulcher*, commonly called the California sheephead (Tegner and Dayton, 1981; Tegner and Levin, 1983; Cowen, 1983). Both species have their center of abundance in Baja California, and southern California is near the northern boundary of both distributions. Spiny lobsters recruit into very shallow (0-4 m) waters and enter kelp forests when they get older (Engle, 1979); the general impact of the El Niño on their recruitment is not yet known. Cowen (1985) reports that spiny lobsters showed strong recruitment success at San Nicolas Is. in 1983 after little or no success in the previous four years. Sheephead recruitment reached Monterey in 1983, nearly 250 km north of their normal range, and was very strong in areas below the northern range limit which do not receive regular recruitment. As sheephead live for 20-25 years in these areas (Cowen, 1985), the recruitment effects of this El Niño on kelp forest community structure may be long lived.

The physical events of the 1982-1984 El Niño and their effects on southern California kelp forest communities are summarized in Table 2.

**Table 2**

Summary of the effects of the 1982-1984 El Niño on Southern California kelp forest communities.

<table>
<thead>
<tr>
<th>Physical events</th>
<th>Effects on kelp forest communities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unprecedented series of large storms</td>
<td>Loss of <em>Macrocystis</em> canopy, considerable <em>Macrocystis</em> mortality, provision of open space</td>
</tr>
<tr>
<td>Relative normal spring upwelling</td>
<td>Outstanding recruitment of <em>Macrocystis</em> and many other species</td>
</tr>
<tr>
<td>Extraordinarily warm summer-fall water temps</td>
<td>Nutrient depletion leading to loss of <em>Macrocystis</em> canopies, considerable mortality and reduced growth rates</td>
</tr>
<tr>
<td>Elevated sea level and depressed thermocline</td>
<td>Nutrient input from coastal upwelling and thermocline motion effectively ceases</td>
</tr>
<tr>
<td>Unusually clear water</td>
<td>Normally light limited, <em>Macrocystis</em> growth becomes nutrient limited</td>
</tr>
<tr>
<td>Altered current patterns</td>
<td>Effects on animal recruitment</td>
</tr>
</tbody>
</table>
VIII. PROSPECTS FOR RECOVERY

Sea-surface temperature finally returned to the mean in November of 1984 and was close to "normal" in 1985 (Fig. 3). *Macrocystis* canopy development followed quickly in most areas of southern California. A notable exception was the stretch of mainland coast west of Santa Barbara, an area protected from most swell activity. These extensive forests were based on a different form of giant kelp, similar to *M. angustifolia*, which produces a very large holdfast, sufficiently large to anchor the plant on sand in some areas. This form reproduces vegetatively as well as sexually (Neushul, 1971). Vegetative reproduction results in large holdfast systems which apparently act as settlement sites for spores. The massive storms of 1982–1983, out of a more westerly direction than usual (Seymour *et al.*, 1984), caused high mortality here as elsewhere. But because these plants grew on unstable sediments, the loss of most holdfasts has left minimal substrate for recruitment. There has subsequently been some recruitment but density is very low (C. Barilotti, D. Glanz, R. McPeak, Kelco, pers. comm.). Recovery here is likely to take many years. W. North (pers. comm.) reports that this variety of *Macrocystis* used to form a continuous forest from Dana Point to San Mateo Rocks in Orange County, a semiprotected stretch of coastline which is largely sand. The forest disappeared during the 1957–1959 El Niño and this form of *Macrocystis* is no longer found in the area.

The massive recruitment of understory algae and two subsequent summer–fall losses of the *Macrocystis* canopy led to the possibility of El Niño-induced changes in kelp community composition. While established stands of understory kelps have considerable resistance to invasion by giant kelp (Dayton *et al.*, 1984), *Macrocystis* rapidly grows above the lower standing species under conditions of scramble competition (Pearse and Hines, 1979; McPeak, 1981; Dayton and Tegner, 1984a; Reed and Foster, 1984). Repeated disturbances of the giant kelp appear to be necessary for understory species such as *Pterygophora* to form a canopy sufficiently dense to inhibit further algal recruitment (Reed and Foster, 1984). Two canopy losses were not adequate disruptions of *Macrocystis* for *Pterygophora* recruits to establish a dense canopy at Point Loma; apparently, the shortened giant kelp plants continued to preempt most of the light. When we compared *Pterygophora* populations under *Macrocystis* with those in a large clearing where the giant kelp was completely removed, it took about a year for the *Pterygophora* in the clearing to establish a canopy dense enough to inhibit further algal recruitment. The *Pterygophora* under *Macrocystis* grew at about one-third the rate of the plants in the clearing, put almost no energy into reproduction and had a significantly higher mortality rate (Tegner *et al.*, in prep.). Similarly, the Channel Is. monitoring program observed a peak in
understory percent cover of 79% in 1983, which rapidly declined to 39% in 1984, and 19% in 1985 (Davis, 1985).

While *Macrocystis* retained its competitive dominance during this period, an apparent secondary effect of the El Niño raised havoc with algal populations at Point Loma in 1985 (Tegner et al., in prep.). With minimal storm activity and cool temperatures, the winter of 1985 was very favorable for kelp growth. However, the canopy which formed soon began losing ground to an infestation of grazing amphipods, especially the kelp curler, *Amphithoe humeralis*. Grazing damage occurred throughout the 10 km forest but large areas of the southern end of the forest were completely denuded of algae. Amphipod outbreaks were also observed in coastal forests west of Santa Barbara (R. McPeak, pers. comm.) and near Point Dume (M. Tegner, pers. obs.). The amphipod species were not exotic; all are found in healthy kelp forests. The most likely explanation was a reduction in the populations of fishes which feed on kelp-associated invertebrates, especially the kelp surf perch (*Brachyistius frenatus*). *Brachyistius* are closely associated with the *Macrocystis* canopy and populations may sharply decline or disappear entirely during decreases in kelp density (Coyer, 1979; Ebeling et al., 1980); the canopy at Point Lorna was lost three times in a two-year period. The *Macrocystis* canopy declined from 632 ha in January 1985 to 275 ha in July, almost a 60% reduction during the seasons when the canopy should have been increasing in area and density. As a result, Kelco's Point Loma harvest for 1985 was only 31% of an average year (R. McPeak, pers. comm.).

**IX. DISCUSSION**

The ENSO event of 1982–1983 produced clear physical and biological signals along the west coast of North America as far north as Alaska (see papers in Wooster and Fluharty, 1985; Mysak, 1986). Fiedler (1984) and McGowan (1985) documented the profound effects in the California Current system: pronounced deepening of the thermocline, significant warming of the mixed layer, weakened coastal upwelling, altered surface currents, reduced productivity and a deep chlorophyll maximum layer, and greatly reduced macrozooplankton biomass. Not surprisingly, these changes were reflected in commercial fish landings; catches of chinook salmon, market squid, crab, shrimp, and other species were down by 70% or more in 1983 (McGowan, 1984). However, this depression was partially offset by great increases in the catch of warm-water species such as albacore, yellowtail, yellowfin and skipjack tuna, marlin, dorado, etc. The northern anchovy of the California Current is an ecological analog of the Peruvian anchoveta; both are relatively small, short-lived, pelagic planktivores in highly variable
eastern boundary currents (Fiedler et al., 1986). Similar to the anchoveta (see Arntz, 1986), the El Niño affected the growth, spawning range, fecundity, and early larval mortality of the northern anchovy. However, due to strong recruitment of the 1984 year class, stock size of the minimally exploited anchovy returned to pre El Niño levels in 1985 (Fiedler et al., 1986). Evaluation of these physical and biological consequences of El Niños has been possible because of the 37 years of the California Cooperative Fisheries Investigations (see McGowan, 1985) and long-term fisheries data.

In contrast, there are very few examples of long-term data for benthic systems. The effects of this El Niño on intertidal algae in southern California were ambiguous; Gunnill (1985) was unable to find a uniform response in seven species of macro-algae. There was considerable mortality during the storms and warm-water episodes but net recruitment by some species was relatively high. He suggested that elevated sea level and fall cloud cover may have mitigated the effects of the El Niño. Similarly, Paine (1986), in a relatively long-term study, was unable to distinguish any changes in the rocky intertidal on the Washington coast from background variability. We speculate that intertidal species, adapted to a variable, more rigorous environment than the subtidal, are better equipped to deal with El Niños. Interestingly, the Peruvian intertidal was dramatically affected in 1983; apparently the extremely high temperatures (10-11°C above normal) killed the barnacles and invertebrate grazers and released the algae (Arntz, 1986).

The effects of the 1982–1983 El Niño on California kelp forest communities varied both locally and regionally. With the exception of the lee side of Santa Catalina Is. (Zimmerman and Robertson, 1985), the storms caused massive damage to forests from San Diego (Dayton and Tegner, 1984a) in the south, to Palos Verdes (Wilson and Togstad, 1983), Naples Reef (Ebeling et al., 1985), and San Nicolas Is. (Harrold, 1985) in southern California, to Diablo Canyon (Kimura, 1985) and the Monterey Bay region (M. Foster, J. Roughgarden, pers. comm.) in central California. While canopy loss was essentially complete, island sheltering of storm waves may have minimized *Macrocystis* mortality in some areas, especially where the islands are very close to shore (Pawka et al., 1984). Negative impacts of the warm summer temperatures, however, were considerably more limited; the major effects were reported from Santa Catalina Is. (Zimmerman and Robertson, 1985) and along the southern mainland coast from Laguna Beach (Gerard, 1984) to San Diego (Dayton and Tegner, 1984a). In part, the differences can be attributed to temperature decrease with latitude. Comparing Fig. 3 with the 1983 temperatures from Naples Reef (Ebeling et al., 1985, Fig. 2), it is apparent that while values were well above normal for that location, both the magnitude and the duration of the warm event at Santa Barbara were considerably less than at La Jolla, some 300 km to the south. In part, the differences can be attributed to ocean circulation.
patterns. Santa Catalina Is.'s position in the southern California Bight is within the area affected by an intrusion of warm, southern, offshore water every year during summer, fall, and winter and is consistently warmer than the adjacent mainland. In contrast, San Nicolas Is., which is offshore and slightly to the south of Santa Catalina Is., lies within an area of the California Current which is consistently colder and more eutrophic (Pelaez and McGowan, 1986). At Santa Catalina Is., the El Niño associated depression of the thermocline and the temperature anomaly added to an already warmer than average environment for *Macrocystis*, leading to the worst El Niño summer effects on kelps reported (Zimmerman and Robertson, 1985). There are no temperature data available from San Nicolas Is., but the rapid recovery of *Macrocystis* after the storms suggests that serious nutrient depletion did not take place (Harrold, 1985). Finally, some of the differences may be ascribed to anthropogenic influences. Water temperatures offshore of the Palos Verdes Peninsula were anomalously warm for an extended period of 1983 but *Macrocystis* flourished (Tegner, unpubl. data). B. Jones (pers. comm.) has recently found high concentrations of NH₄ from the nearby Los Angeles County sewage outfall in kelp forest depths during summer thermally stratified conditions.

Storm damage to *Macrocystis* populations in central California was so severe that in many cases, *Nereocystis leutkeana*, an annual surface canopy former which competes with giant kelp, was able to greatly expand its patch boundaries (Kimura, 1985; M. Foster and G. Van Blaricom, pers. comm.). Kimura (1985) reported that *Nereocystis* populations near Diablo Canyon senesced prematurely during the 1983 El Niño. Diablo Canyon is about the southern range boundary for this species (Abbott and Hollenberg, 1976), so warm-water effects on *Nereocystis* were not surprising. *Macrocystis*, while more susceptible to wave stress than *Nereocystis*, is the competitive dominant, so given adequate sporogenic material and minimal storm activity, is likely to re-establish pre El Niño community structure in the near future (Dayton et al., 1984).

The relevance of El Niños to kelp forest community structure must be related to recurrence rates. Using historical data for evidence of tropical ENSO-type events, Quinn et al., (1978) found an average of 12-3 years between the onsets of strong events and 5-4 years between the onset of strong and moderate El Niños; adding weak events dropped the interval to 3-7 years. While not all tropical El Niños are reflected in the California Current (Chelton et al., 1982), there are mid-latitude warm events which do not occur in concert with tropical El Niños (Simpson, 1984b; Norton et al., 1985). Using the criterion of a minimum time of one month of Scripps pier temperature ≥0.5°C above the 63-year mean (Fig. 3), North (1985) classified one-third of the 1955-1984 period as warm water. There were 33 separate warm-water events, of which seven events lasted six months or more and two
lasted 15 months. Thus warmer than normal periods are a regular feature of the California coastal environment. The effects on kelp community structure will depend upon the season of the warm period (e.g., given the normal summer stress on *Macrocystis*, warm-water events then are more serious than a similar temperature elevation in winter), and the duration and magnitude of warming (North, 1985).

Major storms are another factor strongly affecting the results of warm-water periods on kelp community structure. Seymour *et al.* (1984) found a highly significant correlation between strong El Niños and large wave events in southern California. However, not all El Niños result in large wave events. During 1982–1983, the Aleutian low was not only unusually deep (similar to many El Niño winters), but the low was, on average, large enough in areal extent and displaced eastward sufficiently to affect California (Seymour *et al.*, 1984). During other El Niño winters, high pressure prevails along the west coast and storms generated in the North Pacific make landfall.
in Alaska and British Columbia. The El Niños of 1976–1977 and 1982–1984 were both marked by warm water off southern California but the former event was nearly storm-free (Namais and Cayan, 1984; Cayan and Flick, 1985).

Two major El Niños stand out in recent California history, the events of 1957–1959 and 1982–1984. Both were catastrophic-scale disturbances but the two events differed physically and had very different implications for kelp forest community structure. There were four wave episodes exceeding 3 m during 1957–1959; there were ten such episodes during the latter El Niño, an unprecedented record (Seymour et al., 1984). The former warm-water period was longer but the 1982–1984 event included a substantial period of unparalleled high sea-surface temperature anomaly (North, 1985). Because the large temperature anomalies exacerbated the effects of the storms, we believe the recent El Niño to be the larger disturbance, but many coastal kelp forests showed strong recoveries in 1985, something that took several years in the 1960s (Fig. 11). Two critical factors are different. First,
spiny lobsters and sheephead, the important predators of red and purple sea urchins in southern California, have been heavily fished for many years. Thus even small reductions in drift availability during 1957–1959 were likely to have been enough to push an already out-of-balance situation towards destructive grazing (Tegner, 1980; Tegner and Dayton, 1981; Tegner and Levin, 1983; Dean et al., 1984; Harrold and Reed, 1985). A red sea urchin fishery developed in the early 1970s (Kato and Schroeter, 1985) and has had a major impact on standing stocks of this species, the largest and most destructive of the California sea urchins. The role of urchin grazing was consequently much less in 1982–1984 than in 1957–1959. Second, waste water disposal practices of the 1940s and 1950s had led to substantial decreases in *Macrocystis* standing stocks in several coastal kelp forests, notably at Palos Verdes and Point Loma, before the El Niño of 1957–1959 (Wilson et al., 1977). The eventual recovery of these forests was facilitated by improvements in waste water treatment, kelp restoration and sea urchin control efforts, and the sea urchin fishery. Thus while the disturbances caused by the El Niño of 1982–1984 were larger, the destabilized kelp forests of the late 1950s were much more severely affected.

While attempting to integrate local ecological factors with the physical parameters of the 1957–1959 and 1982–1984 El Niños, it is important to remember that tropical ENSO events vary considerably in magnitude (Quinn et al., 1978). Furthermore, even the large-scale events may be very different from each other; recall that the recent El Niño was not preceded by an intensification of the trade winds, something formerly believed to be a necessary condition for an ENSO event (Ramage, 1986). Physical differences are also apparent in the California record. Both the 1957–1959 and the 1982–1984 events were characterized by very high temperatures, but the former had anomalously high salinity and the latter had anomalously low salinity water (McGowan, 1985). High-temperature, high-salinity water is consistent with transport from the south, but the only possible low salinity source is Pacific Subarctic water from the west (Simpson, 1984a). This suggests different physical forcing mechanisms. Simpson (1984a,b) argues that anomalous atmospheric circulation, an atmospheric teleconnection to the tropical ENSO event, produced the 1940–1941 and 1982–1984 California El Niños. However, there is biological evidence that planktonic larvae of southern species moved far to the north during 1983 (Cowen, 1985). Other physical oceanographers present evidence for both oceanic and atmospheric forcing of the recent event off the west coast of North America (Huyer and Smith, 1985; Norton et al., 1985; Reinecker and Mooers, 1986). Although there is clearly much to be learned about these large-scale oceanographic phenomena, we know that there are physical differences between events, and that different forcing mechanisms are likely to have very different biological ramifications.
Fig. 12. Summer sea temperatures 5 m below surface at La Jolla, California reconstructed from standardized tree ring indices for *Pseudotsuga macrocarpa* from 1214 m on the Santa Ana Mountains, California. Data from Douglas (1976, p. 188) were put into graphical form by Gerry Kuhn (Dayton and Tegner, 1984b).
Finally, from the biological perspective, the opposite side of the coin may be even more important to the California Current system. Anti El Niño years, characterized by strong southward transport, low sea level, reduced temperature and salinity, and high zooplankton abundance (Chelton et al., 1982), are years of high biological productivity. Indeed, Barilotti et al. (1984) have developed an index based on the depth of the 14°C isotherm which correlates with *Macrocytis* standing crop and two measures of ENSO activity, sea level and the Southern Oscillation index (Fig. 4). Ocean temperatures extrapolated from tree ring data (Fig. 12) suggest that in the decade to century time scales, these anti El Niños could also be very important to the entire coastal system.

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