

IS THERE EVIDENCE FOR LONG-TERM CLIMATIC CHANGE IN SOUTHERN CALIFORNIA KELP FORESTS?

MIA J. TEGNER, PAUL K. DAYTON, PETER B. EDWARDS, AND KRISTIN L. RISER

Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093-0201

ABSTRACT

Evidence for long-term natural change in coastal ecosystems has to be separated from the effects of intense anthropogenic impacts, especially in heavily populated areas. The kelp forests of southern California, highly productive ecosystems organized around the giant kelp, *Macrocystis pyrifera*, support a variety of fisheries, and the kelp is harvested for extraction of alginates. Because of the importance of *Macrocystis* itself to the diverse assemblage within the kelp forest community, research in this ecosystem has focused on changes in giant kelp populations. Canopy maps of the Point Loma kelp forest near San Diego illustrate major changes over the last century; these changes have been ascribed to a variety of different causes, including temperature. To understand the role of physical forcing on interannual variability in the *Macrocystis* canopy at Point Loma, we compared two 31-year kelp data sets with available physical records. Annual average surface temperature was significantly correlated with kelp harvest, but explained only 24% of the variance. Because the canopy of giant kelp is susceptible to disturbances that may not affect plant survival, we evaluated two subsurface measures—stipe number as an index of individual plant growth, and stipe density as a measure of carrying capacity. Both stipe measures were sensitive to interannual variability in surface temperature for the period 1983–95 and were more sensitive than plant survival. Plant size and carrying capacity were very low following 1992–93 El Niño conditions and the anomalously warm 1994. Comparison with historical stipe data from 1957, 1973, and 1974 indicates up to two-thirds reductions in standing biomass since 1957. There is a strong inverse trend between median plant size and the sums of anomalies in Scripps Institution of Oceanography Pier surface temperature, calculated quarterly for three years. It appears, however, that these large, interdecadal changes in biomass can be explained by the location of the data sets within multiyear warm and cold periods. We conclude that stipe numbers and stipe density—measures of individual plant size and carrying capacity—are useful tools for evaluating long-term change in *Macrocystis* populations within specific locations. Although limited by the paucity of historical observations, the sensitivity of stipe counts to surface temperature argues strongly for their incorporation into ongoing and future kelp forest research.

INTRODUCTION

Roemmich and McGowan's (1995) report of a 70% decrease in the biomass of macrozooplankton associated with warming of the surface layers off southern California since 1951 suggests that climatic warming may be strongly affecting productivity of the California Current region. Is there evidence for similar long-term change in the nearshore zone of southern California? Such a determination for the nearshore zone faces major confounding factors relative to offshore waters; the effects of climate change on coastal populations have to be separated from those of intense human exploitation, disturbance, and pollution. Further complications for detecting long-term change in the nearshore zone include very different life spans and time scales of some coastal organisms and communities relative to pelagic macrozooplankton. The coastal zone receives nutrients from some sources that may have little to no effect on the California Current; these sources include runoff, sewage discharge, and benthic topographic effects on turbulence and mixing. Even the spatial scale of coastally linked upwelling is within a few km of shore (Jackson 1986). Furthermore, nutrient availability will be different for fixed and free-floating plants; for example, internal waves, which constitute an important nitrogen source for giant kelps (Zimmerman and Kremer 1984, 1986; Zimmerman and Robertson 1985), are inherently less valuable to phytoplankton, which float within a water mass. The importance of coastally linked sources and processes affecting nutrients is supported by satellite studies showing a trend for high chlorophyll in the very near coastal zone in all seasons (Fargion et al. 1993). Thus, for several reasons, long-term change is likely to be more difficult to demonstrate in the coastal zone.

Nevertheless, Barry et al. (1995) reported a long-term shift in invertebrate species composition in a central California rocky intertidal community. Barry et al. relocated fixed quadrats established in the 1930s at Hopkins Marine Station in Pacific Grove, which has been closed to public access since 1917. The abundances of eight of nine species with southerly distributions increased significantly, and the abundances of five of eight northern species decreased significantly between 1931–33 and 1993–94; there was no trend for cosmopolitan species. Barry et al. associated the species shifts with a small,

0.75°C increase in annual sea-surface temperature and a larger, 2.2°C increase in summer temperature.

The kelp forests of southern California are highly productive nearshore ecosystems centered around the giant kelp, *Macrocystis pyrifera*. Kelp forests support sport and commercial fisheries for sea urchins, abalones, spiny lobsters, and various finfishes; the kelp itself is harvested for the production of alginates. Providing the preponderance of the primary productivity and three-dimensional structure to the kelp community, as well as considerable food to adjacent communities, *Macrocystis* is a key species for a diverse assemblage of invertebrates, fishes, and marine mammals. Thus research in this ecosystem has focused not on species composition but on changes in populations of *Macrocystis* itself.

Understanding patterns of productivity and long-term change in giant kelp populations presents a very different set of challenges than for phytoplankton. *Macrocystis* is a very large plant with complex morphology, a life history that involves alternation of generations, and a macroscopic sporophyte which can live for several years, leading to population cycles of three to four years. Macrophytes of rocky shores are generally adapted to vigorous water movement, which allows them to benefit from high levels of turbulent diffusion as well as coastal upwelling; these in turn permit high levels of nutrient uptake, photosynthesis, and growth (Mann 1982). *Macrocystis* forms an extensive surface canopy which allows it to outcompete lower-standing kelps for light but increases its susceptibility to storm damage (reviewed by Murray and Bray 1993). Thus both the morphology and the habitat of *Macrocystis* contribute to its dynamic nature; its populations are highly variable in space and time, and environmental forcing clearly plays a large role in this variability (Dayton and Tegner 1984a, 1990; Tegner and Dayton 1987; Dayton et al. 1992; Tegner et al.¹).

The health of *Macrocystis* populations in southern California has long been associated with temperature and nutrients. The widespread destruction of populations during 1958 and 1959 and the deterioration of surface canopies during warm summer/fall periods were attributed to long periods of water temperatures greater than 20°C (North 1971). The demonstration of the inverse relationship between temperature and nutrients (Jackson 1977; Zimmerman and Kremer 1984) led to experimental uncoupling of these factors. If nutrients are present, *Macrocystis* can tolerate temperatures at which damage has been observed in the field; both photosynthesis and nutrient uptake occur unimpeded above 20°C (reviewed by Murray and Bray 1993; North 1994). The

sensitivity of *Macrocystis* to higher-frequency temperature variation, notably El Niño–Southern Oscillation events (Dayton and Tegner 1984a, 1990; Tegner and Dayton 1987; Dayton et al. 1992; Tegner et al.²), may offer some insight into the future, allowing predictions of short-term responses to longer-term global warming (Peterson et al. 1993; Lubchenco et al. 1993).

Here we report changes to *Macrocystis* forests over the last century, evaluate several sets of physical data for their effects on two measures of the kelp canopy in the Point Loma forest near San Diego, propose and evaluate subsurface indicators of plant size and carrying capacity, and consider the evidence for long-term climatic change in giant kelp populations.

CANOPY HISTORY

Against the backdrop of inherent variability, there is well-known evidence for major changes in *Macrocystis* populations. Kelp's importance to sailors as an indicator of shallow water led to many recorded observations and canopy diagrams on nautical charts documenting the entrances to major ports. Concern over dependence on imports for potash—important to farmers for fertilizer and to the munitions industry of the early twentieth century—led to a survey of all kelp forests from Alaska to Baja California by the U.S. Department of Agriculture in 1911–12 (Crandall 1915). Sporadic and eventually annual aerial mapping illustrated long-term changes in canopy coverage. Comparisons of these early maps with recent surveys indicated overall declines of 30%–70% in canopy area of kelp beds in southern California since Crandall's surveys (reviewed by Foster and Schiel 1985). The decline has been attributed to many factors (e.g., Foster and Schiel 1985; Tarpley and Glantz 1992; Neushul and Neushul 1992) including grazing, fisheries on predators of grazers, storms, abnormal oceanographic conditions such as El Niño events, discharge of wastes (sewage, industrial, thermal, oil drilling), harbor dredging, competition for substrate, and different mapping techniques—all of which have to be filtered out of any consideration of long-term change in productivity. Furthermore, kelp has been harvested since 1911 (Tarpley and Glantz 1992); as for any natural resource, the harvest data reflect changing markets as well as natural disturbances and variable productivity.

The Point Loma kelp forest near San Diego, California, one of the largest *Macrocystis* forests in the world, is generally about 8–10 km long by 1 km wide. It is also one of the scientifically best known; the pioneering studies of Wheeler North and colleagues date back to the mid 1950s. North's Kelp Habitat Improvement Program continued until 1975, overlapping with research conducted

¹Tegner, M. J., P. K. Dayton, P. B. Edwards, and K. L. Riser. Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. MS submitted to Mar. Ecol. Prog. Ser.

²Ibid.

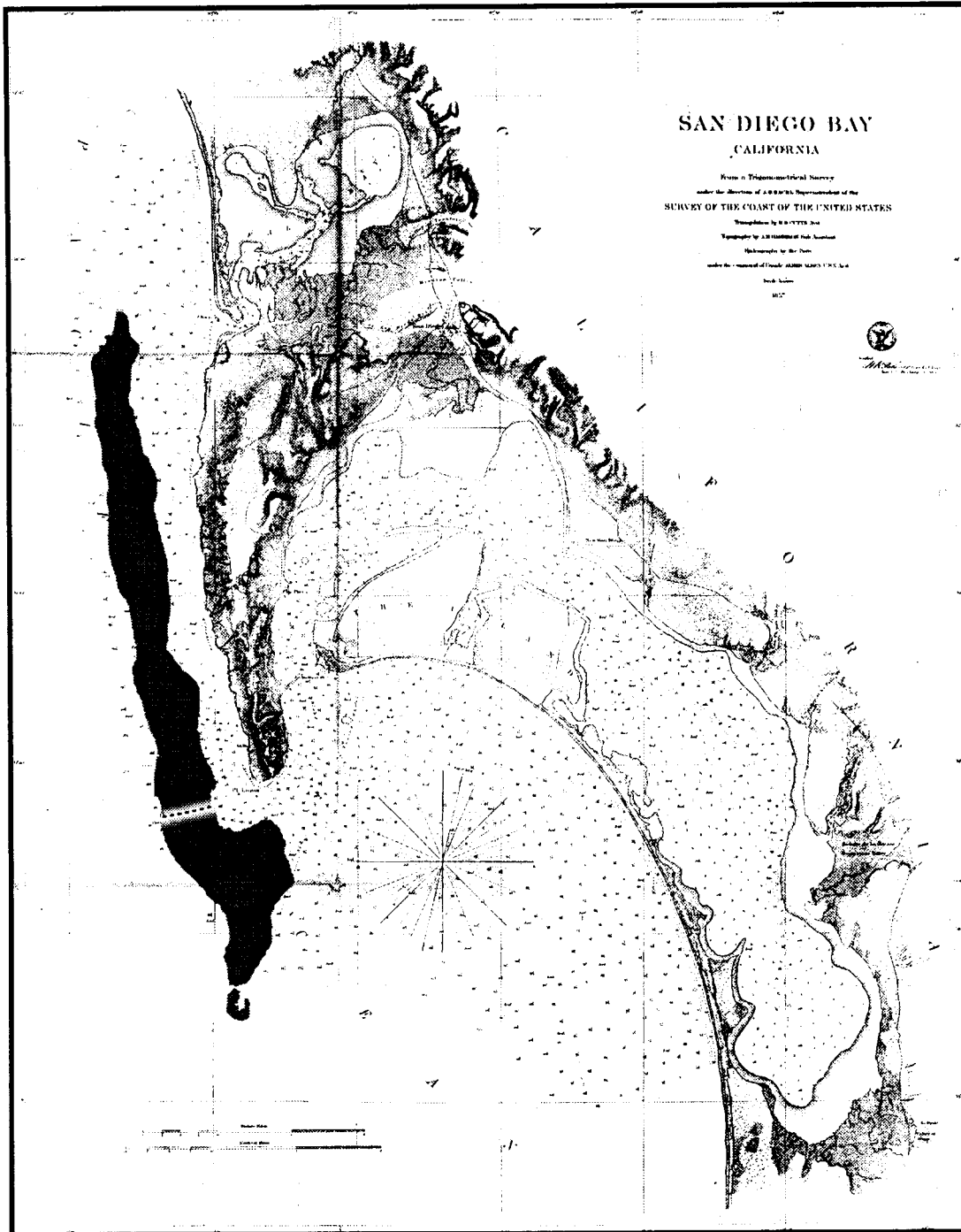


Figure 1. Point Loma in 1857, after a United States Coast Survey chart; the kelp canopy has been shaded to increase its visibility.

by Kelco—the San Diego-based harvesting company—and Scripps Institution of Oceanography (SIO), which began in 1970. Point Loma's proximity to Kelco has led to steady, maximal rates of harvest (the upper four feet is harvested up to three times a year), and the presence of San Diego's sewage outfall has ensured annual photographic assessments of canopy cover for regulatory purposes since 1964.

An 1857 chart of the San Diego Bay region by the United States Coast Survey (figure 1) with sailing directions describes a *Macrocystis* canopy extending three miles south of the tip of Point Loma. Crandall (1915) mapped a similar canopy extent in 1911, but by 1949, the Point Loma kelp forest exhibited considerable decline, which culminated in virtual disappearance of the canopy in the late 1950s–early 1960s (figure 2). The dis-

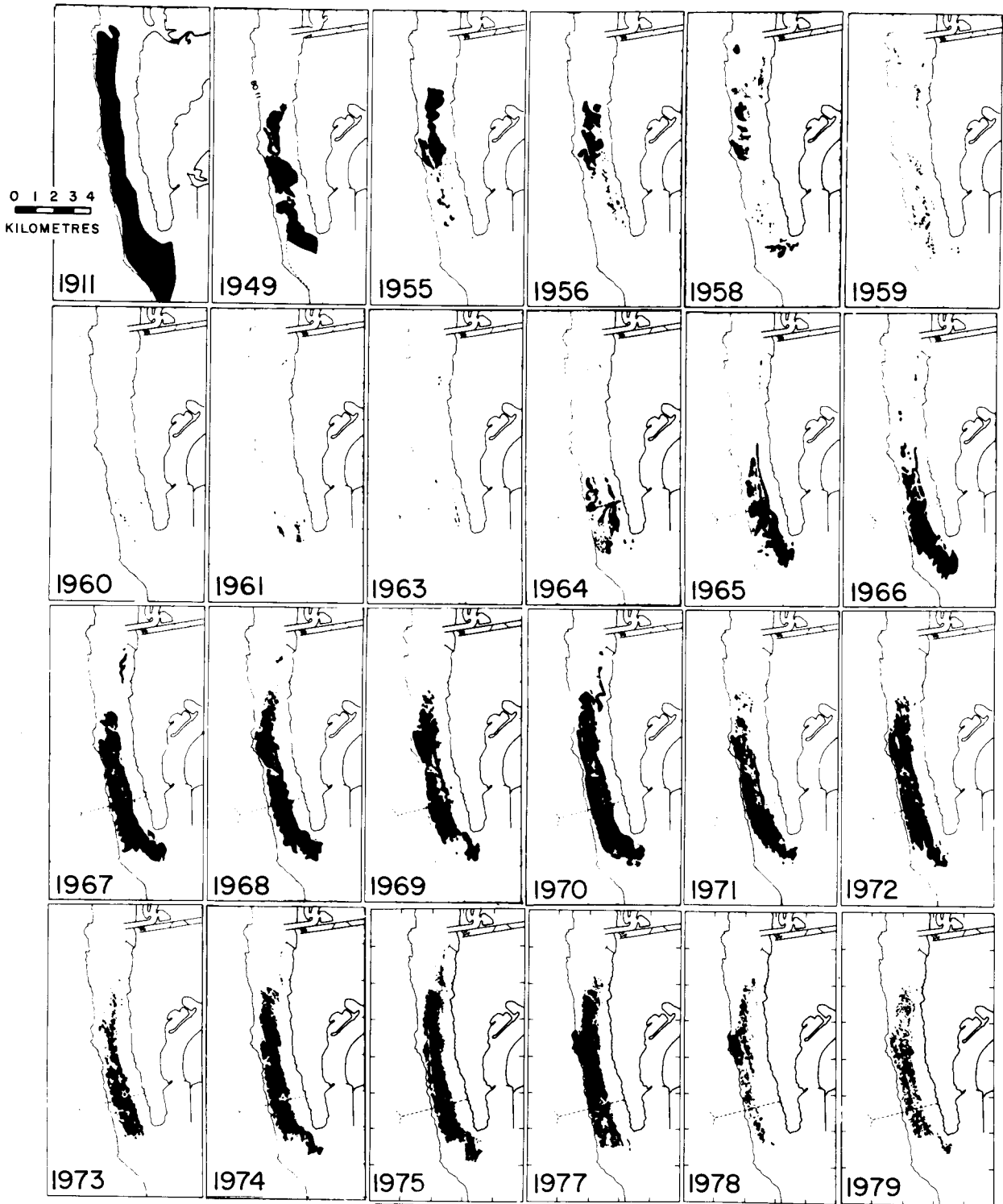


Figure 2. Montage of canopy maps of the Point Loma kelp forest assembled by Wheeler North (see North et al. 1993 for methods). Note the changes in vertical and horizontal extent after 1980. Mission Bay is a recreational bay to the north of the kelp forest; its entrance channel and the westernmost portion of the bay are visible at the top of each panel. The entrance to San Diego Bay, a large natural harbor, is south of the kelp forest and east of the tip of the Point Loma peninsula; the Zuniga jetty forms the eastern boundary of the entrance channel. The Point Loma sewage outfall, the dotted line crossing the kelp forest, was constructed in 1963. Figure 2 continues on next page.

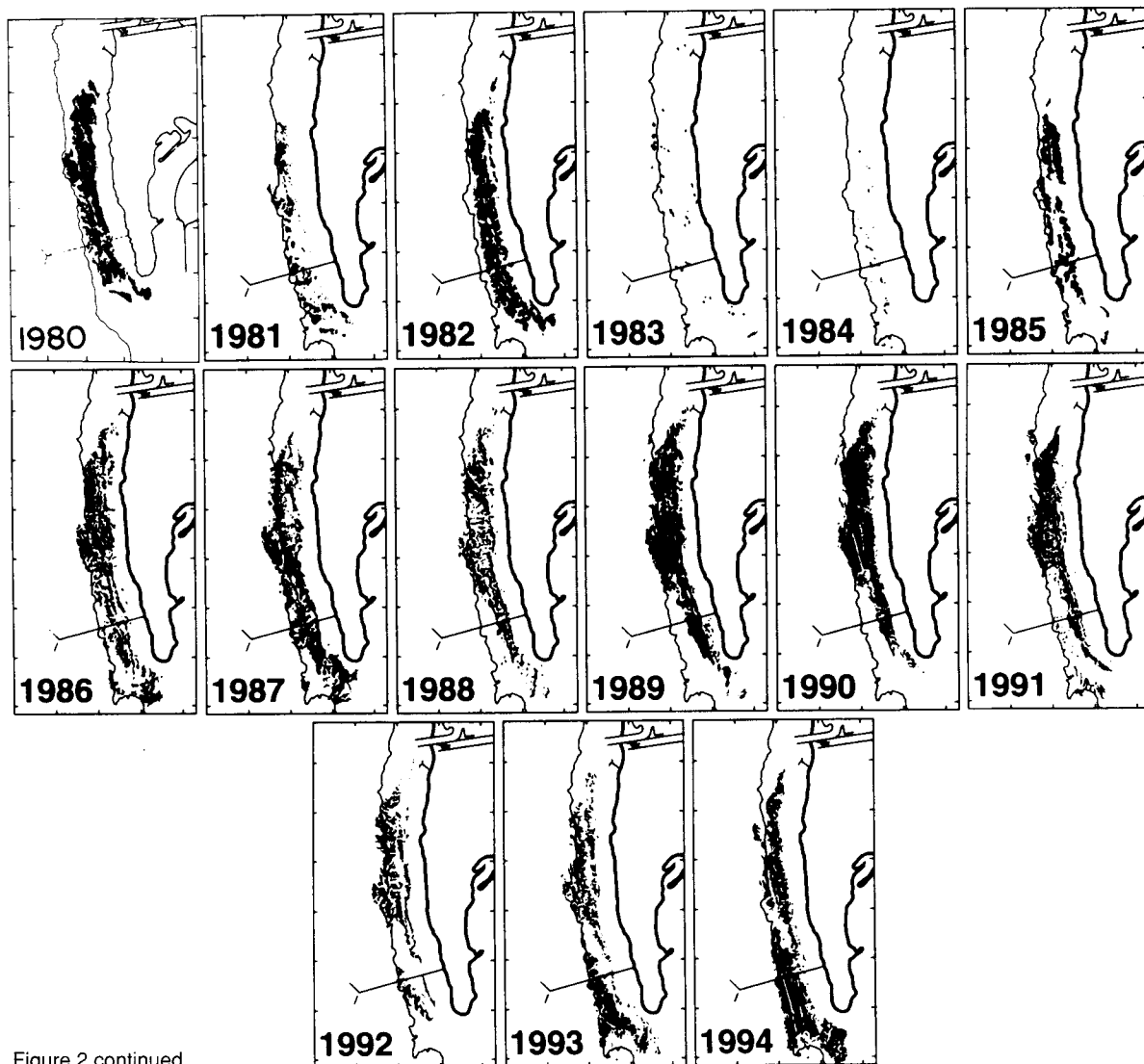


Figure 2 continued

appearance was attributed to intense grazing by sea urchins, the 1957–59 El Niño, and the discharge of poorly treated sewage in San Diego Bay (reviewed by Tegner and Dayton 1987, 1991).

Recovery began after the sewage outfall was moved to a deepwater, offshore location, and kelp restoration efforts began controlling sea urchin populations. There was considerable regrowth, and the *Macrocystis* canopy was relatively stable in the late 1960s–1970s; the sea urchin fishery that began in the 1970s contributed to this stability. The 1980s were marked by the massive 1982–84 El Niño and the 200-year storm of 1988, but the canopy recovered quickly from these natural disturbances. Although the size of the forest has grown considerably from its low points, the Point Loma canopy has not approached the northern or southern maximum extents of 1857 or 1911; these may be permanent changes

related to the dredging of Mission and San Diego Bays, and the effects of the Zuniga jetty on tidal outflow from San Diego Bay (see figure 2).

ENVIRONMENTAL CORRELATES OF KELP CANOPY

Kelp Harvest vs. Canopy Area

In an effort to understand the role of physical forcing on interannual variability in the *Macrocystis* canopy at Point Loma, we compared two long-term (1964–94) data sets—annual harvest and annual maximum canopy area—with various long-term physical records. Point Loma kelp harvest data for 1964–94 were provided by D. Glantz of Kelco, a unit of Monsanto Company. To protect proprietary information, the maximum harvest year of this time series (1972) was treated as 100%, and other years were scaled accordingly. Approximate annual

maximum kelp-canopy coverage data from Point Loma were compiled from aerial photographs by W. J. North (see North et al. 1993 for methods).

Surface and 5-m depth temperatures were collected daily on the SIO Pier; in situ bottom temperatures were collected from the 18-m Central site at Point Loma (Dayton et al. 1992). Monthly Secchi disk data (a measure of near-surface transparency) from three sites along the outer edge of the Point Loma kelp forest, and annual mass emission rates from the Point Loma wastewater treatment plant were provided by the City of San Diego. A significant ($p = 0.02$) degree of concordance was found to exist through time among the three Secchi disk stations by testing with Kendall's concordance test (Zar 1984). A Kruskal-Wallis test showed that the Secchi depths at the three sites did not differ ($p = 0.12$), so the data were pooled to calculate annual averages. Wave data from the Mission Bay buoy (lat. $32^{\circ}45.9'$, long. $117^{\circ}22.5'$, about 13 km offshore of the entrance to Mission Bay) were collected by the Coastal Data Information Program. Seymour et al. (1985) detail the data-gathering system and analysis techniques. Significant wave height is defined as the average of the one-third highest waves. Sea-level data for San Diego Bay were downloaded off the Internet from the Integrated Global Ocean Services System (IGOSS) at the University of Hawaii, courtesy of G. T. Mitchum and K. Wyrki. Anomalies were calculated from the 1975-to-1986 mean annual cycle of sea level and corrected for the inverted barometer effect by IGOSS.

Simple linear regressions were used to compare kelp harvest data with canopy coverage data, and to determine the effect of environmental variables on the kelp forest, with kelp harvest as the dependent variable. In each case, untransformed data met the assumptions of regression analysis. Because these data sets varied in length from 11 to 31 years, individual regressions were run to make use of all available data; this represents more testing than optimal, but appears to be the best way to extract the most information.

To determine the more appropriate measure of *Macrocystis* for these analyses, we compared time series data of annual kelp harvest with the approximate annual maximum canopy coverage (figure 3). Harvest data have the advantages of integrating growth over a longer period and of less measurement subjectivity. Areal coverage offers better spatial information, but is a snapshot in time and a poor indicator of canopy density. The two measures are significantly correlated ($r^2 = 0.343$, $p = 0.0005$), but there are differences in maximal years and in the relationship between harvest and coverage. The highest canopy coverage in this time period occurred in 1994, but that year's harvest was relatively low, probably because of warm surface temperatures. In contrast,

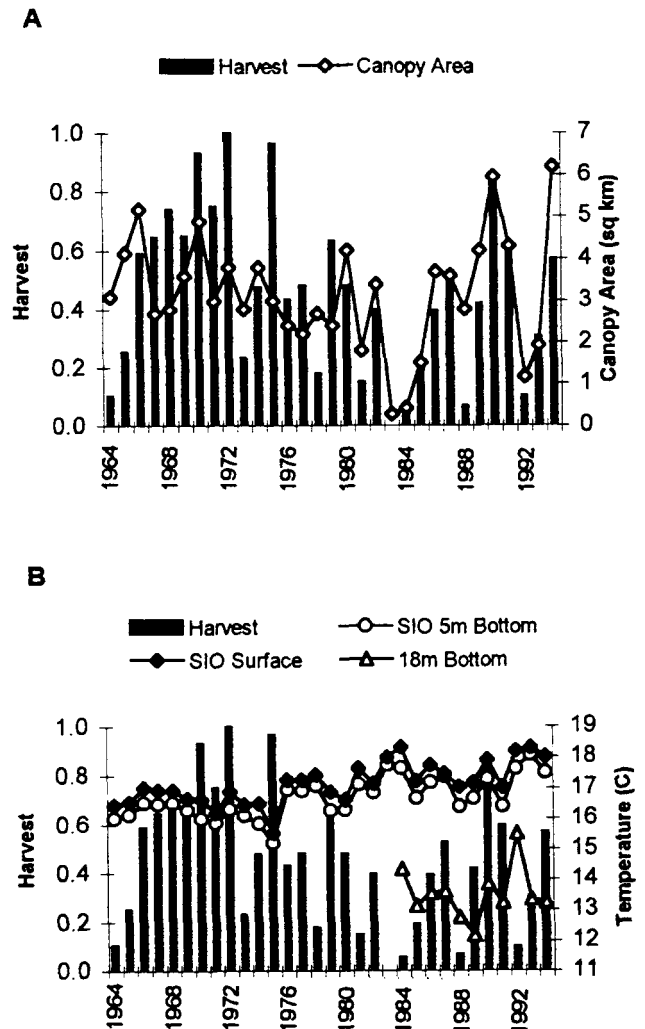


Figure 3. A, Comparison of kelp harvest data with canopy coverage, 1964–94. B, Relationship between kelp harvest data and the SIO Pier surface temperature 1964–94, SIO Pier 5-m temperature 1964–94, and 18-m in situ bottom temperature 1984–94. Harvest is scaled to the maximum year in this time series—1972.

surface temperatures were relatively cool in the late 1960s through the mid-1970s (e.g., Smith 1995), when harvest rates were high relative to canopy cover. Because of the strong inverse relationship between temperature and nutrients (Jackson 1977; Gerard 1982; Zimmerman and Kremer 1984), we compared both harvest and canopy coverage with surface temperature; both kelp-canopy measures were significantly ($p = 0.005$ and 0.019 , respectively) negatively correlated with surface temperature. Because of the advantages discussed above and because surface temperature explained more of the variance in harvest data ($r^2 = 0.24$ vs. 0.17), we chose to use harvest data for further comparisons.

Kelp Harvest vs. Physical Parameters

Two measures of subsurface temperature were examined: the daily determination at 5 m from the SIO Pier

TABLE 1
 Results of Simple Regressions of Relative Kelp Harvest (% 1972), SIO Surface Temperatures, SIO 5-m Bottom Temperatures, and 18-m Bottom Temperatures on Various Environmental Factors Using Yearly Means, Totals, or Maxima

Variable	N*	Intercept	Slope	R ²	P
Harvest					
Canopy area	31	0.083	0.118	0.343	0.0005
SIO surface temperature	31	3.997	-0.207	0.237	0.0050
SIO 5-m bottom temperature	31	4.022	-0.214	0.239	0.0052
18-m bottom temperature	11	1.258	-0.066	0.050	0.5067
Secchi depth	18	0.504	-0.006	0.010	0.6981
Mass emissions	30	0.853	-0.001	0.078	0.1361
Max sig wave height	12	0.538	-0.001	0.054	0.4687
Sea-level anomaly	20	0.394	-0.004	0.231	0.0300
SIO surface temperature					
SIO 5-m bottom temperature	60	0.5915	0.935	0.787	0.0000
18-m bottom temperature	11	10.747	0.507	0.502	0.0147
Sea-level anomaly	20	17.342	0.014	0.466	0.0009
SIO 5-m bottom temperature					
18-m bottom temperature	11	12.149	0.371	0.331	0.0640
Sea-level anomaly	20	16.939	0.014	0.559	0.0002
SIO 18-m bottom temperature					
Sea-level anomaly	11	13.399	0.026	0.636	0.0033

*Number of years of data available.

and the 18-m in situ records. The former has the advantage of 31 years of available data, but is shallow for kelps, and is located some distance from Point Loma in an area where topographic complexities may affect temperature patterns. The latter data set is from the Point Loma kelp forest and is based on eight values per day, but only 11 years of data.

The 5-m temperature was significantly correlated with harvest, as was surface temperature, and explained an identical amount of its variance (figure 3, table 1). Not surprisingly, surface and 5-m temperatures were very highly correlated ($r^2 = 0.79$). In contrast, in situ 18-m temperature explained very little of the variance in kelp harvest over the shorter period. The deeper measure was significantly correlated with surface temperature ($p = 0.015$), although less so than 5-m temperature. Nevertheless, while annual averages of surface and bottom temperatures are related, their relationship varied within and between years (figure 3). The implications for kelp harvest, however, are clear: most of the growth of giant kelp is responding to temperature in the upper part of the water column, not at 18 m.

The City of San Diego has collected monthly Secchi disk data immediately offshore of the Point Loma kelp forest for 18 years. There was interannual variability in the averaged Secchi data, with the 1982-84 El Niño years notably clearer (figure 4). Nevertheless, there was no significant relation between kelp harvest and annual Secchi depth averages (table 1). Conversi and McGowan (1992) detected no trends in Secchi depth for the pe-

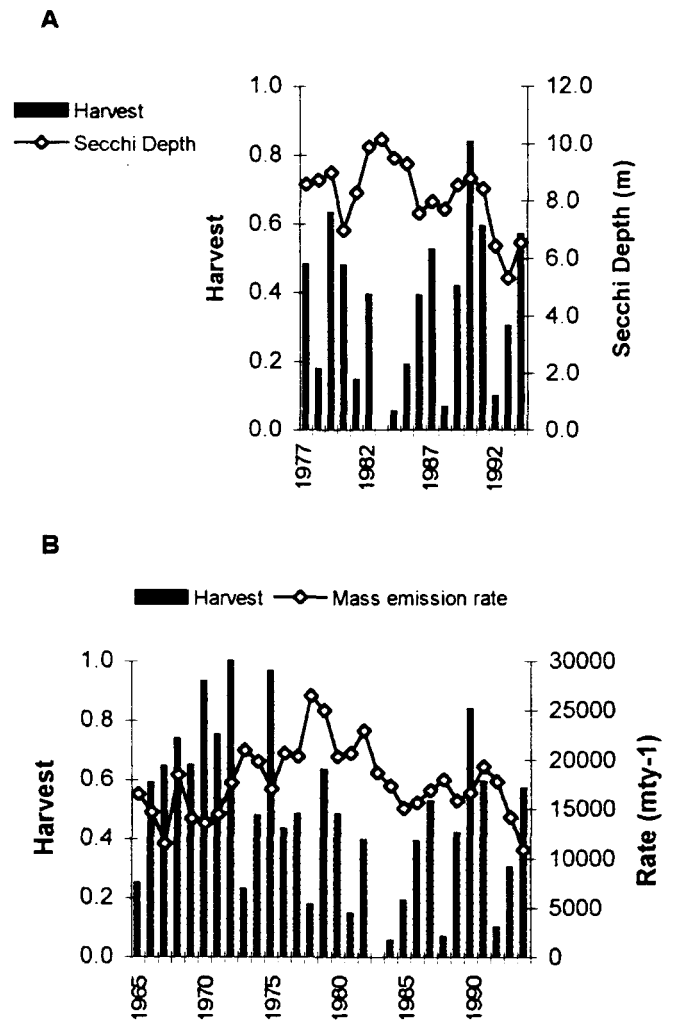


Figure 4. A, Kelp harvest data vs. average annual Secchi depth, 1977-94. B, Kelp harvest data vs. annual mass emission rate of suspended solids from the Point Loma wastewater treatment plant, 1964-94. Harvest is scaled to the maximum year in this time series—1972.

riod 1972-87 at these sites, and demonstrated the independence of water clarity, as measured by Secchi depth, and mass emissions rate from the Point Loma outfall. Because of the strong inverse relationship between mass emission rates of suspended solids from the Los Angeles County outfall and the area of the Palos Verdes kelp canopy (Stull and Haydock 1989), we compared these data from the Point Loma wastewater treatment plant with kelp harvest data (figure 4). The relation between mass emissions and kelp harvest was not significant for the period 1965-94 (table 1).

Wave damage has devastated the Point Loma kelp forest in recent years (Seymour et al. 1989; Dayton et al. 1992), and 1983 and 1988 were peak years of maximum significant wave height; however, the relation between maximum significant wave height and Point Loma kelp harvest was not significant (figure 5, table 1). Other mea-

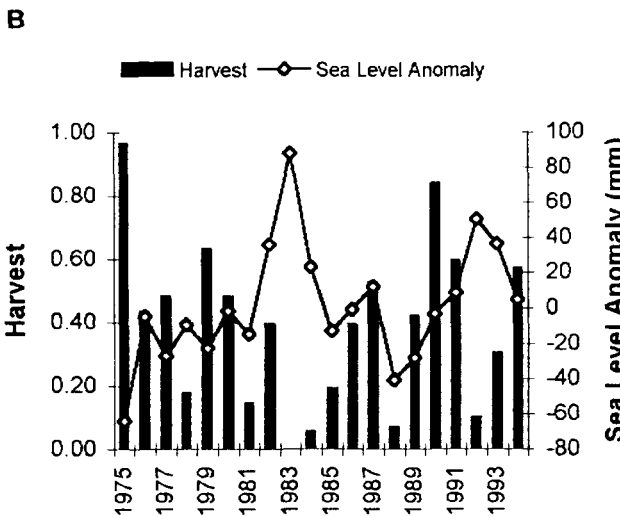
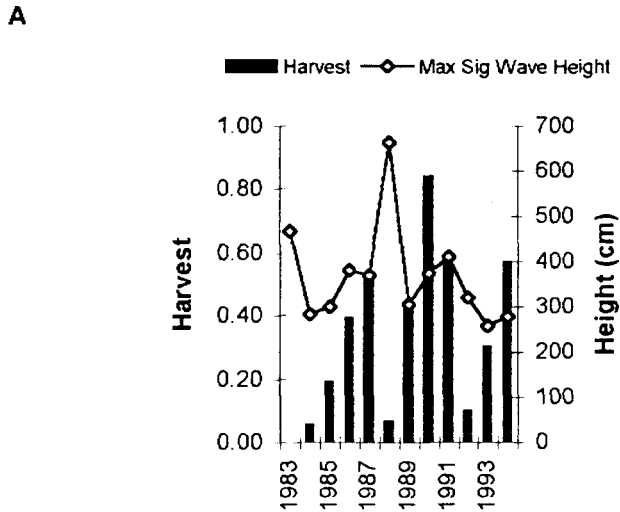


Figure 5. A, Kelp harvest data vs. annual maximum significant wave height, 1983-94. B, Kelp harvest data vs. sea level anomaly, 1975-94. Harvest is scaled to the maximum year in this time series—1972.

sures of wave energy, including the number of days with significant wave height greater than 2 m, and the average significant wave height for the year, explained even less of the variance; extreme values are apparently the most relevant parameter (e.g., Gaines and Denny 1993).

The productivity of the California Current, as indicated by zooplankton volume, is heavily influenced by large-scale, interannual variations in flow, which are strongly related to the coastal sea-level anomaly (Chelton et al. 1982). There is a significant inverse relationship between sea-level anomaly and Point Loma kelp harvest data for 1975-94 (figure 5, table 1; $r^2 = 0.23$, $p = 0.03$). Sea-level anomaly is also correlated with sea-surface temperature (figure 6, $r^2 = 0.47$, $p = 0.0009$), 5-m pier temperature ($r^2 = 0.56$, $p = 0.0002$), and in situ bottom temperature ($r^2 = 0.64$, $p = 0.0033$). The increasing amount of variance explained with decreasing depth sug-

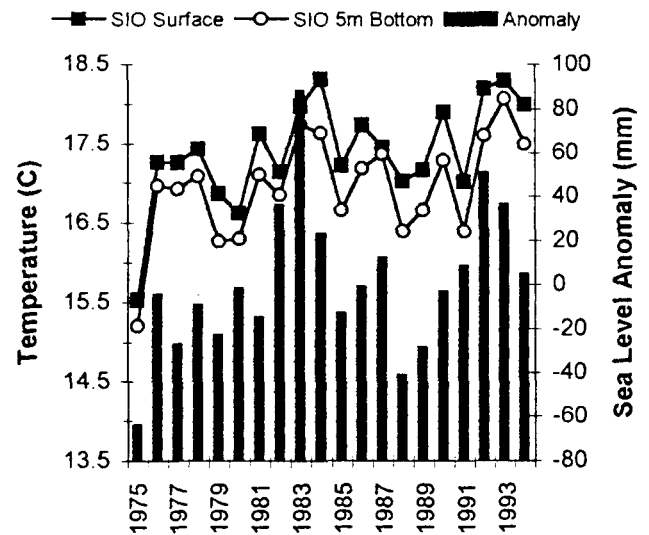


Figure 6. Sea-level anomaly vs. SIO Pier surface temperature and SIO Pier 5-m temperature, 1975-94.

gests that local processes are relatively more important to surface temperature, whereas deeper temperatures are more influenced by larger-scale phenomena.

STIPE COUNTS AS SUBSURFACE INDICATORS OF ENVIRONMENTAL CHANGE

Both areal estimates and harvest are correlates of the canopy that can be strongly affected by storms and warm summer-fall sea-surface temperatures with lesser or no impacts on survival of the plants themselves. This suggests that some measure from the less variable bottom environment of *Macrocystis* would be a better indicator. The density of giant kelp plants is generally a function of disturbance history and cohort age (figure 7; Dayton et al. 1992). High levels of disturbance lead to high initial cohort density (Reed et al. 1988; Tegner et al.³); after recruitment, intraspecific competition leads to gradual self-thinning (Dayton et al. 1984). Thus, some measure of individual plant status is required.

Giant kelp plants consist of a holdfast, which anchors the plant to the substratum; bundles of fronds analogous to the branches and leaves of a land plant; and reproductive tissues called sporophylls, which are located just above the holdfast. Fronds, made up of stemlike stipes and leaflike blades, originate at the basal meristem above the holdfast and grow up through the water column to form the surface canopy; fronds generally increase in number as plants age. *Macrocystis* plants are perennial, living up to about five years in the San Diego region (Rosenthal et al. 1974; Dayton et al. 1992), but the maximum lifetime of individual fronds is six to nine months (North 1994). The frond population of a plant turns

³See footnote 1 on p. 112.

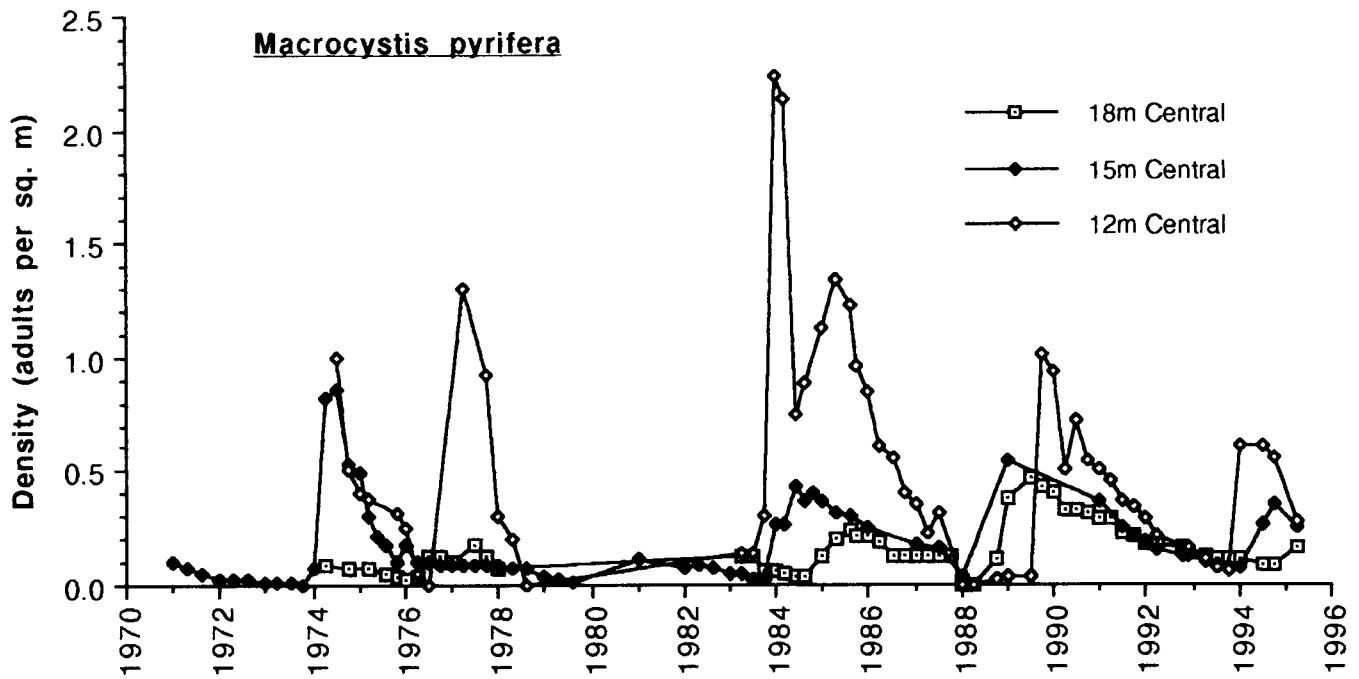


Figure 7. Density of adult (defined as four or more stipes, Dayton et al. 1992) *Macrocystis pyrifera* determined quarterly at long-term study sites in the central Point Loma kelp forest, 1983–94. Continuation of data from Dayton et al. 1992.

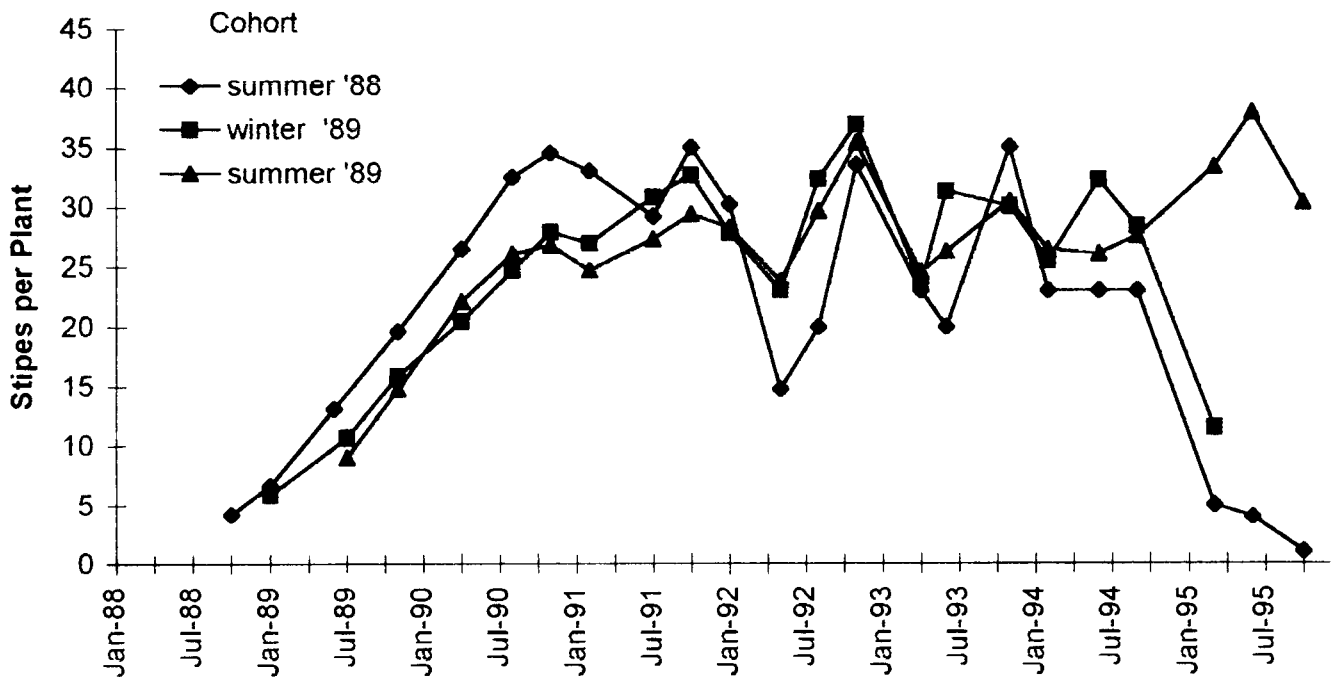


Figure 8. Changes in the mean number of stipes per *Macrocystis pyrifera* plant by cohort at 18-m Central, 1988–94.

over once or twice a year as fronds lost to senescence or disturbance are replaced with juveniles; at any given time the frond population consists of a complex mixture of different ages. This constant turnover of biomass contrasts sharply with terrestrial forests, where biomass

in woody trunks and branches of trees often remains fixed for decades (North 1994), and is the basis for the rich invertebrate-grazer fisheries of this ecosystem.

We began regularly collecting stipe data at five permanent sites at Point Loma in 1983 (Dayton et al. 1992;

Tegner et al.⁴). All adult (defined as four or more stipes) giant kelp plants are mapped quarterly in 400 m² per site, and stipes are counted at a height of one meter above the bottom. Stipes are not tagged, so stipe number data encompass both attrition and growth. Cohorts are defined as those plants which newly achieve adult status in a quarterly census. Jackson (1987) modeled *Macrocystis* stipe numbers and showed their sensitivity to season, depth, latitude, degree of wave exposure, upwelling, and other factors. Indeed, stipe density decreases with depth at Point Loma, and appears to be a good indicator of carrying capacity (Dayton et al. 1992). Thus stipe data should be compared within locations through time, and the comparative data presented here are all from 15 m in central Point Loma. Generally, frond number varies seasonally, independent of cohort age. In this example from our 18-m Central site (figure 8), there were clear decreases in average stipe number associated with seasonal decrease in light and winter storms, and increases in stipe number with the onset of spring upwelling and longer days in 1992 and 1993. Generally, there is also an inverse relationship between plant density and average plant size, in terms of fronds per plant (North 1994).

The relationships between disturbance, oceanographic conditions, plant density, and stipe carrying capacities have been explored in detail (Dayton et al. 1992; Tegner et al.⁵). Here we summarize these findings to establish the basis for using stipe counts as a useful indicator for long-term change in *Macrocystis* populations. Different stipe patterns were observed following the 1982–84 El Niño in comparison with after the 1988 storm. Data from 15-m Central (figure 9) are typical, although this site had a few adult survivors of both disturbances which led to brief peaks in stipes per plant before these large adults died.

After the extreme warm-water conditions of 1983–84, the number of stipes per plant steadily increased until the catastrophic storm of 1988 caused extensive mortality (Dayton et al. 1992); presumably these plants would have continued to grow in the absence of disturbance. Stipes per plant increased as plant density decreased, and thus stipe density remained relatively stable from 1986 until the storm (figure 9). In other words, there was an apparent stipe carrying capacity of about 5 m⁻² at the 15-m site between 1986 and 1988 (Dayton et al. 1992; Tegner et al.⁶). After the 1988 storm (excluding the prestorm survivors), there were three years (fall 1988–fall 1991) of steady increase in the number of stipes per plant during cold conditions associated with the 1988–89 La

Niña (Dayton et al. 1992), but then this value leveled off except for seasonal variation.

There was widespread sea-surface warming in the California coastal zone during 1992 and 1993 associated with the 1991–93 El Niño (Lynn et al. 1995). During 1994, circulation returned to a more normal pattern, but sea-surface temperatures were again anomalously warm during most of the year (Hayward et al. 1995). This leveling off of stipe number per plant during three years of warm-water conditions contrasts with the relatively steady increase observed after 1984, when water temperatures were closer to the mean. The general decline in stipe density to <2 m⁻² in early 1994, along with the decline in plant density after summer 1991, as well as the lack of increase in stipes per plant, suggests that warm-water conditions negatively affected growth and carrying capacity. Thus, both plant and stipe densities were much higher in 1988–90 than in 1985–86, but the initial success of these cohorts did not persist, and both indices dropped well below the 1986–88 carrying capacities. New plants recruited in mid-1994 after the decline of the post-1988 storm cohorts, and data from the early stages of the 1994 cohort indicate that the plants are growing in size as plant density decreases, and that the stipe density has remained relatively constant at about 4 m⁻² under more normal surface temperatures in 1995 (figure 9).

Thus we have two measures of kelp biomass independent of the canopy: stipe number per plant—an index of individual growth—and stipe density per square meter—which appears to reflect carrying capacity of the habitat. These are both very sensitive to water temperature and more sensitive than plant survival; witness the decline in stipe density in 1992–94 (figure 9) without unusual mortality (figure 7).

Analysis of long-term change depends on the availability of historical data; we located three earlier stipe data sets from 15 m in central Point Loma to compare with the last 12 years (table 2). Wheeler North surveyed all plants in an 800-m² area in September 1957 (North 1994); Ron McPeak (unpubl. data) of Kelco haphazardly measured 19 plants in September 1973; and Paul Dayton (unpubl. data) measured all plants in 225 m² a few months later, in January 1974, after winter storms would have caused some decreases in frond number from when McPeak's data were gathered. To represent our data from the last 13 years, we selected the peaks in number of stipes per plant for each of the post-disturbance populations, June 1986 and September 1993. Figure 10 illustrates the log of plant size (in terms of stipes per plant) plotted against cumulative percentage for four of the size-frequency distributions; the small McPeak data set was left off this figure for legibility. Median plant size has decreased by about two-thirds since 1957. Note also

⁴See footnote 1 on p. 112.

⁵See footnote 1 on p. 112.

⁶See footnote 1 on p. 112.

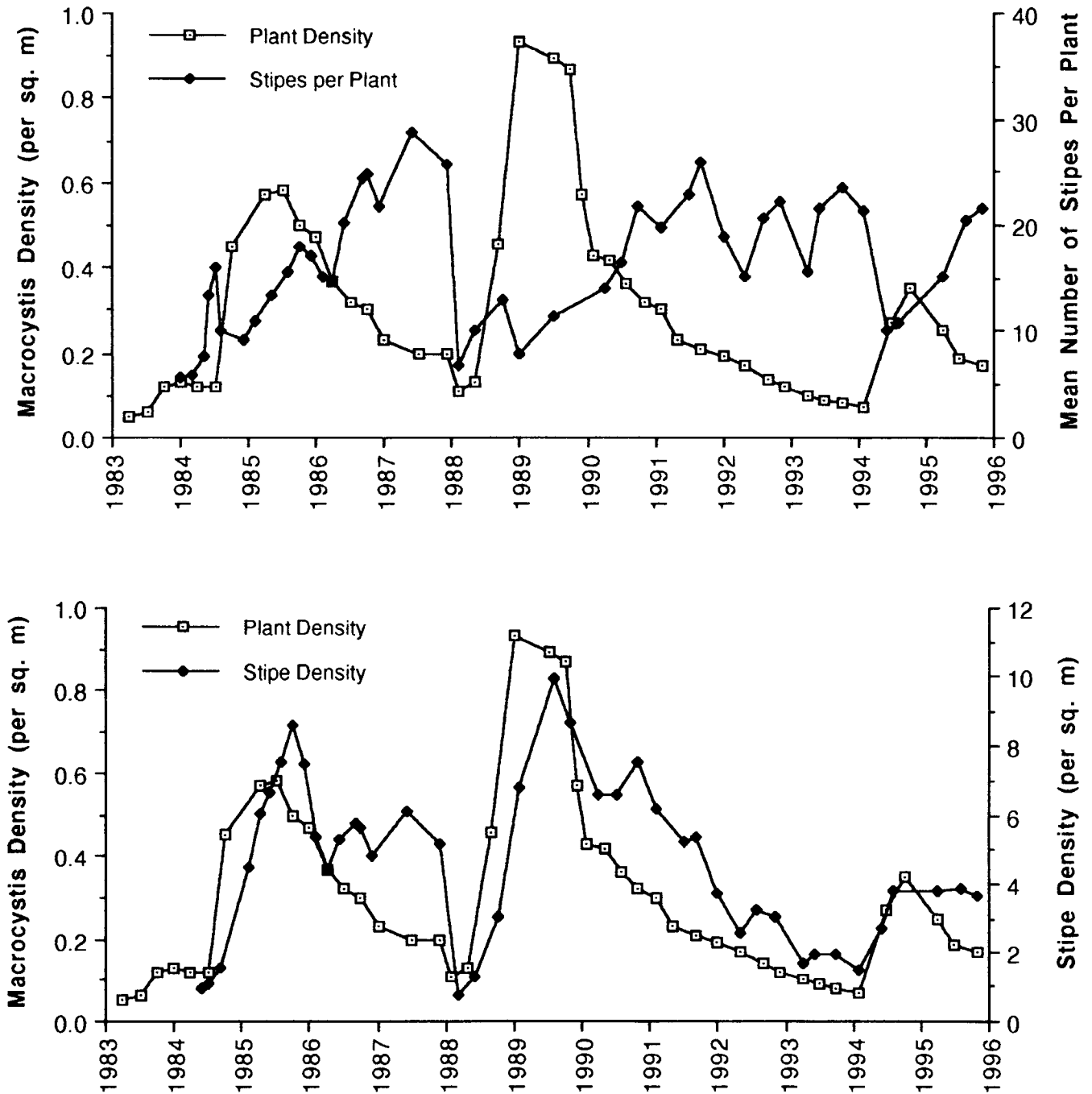


Figure 9. Changes in the mean number of stipes (growth) per *Macrocytis pyrifera* plant and in stipe density (carrying capacity) as functions of plant density at 15-m Central, 1983–94.

the changes in maximum plant size (table 2). Because of the strong inverse relationship between plant size and density (e.g., North 1994), it is important to compare plant densities among these years; despite the large discrepancy in size, the very large plants of September 1957 were found at the same density as the 1993 plants, suggesting very different carrying capacities. We reiterate that the earlier data represent haphazard points in time; only the 1983–95 data are continuous.

Because surface temperature was the best predictor of kelp harvest (table 1) in our data set, and because the plants live for several years, we plotted median stipe number against the sums of anomalies in SIO Pier temperature, calculated quarterly for three years (figure 11). There was a strong inverse trend between the accumulated pier temperature anomalies and median stipe number. Note that four of the five points were collected between June and September; it is probably because

TABLE 2
 Data Sets for Comparison of *Macrocystis pyrifera* Stipe Distributions among Years

Date	N	Plant density (per sq m)	Stipe number			Mean stipe density (per sq m)	Sum of anomalies (12 quarters)	Source	Notes
			Min	Max	Med				
Sept. 1957	60	0.08	1	192	55.0	4.11	-3.98	North (1994)	800 sq m
Sept. 1973	19	N.A.	12	194	48.0	N.A.	-4.26	McPeak (unpubl.)	Haphazardly selected plots
Jan. 1974	44	0.20	1	91	40.5	8.89	-5.80	Dayton (unpubl.)	225 sq m
June 1986	79	0.20	5	88	26.0	6.00	8.78	Tegner et al.*	Peak of 1983-88 cohorts (400 sq m)
Sept. 1993	33	0.08	1	69	19.0	1.92	11.40	Tegner et al.*	Peak of 1988-94 cohorts (400 sq m)

All data were collected from 15-m depths in the central Point Loma kelp forest. Anomalies refer to SIO Pier surface-temperature measurements.
 *See footnote 1 on p. 112.

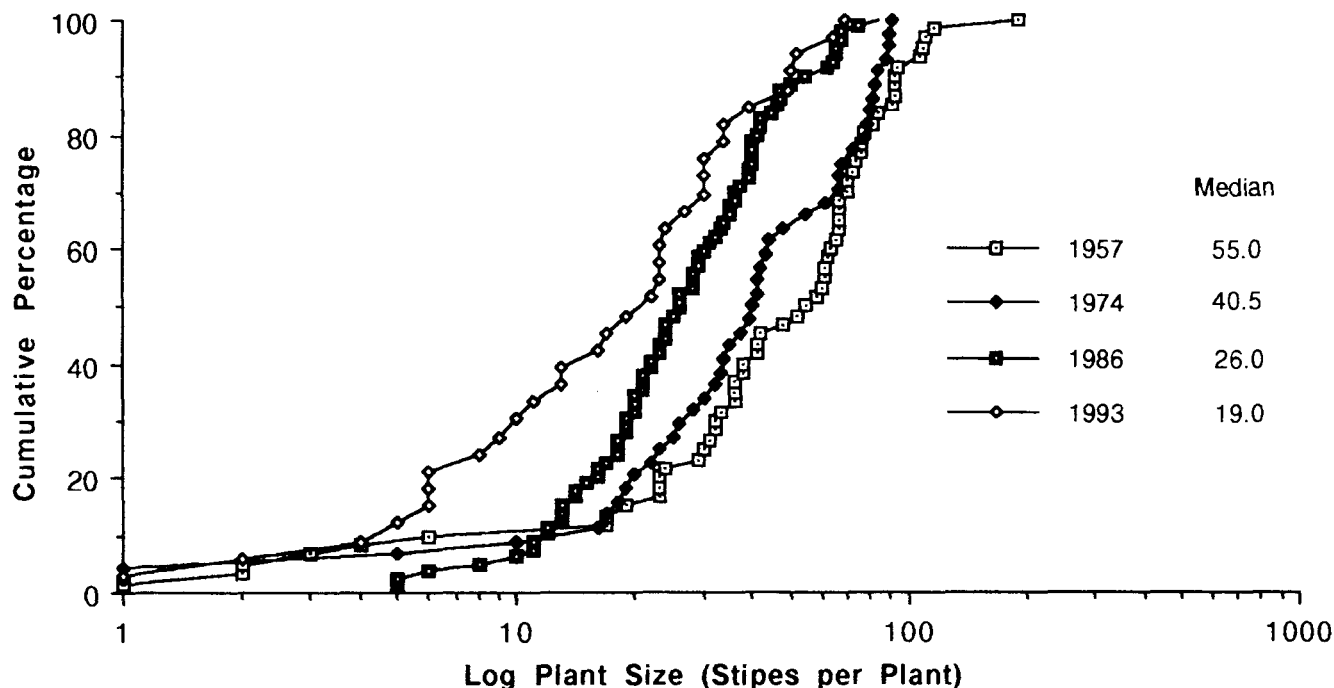


Figure 10. Log of *Macrocystis pyrifera* size vs. cumulative percentage for size-frequency distributions collected in four different years.

of the seasonal cycle in stipe number (figure 8) that the January 1974 data point appears low. Furthermore, because we selected the two peaks in stipe numbers between 1983 and 1995, the slope of this line is conservative. This figure explains the variable relationship between kelp harvest and canopy area (figure 3). The large canopy area but relatively low harvest of 1994 was due to low stipe counts, whereas the relatively high harvests of the late 1960s to mid-1970s almost certainly reflect high stipe counts.

DISCUSSION

Schiel and Foster (1986) review the problems of factor covariance (e.g., with depth) and interactions; changing relationships between abiotic variables and plant responses with the scale of measurement; and differences in responses among life-history stages in simple corre-

lation analyses. Such analyses, problematic when used to deduce cause-and-effect relationships, are useful when based on independent information on mechanisms and within the context of the proper time and space scales. Our analyses of the effects of environmental parameters on kelp harvest offer information on large-scale, inter-annual variability; these data are not relevant to processes with shorter time scales such as two-week kelp-recruitment windows (Deysher and Dean 1986) or restricted spatial scales (Dayton et al. 1984).

Surface temperature (as a surrogate for nutrient availability) is the best environmental predictor of kelp harvest and canopy area of those parameters for which we have historical data (see also North et al. 1993). The very high correlation between surface and 5-m pier temperatures and subjective evidence of thermocline depth at Point Loma suggest that the 5-m record is too shallow

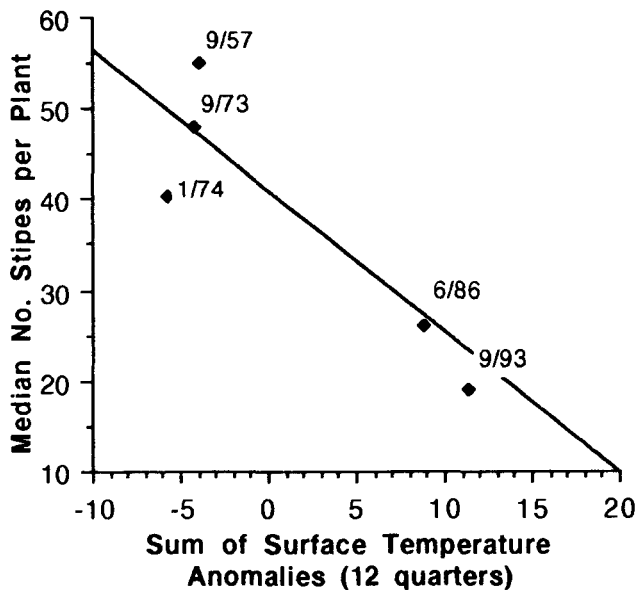


Figure 11. Anomalies in SIO Pier surface temperature, calculated quarterly and summed for three years, versus median stipe number of *Macrocystis pyrifera*.

to represent bottom temperatures in the kelp forest, and a longer 18-m in situ record would be desirable. The predictive value of surface temperature is somewhat counterintuitive—given the long period of the year that surface temperatures are warm; the colder, presumably more nutrient-rich bottom waters; and the importance of thermocline motion to the health of *Macrocystis* plants at Santa Catalina Island (Zimmerman and Kremer 1984, 1986; Zimmerman and Robertson 1985). However, with up to 60% of giant kelp biomass in the surface canopy (North 1968), and more than 98% of the production of *Macrocystis* in the upper 3 m of the water column (Towle and Pearse 1973), the portion of giant kelp plants above the thermocline probably overwhelms capacity for nutrient transport from below much of the time (e.g., Jackson 1977).

The greater importance of surface temperature as opposed to bottom temperature for kelp harvest was supported by R. W. Eppley and R. McPeak (unpubl. MS). They were able to account for less than 10% of the variance in coastal kelp harvest by using the depth of the nitrate concentration gradient ($\geq 1 \mu\text{g atom/L NO}_3$), which ranged from about 10 to 50 m. North et al. (1993), in their study of kelp forests in Orange and San Diego Counties, illustrate one spatial scale of temperature effects: 10 of the 12 forests in existence in the early 1980s displayed their lowest canopy coverage during El Niño conditions in 1983 or 1984, and 12 of 20 beds in existence in the late 1980s had their highest or next highest coverage during the 1989 La Niña.

The high correlations between all temperature measures and sea-level anomaly (r^2 values from 0.46 to 0.64,

table 1) indicate the importance of very large scale events to kelp harvest in coastal forests; Hickey (1993) reviews evidence that more than 75% of the variance in sea level in the Southern California Bight is accounted for by equatorial forcing. Such El Niño and La Niña events affect the California Current and the nearshore, although the largest interannual effects occur nearshore. Regional scales are also important to temperature; for example, sea level in 1984 was greatly reduced relative to 1983, and the tropical El Niño dissipated by fall 1983. However, anomalous conditions, including the warm surface temperatures associated with this event, persisted through 1984 in the California Current region (see references in Tegner and Dayton 1987; Dayton and Tegner 1990).

Some processes supplying nutrients to the nearshore are both temperature and coastally dependent. Coastal upwelling, where the land provides a barrier that forces water to flow away from the coast under appropriate wind conditions, is minimal in the Southern California Bight relative to other regions along the West Coast. However, coastal upwelling does occur within a few km of shore (the scale appropriate for kelp forests) in the bight, and is especially prominent at Point Conception, Palos Verdes, and Point Loma (Jackson 1986). El Niño events depress the depth of the thermocline, and thus may greatly reduce coastal upwelling or render it ineffective (Fiedler 1984; Shkedy et al. 1995). Other sources of nutrients to the nearshore, such as runoff from land, sewage discharge, and benthic topographic effects on turbulence and mixing, are less related to temperature. Thus, nutrients are provided to kelp forests in the nearshore zone by physical processes on a variety of scales, but the lesson of recent years has been the dramatic importance of very large scale events.

The history of Point Loma kelp populations since 1982 leaves no doubt that wave disturbance can decimate this community (Seymour et al. 1989; Dayton et al. 1992). Annual maximum significant wave height alone, however, does not predict kelp harvest. This may not be surprising, given the importance of wave period and wind in addition to significant wave height to kelp damage (Seymour et al. 1989); the strong age dependence of mortality rates for *Macrocystis* (Dayton et al. 1984, 1992); the strong dependence of kelp recovery on temperature; and annual harvest data.

Light is critical for all plants, and successful competition for light appears to explain the dominance of *Macrocystis* over understory kelps (reviewed by Murray and Bray 1993). Gerard and North (1984) report evidence that giant kelp growth is affected by light conditions the week preceding the growth determination, as opposed to the week of the determination. Interannual variability in light, as measured by averages of monthly Secchi depths on the outer edge of the Point Loma kelp

forest, however, explained little of the variance in kelp harvest. This is perhaps not surprising, given that canopies, the basis of kelp harvest, capture full sunlight before much radiant energy is absorbed by the water column (North et al. 1986). Secchi data, as an indicator of euphotic depth (the uses of this tool are reviewed by Conversi and McGowan 1992), would be more relevant to earlier life-history stages. Light and temperature requirements for germination and growth of microscopic stages of kelps define recruitment windows (Deysher and Dean 1986), which ultimately affect kelp harvest, but clearly growth conditions affecting intermediate life-history stages have a more direct effect. That understory recruitment events appear to depend on major canopy disruption by storms, sea urchins, or significant self-thinning of *Macrocystis* populations (Tegner et al.⁷) suggests that disturbance and the age structure of giant kelp are more important than interannual variability in water clarity for these lower-standing kelp guilds.

The anthropogenic factor most clearly associated with the health of southern California kelp forests is particulate emissions from sewage outfalls. Past high emissions from the Los Angeles County outfall reduced light penetration, introduced flocculant material and toxicants, and buried the substratum in the Palos Verdes kelp forest (Stull and Haydock 1989). There was a strong inverse relation between annual mass emissions and kelp canopy coverage from the mid-1940s to 1990. At Point Loma, the relation between mass emissions and kelp harvest was not significant for the 1964–94 period for which we have data (figure 4). We note, however, a strong inverse trend over the last three years. Fine-tuning of the advanced primary treatment process has reduced suspended solids emissions annually since 1991 (A. Langworthy, pers. comm.), and the outfall was extended an additional 3.7 km in 1993; the present discharge is 7.1 km offshore in 93 m of water. In this case, however, we know that the recent increase in *Macrocystis* harvest and canopy coverage resulted from release in grazing pressure due to a disease that eliminated a large sea urchin barren in the southwestern portion of the kelp forest and affected about a third of the bed (figure 2; see also figure 2 of Tegner et al. 1995). Subsequent kelp recruitment and growth led to dramatic changes in this region; the canopy at the end of 1994 extended more than a kilometer farther south than we have seen in the last two decades. Finally, the strong recovery of the Point Loma kelp forest after the catastrophic storm of 1988 in comparison with the weak recovery after the 1982–84 El Niño event argues that oceanographic conditions have been the critical determinant of resiliency in this ecosystem in recent years.

Stipe counts appear to be a useful tool for assessing *Macrocystis* carrying capacity and plant response to environmental change. Stipe counts are sensitive to temperature/nutrient conditions, integrate conditions over at least a three-year period, and are much less susceptible to disturbance than are measures of the canopy such as harvest or surface area. But most important, stipe counts are more sensitive to environmental conditions than is plant survival. Unfortunately this tool's usefulness as a historical record is limited because data cannot be compared across sites and depths (Jackson 1987; Dayton et al. 1992). Furthermore, there are few historical data where giant kelp populations have consistently been followed for any length of time, let alone the time-consuming stipe counts made. Nor will this tool be easy to apply, given that the plants in a cohort apparently need to be at least two years old for competition to govern their size and thus make the tool useful. The relationship between plant size, density, and nutrient availability bears further investigation. Nevertheless, the strong trend in the relation between accumulated surface temperature anomalies and median plant size (figure 11) clearly justifies further use of this tool—and constitutes yet another argument that long-term population studies are critical to our understanding of ecology and responses to long-term change (e.g., Dayton and Tegner 1984b).

What is the significance of these large interdecadal changes in giant kelp plant size as determined by stipe counts (figure 10) for the issue of long-term change? These data are inadequate to determine whether the decline in plant size was continuous from 1957 to before 1983, or whether the three historical data sets all happened to fall within cold periods, and the last twelve years have all been in a very warm period. Smith (1995) analyzed monthly SIO Pier temperature anomalies for the period 1940–93 for longer-term variability using a 24-month running mean. His results describe a long 1942–57 cold period followed by the 1957–59 El Niño, a cold period during 1960–66, a brief warm interval, a 1969–76 cold period, and finally the extraordinary 1977–93 warm period. North's 1957 data were from plants that had grown through the longest cold interval in this record before the ENSO had much impact in southern California; the 1973 and 1974 data came from plants which integrated the 1969–76 cold period. Thus much of the change in kelp biomass shown in figure 10 may be due to the location of these sample dates within warm and cold periods. Only time can resolve whether the 17-year warm anomaly that started in 1977, the longest in the 1922–94 period, is a harbinger of long-term increase in temperatures. We note that 1995 temperatures were much closer to the long-term mean and that more normal relationships between plant density, stipes per plant, and stipe density appear to

⁷See footnote 1 on p. 112.

be establishing with the plants that recruited in 1994 (figure 9).

There was a two-thirds reduction in median plant size as measured by frond number from 1957 to 1993 at the same plant density. Given that the average wet weight of a frond in the 10–20-m depth range is about one kilogram (North 1994), this substantial reduction in *Macrocystis* biomass suggests the possibilities of secondary effects on kelp forest community structure and on the export of material to surrounding communities. The relationship between giant and understory kelps is governed by competition for light (e.g., Dayton et al. 1984, 1992); the range in stipe densities observed since 1957 suggests important effects on benthic light levels. Comparing the structure of the Point Loma kelp forest community following the large-scale disturbances of the winter 1982–83 and the January 1988 storms, we found major differences in *Macrocystis* population dynamics and its competitive interactions with lower-standing species (Tegner et al.⁸). There was intense kelp recruitment after both disturbances. Poor giant kelp growth, canopy formation, and survival during El Niño conditions in 1983–84 apparently allowed the persistence of understory populations. Extraordinary *Macrocystis* growth during 1988–89 La Niña conditions led to the near extinction of understory kelps in our study sites. In both cases, the anomalous oceanographic conditions at the beginning of these cohorts lasted about two years after the disturbances, but the effects on kelp community structure persisted for the lives of the *Macrocystis* cohorts, despite average or poor conditions later.

Once established, understory kelp patches have considerable resistance to invasion (Dayton et al. 1984; Dayton and Tegner 1984a). Thus one scenario for long-term change would be increased understory populations and less *Macrocystis*. This has obvious implications for the giant kelp harvest and is likely to affect animal populations as well, given the enhancing effects of *Macrocystis* on fish recruitment and abundance (reviewed by Cross and Allen 1993) or the importance of giant kelp drift to sea urchins (Tegner and Dayton 1991; Dayton et al. 1992). Kelp detritus exported to surrounding communities supports high secondary production and prey for many fishes (Vetter 1995); thus reduced *Macrocystis* production could have ramifications well beyond the kelp forest.

Differences between high-frequency ENSO events or even these longer-term warm and cold periods and long-term change include the rate of change and the time available for species to acclimate or evolve adaptations to cope with changing conditions (Lubchenco et al. 1993). Perhaps not surprising for a species ranging from cen-

tral Baja California, Mexico, to north of Santa Cruz, California, *Macrocystis pyrifera* varies physiologically within its range. North (1971) observed giant kelp populations in Bahía Tortugas, near the southern end of the range, flourishing during 1957 when warm temperatures were associated with the deterioration of more northerly forests. Kopczak et al. (1991) demonstrated significant quantitative differences in the physiological responses to nitrate limitation in three geographically isolated populations of giant kelp with different natural patterns of nutrient availability. Kopczak et al. suggest that these populations have undergone genetic divergence that can be explained by ecotypic adaptation to widely differing habitat nutrient conditions. Thus, over long time scales, *Macrocystis* may be able to adapt, at least in part, to global warming, as changing conditions select for ecotypes similar to that which Kopczak and colleagues found at their most oligotrophic site.

These rate-of-change and time-scale differences in biotic responses to ENSOs or warm and cold periods and to long-term global change clearly limit our ability to use these higher-frequency events as a look into the future. For the near-term future, however, we believe that *Macrocystis* stipe counts are a useful indicator of temperature effects on the carrying capacity of southern California kelp forest communities.

ACKNOWLEDGMENTS

We thank M. Curtis, D. Glantz, W. Konopka, A. Langworthy, R. McPeak, W. North, T. Parr, T. Rothans, P. Vainik, and L. Verecker for discussions and data, E. Venrick for statistical advice, L. Basch and M. Mullin for comments on the manuscript, and many divers for their help in the field over the last two decades. This research was supported by the National Science Foundation and the City of San Diego.

LITERATURE CITED

- Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995. Climate-related, long-term changes in a California rocky intertidal community. *Science* 267:672–675.
- Chelton, D. B., P. A. Bernal, and J. A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. *J. Mar. Res.* 40:1095–1125.
- Conversi, A., and J. A. McGowan. 1992. Variability of water column transparency, volume flow, and suspended solids near San Diego sewage outfall (California): 15 years of data. *Chem. Ecol.* 6:133–147.
- Crandall, W. C. 1915. The kelp beds from lower California to Puget Sound. *In* Potash from kelp, F. K. Cameron, ed. U.S. Department of Agriculture Rep. 100, Washington, D.C.
- Cross, J. N., and L. G. Allen. 1993. Fishes. *In* Ecology of the Southern California Bight, M. D. Dailey, D. J. Reish, and J. W. Anderson, eds. Berkeley: Univ. Calif. Press, pp. 459–540.
- Dayton, P. K., and M. J. Tegner. 1984a. Catastrophic storms, El Niño, and patch stability in a southern California kelp forest community. *Science* 224:283–285.
- . 1984b. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. *In* Novel approaches to interactive systems, P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, eds. New York: Wiley, pp. 457–482.

⁸See footnote 1 on p. 112.

- . 1990. Bottoms below troubled waters: benthic impacts of the 1982–1984 El Niño in the temperate zone. *In* Global consequences of the 1982–1983 El Niño—Southern Oscillation, P. Glynn, ed. Amsterdam: Elsevier, pp. 433–472.
- Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal, and D. Ven Tresca. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54:253–289.
- Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62:421–445.
- Deysher, L. E., and T. A. Dean. 1986. *In situ* recruitment of giant kelp, *Macrocystis pyrifera* (L.) C. A. Agardh: effects of physical factors. *J. Exp. Mar. Biol. Ecol.* 103:41–63.
- Fargion, G. S., J. A. McGowan, and R. H. Stewart. 1993. Seasonality of chlorophyll concentrations in the California Current: a comparison of methods. *Calif. Coop. Oceanic Fish. Invest. Rep.* 34:35–50.
- Fiedler, P. C. 1984. Satellite observations of the 1982–83 El Niño along the U.S. Pacific coast. *Science* 224:1251–1254.
- Foster, M. S., and D. R. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. *U.S. Fish Wildl. Serv. Biol. Rep.* 85(7.2), 152 pp.
- Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecol.* 74:1677–1692.
- Gerard, V. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. *Mar. Biol.* 66:27–35.
- Gerard, V., and W. J. North. 1984. Measuring growth, production, and yield of giant kelp, *Macrocystis pyrifera*. *Hydrobiologia* 116/117:321–324.
- Hayward, T. L., D. R. Cayan, P. J. S. Franks, R. J. Lynn, A. W. Mantyla, J. A. McGowan, P. E. Smith, F. B. Schwing, and E. L. Venrick. 1995. The state of the California Current in 1994–1995: a period of transition. *Calif. Coop. Oceanic Fish. Invest. Rep.* 36:19–39.
- Hickey, B. M. 1993. Physical oceanography. *In* Ecology of the Southern California Bight, M. D. Dailey, D. J. Reish, and J. W. Anderson, eds. Berkeley: Univ. Calif. Press, pp. 19–70.
- Jackson, G. A. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. *Limnol. Oceanogr.* 22:979–995.
- . 1986. Physical oceanography of the Southern California Bight. *In* Lecture notes on coastal and estuarine studies, vol. 15. Plankton dynamics of the Southern California Bight, R. W. Eppley, ed. New York: Springer-Verlag, pp. 13–52.
- . 1987. Modelling the growth and harvest yield of the giant kelp, *Macrocystis pyrifera*. *Mar. Biol.* 95:611–624.
- Kopczak, C. D., R. C. Zimmerman, and J. N. Kremer. 1991. Variation in nitrogen physiology and growth among geographically isolated populations of the giant kelp, *Macrocystis pyrifera* (Phaeophyta). *J. Phycol.* 27:149–158.
- Lubchenko, J., S. A. Navarette, B. N. Tissot, and J. C. Castilla. 1993. Possible ecological responses to global climate change: nearshore benthic biota of the northeastern Pacific coastal ecosystems. *In* Earth system responses to global change, H. A. Mooney and B. I. Kronberg, eds. San Diego: Academic Press, pp. 147–166.
- Lynn, R. J., F. B. Schwing, and T. L. Hayward. 1995. The effect of the 1991–1993 ENSO on the California Current System. *Calif. Coop. Oceanic Fish. Invest. Rep.* 36:57–71.
- Mann, K. H. 1982. Ecology of coastal waters: a systems approach. *Studies in ecology*, volume 8. Berkeley and Los Angeles: Univ. Calif. Press, 322 pp.
- Murray, S. N., and R. N. Bray. 1993. Benthic macrophytes. *In* Ecology of the Southern California Bight, M. D. Dailey, D. J. Reish, and J. W. Anderson, eds. Berkeley: Univ. Calif. Press, pp. 304–368.
- Neushul, M., and P. Neushul. 1992. Marine plants: discussion. *In* California's living marine resources and their utilization, W. S. Leet, C. M. Dewees, and C. W. Haugen, eds. Calif. Sea Grant Extension Pub. UCSGEP-92-12, pp. 6–7.
- North, W. J. 1968. Effects of canopy cutting on kelp growth: comparison of experimentation with theory. *Calif. Dep. Fish Game, Fish Bull.* 139:223–254.
- . 1971. Introduction and background. *In* The biology of giant kelp beds (*Macrocystis*) in California, W. J. North, ed. Beihefte Nova Hedwegia 32:1–97.
- . 1994. Review of *Macrocystis* biology. *In* Biology of economic algae, I. Akatsuka, ed. The Hague, The Netherlands: SPB Academic Publishing bv., pp. 447–527.
- North, W. J., G. A. Jackson, and S. L. Manley. 1986. *Macrocystis* and its environment, knowns and unknowns. *Aquat. Bot.* 26:9–26.
- North, W. J., D. E. James, and L. G. Jones. 1993. History of kelp beds (*Macrocystis*) in Orange and San Diego Counties, California. *Hydrobiologia* 260/261:277–283.
- Peterson, C. H., R. T. Barber, and G. A. Skilleter. 1993. Global warming and coastal ecosystem response: how northern and southern hemispheres may differ in the eastern Pacific Ocean. *In* Earth system responses to global change, H. A. Mooney and B. I. Kronberg, eds. San Diego: Academic Press, pp. 17–34.
- Reed, D. C., D. R. Laur, and A. W. Ebeling. 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58:321–335.
- Roemmich, D., and J. McGowan. 1995. Climatic warming and the decline of zooplankton of the California Current. *Science* 267:1324–1326.
- Rosenthal, R. J., W. D. Clarke, and P. K. Dayton. 1974. Ecology and natural history of a stand of giant kelp, *Macrocystis pyrifera*, off Del Mar, California. *Fish. Bull. U. S.* 72:670–684.
- Schiel, D. R., and M. S. Foster. 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.* 24:265–307.
- Seymour, R. J., M. H. Sessions, and D. Castel. 1985. Automated remote recording and analysis of coastal data. *J. Waterway, Port, Coastal, and Ocean Engineering, ASCE*, 111(2):388–400.
- Seymour, R. J., M. J. Tegner, P. K. Dayton, and P. E. Parnell. 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuarine Coastal Shelf Sci.* 28:277–292.
- Shkedy, Y., D. Fernandez, C. Teague, J. Vesceky, and J. Roughgarden. 1995. Detecting upwelling along the central coast of California during an El Niño year using HF-radar. *Cont. Shelf Res.* 15:803–814.
- Smith, P. E. 1995. A warm decade in the California Current. *Calif. Coop. Oceanic Fish. Invest. Rep.* 36:120–126.
- Stull, J. K., and C. I. Haydock. 1989. Discharges and environmental responses: the Palos Verdes case. *In* Managing inflows in California's bays and estuaries. Sausalito, Calif.: The Bay Institute, pp. 44–49.
- Tarpley, J. A., and D. A. Glantz. 1992. Giant kelp. *In* California's living marine resources and their utilization, W. S. Leet, C. M. Dewees, and C. W. Haugen, eds. Calif. Sea Grant Extension Pub. UCSGEP-92-12, pp. 2–5.
- Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. *Adv. Ecol. Res.* 17:243–279.
- . 1991. Sea urchins, El Niños, and the long term stability of southern California kelp forests. *Mar. Ecol. Prog. Ser.* 77:49–63.
- Tegner, M. J., P. K. Dayton, P. B. Edwards, K. L. Riser, D. B. Chadwick, T. A. Dean, and L. Deysher. 1995. Effects of a large sewage spill on a kelp forest community. *Mar. Environ. Res.* 40:181–224.
- Towle, D. W., and J. S. Pearse. 1973. Production of giant kelp, *Macrocystis*, estimated by in situ incorporation of ¹⁴C in polyethylene bags. *Limnol. Oceanogr.* 18:155–159.
- Vetter, E. W. 1995. Detritus-based patches of high secondary production in the nearshore benthos. *Mar. Ecol. Prog. Ser.* 120:251–262.
- Zar, J. H. 1984. *Biostatistical analysis*. Englewood Cliffs, N.J.: Prentice-Hall, 718 pp.
- Zimmerman, R. C., and J. N. Kremer. 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. *J. Mar. Res.* 42:591–604.
- . 1986. In situ growth and chemical composition of giant kelp, *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. *Mar. Ecol. Prog. Ser.* 27:277–285.
- Zimmerman, R. C., and D. L. Robertson. 1985. Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island. *Limnol. Oceanogr.* 30:1298–1302.