CATALINA ISLAND KELP FORESTS: 1992 TO 1998

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ABSTRACT

To assess long-term changes in kelp forests at Santa Catalina Island, the Catalina Conservancy Divers recorded benthic water temperatures and conducted quarterly censuses of giant kelp (*Macrocystis pyrifera*) and sea urchins along three permanent 120 m^2 transects at 4-m, 10-m, and 20-m depths since1992. Catastrophic declines of *Macrocystis* occurred in 1992 and 1997 El Niño events. Rates of frond elongation (RFE) correlated with fluctuations in plant biomass and population density, but not plant size, which emphasized recruitment in maintaining giant kelp at this site. Within seasons, RFE were highest at the lowest mean temperatures and declined significantly with exposure to water above 18°C. Data suggest that thermal anomalies such as El Niño led to the reduction of giant kelp by intensifying stressful conditions in summer (high temperatures, low nutrients) and, also, by limiting production during winter and spring. Overgrazing of kelp by sea urchins was not observed. Depth distributions for three species of sea urchins remained stable from 1992 to 1998. Densities of *Strongylocentrotus purpuratus* and *S. franciscanus* declined, especially in 1992 and 1993, with the disappearance of giant kelp and signs of echinoderm wasting disease. Increases in the density of *Centrostephanus coronatus*, a species with tropical affinities, exemplify the potential shift toward warm water species.

Keywords: California Channel Islands, kelp forest, *Macrocystis pyrifera*, monitoring, El Niño, sea urchins, ocean temperatures, ocean climate change, Santa Catalina Island.

INTRODUCTION

Kelp forests in southern California represent a major economic and ecological component of coastal marine habitats in the temperate eastern Pacific. Their characteristic episodes of luxuriance and disappearance have drawn increasing interest since the 1950s when large scale reductions occurred in conjunction with warm water, strong winter storms, and extensive grazing by sea urchins (North 1971; Dayton and Tegner 1984; Tegner and Dayton 1987, 1991). To track the impact and interaction of different environmental variables a number of experimental and long-term field studies have served to identify critical life history variables and to outline historical patterns of discrete populations (e.g. Davis 1989; Dean and Deysher 1983; Tegner and Dayton 1991; Dayton et al. 1992; Tegner et al. 1996, 1997). Most recently, indications of major shifts in local oceanic climate regimes in the north Pacific (McGowan et al. 1998), brings to the fore the question of how susceptible these highly productive kelp forests are to long-term transformation or depletion (McFarland and McAlary 1991).

Kelp forest monitoring at Santa Catalina Island developed from the efforts of the Catalina Conservancy Divers in conjunction with the Wrigley Institute of Environmental Science. Biologically, the Catalina site is significant for two major reasons. First, the waters surrounding Catalina are the warmest in the Channel Islands region. Sea surface temperatures (SST) regularly exceed 20°C in the summer and mean monthly SSTs generally fall between 15° and 21°C (Engle 1993; Bushing 1997). Thus, giant kelp is near the limits of its preferred temperature range (North 1971; Engle 1993; Bushing 1997) and warm waters, especially above 16° to 17°C, are generally nutrient-poor (Jackson 1977; North and Zimmerman 1984; Zimmerman and Kremer 1984; Reitzel et al. 1987). Second, due to the strong thermal gradient from north to south across the relatively short distance of the Southern California Bight, the marine biota at Catalina is a mixture of species with temperate or tropical affinities (Neushul et al. 1967; Murray et al. 1980; Seapy and Littler 1980; Engle 1993, 1994). The island, thus, provides a biogeographically sensitive site for the detection of shifts in marine climate. The data presented in this paper augment and extend an earlier report on kelp forests at Catalina Island presented at the Fourth California Channel Islands Symposium (McAlary and McFarland 1994).

METHODS AND MATERIALS

The kelp forest monitoring area is located on the lee side of Catalina Island in the Catalina Marine Life Refuge adjacent to the Wrigley Institute of Environmental Studies (See Figure 1, McAlary and McFarland 1994). Since May 1992, the Catalina Conservancy Divers (CCD) in cooperation with the University of Southern California have conducted quarterly censuses of giant kelp (*Macrocystis pyrifera*) and sea urchins at this site along three permanent 120 m^2

transects at 4-m, 10-m, and 20-m depth. Between May 1992 and October 1997, relative rates of frond elongation (RFE) were included to index kelp growth. Benthic ocean temperatures were recorded at intervals of 30 min or 1 hour at each transect depth beginning in August 1992 using Ryan thermographs. A fourth thermograph was placed at 30-m in June 1993. Diver training and monitoring protocols are outlined in Turney (1995) and McAlary and McFarland (1994), except that sea urchins were counted annually beginning in 1993.

Selected census data from the kelp forest monitoring project and other CCD projects around Catalina Island are available on the Internet at: **www.ccd.org.**

RESULTS

Temperature

Benthic thermographs provided an almost continuous record of ocean temperatures in the monitoring area from August 1992 onward (Figure 1). As expected, annual temperatures followed a typical pattern of seasonal warming and cooling. Beginning in the spring, variance in temperature increased significantly with depth as surface waters warmed and the thermocline strengthened. Mean monthly temperatures and thermal stratification reached maximums in August or September with daily temperature excursions of as much as 8°C at the 30-m depth. The thermocline disappeared during the fall and temperatures remained uniform to 30 m throughout the winter. Minimum monthly temperatures occurred in January or February. A comparison of seasonal trends from 1992 to 1998 showed considerable variation in the strength and depth of the thermocline between seasons and years. Rates of heating and cooling, thermal variance, and the absolute range of temperatures for different years varied slightly, but over a significant physiological range for kelp forest biota.

Temperatures for 1997 followed the thermal trend recorded at the same location during the 1983-1984 and 1991-1992 El Niños, except that warming persisted later in the year, especially at 30 m. In 1997, 86% of the temperature records for August and September at 10 m were ≥20°C, with a low of 18.9°C. In 1995, a cooler year, only 9.4% of the temperature records were ≥20°C, with a low of 13.9°C. Ocean temperatures reached a record high of 23.7°C at 4 m, on September 7, 1997, and the mean monthly temperature for September 1997 was 22.3°C, the highest over 28 years (McAlary and McFarland 1994). Winter 1997-1998 was the warmest winter on record with mean monthly temperatures >17°C from December through February to 30-m depth. Available records at the Wrigley Center for Environmental Studies suggest that the annual average SST at Catalina Island has increased about 0.5°C since the mid 1970s.

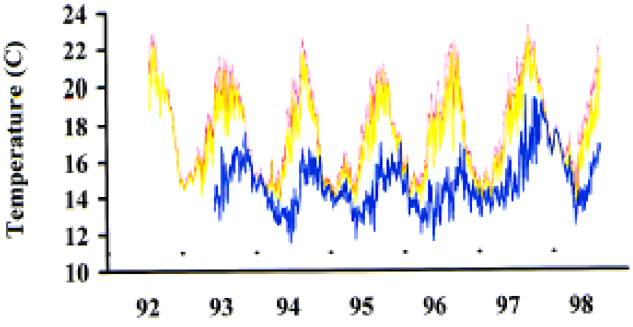

Figure 1. Mean daily temperatures at four depths smoothed using a moving average (period = 30). Depths: 4 m = red; 10 m = yellow; 20 m= green; 30 m = blue. Horizontal bar = January 1 to 10th. Catalina Marine Life Refuge, Catalina Island.

Kelp

The density of adult *Macrocystis pyrifera* (≥1 m tall) declined dramatically at the study site during the first half of 1993 and, despite varying degrees of recovery during the intervening period, all but disappeared in the fall of 1997. Increases in the density of adult plants at different times between 1992 and 1998 followed the general pattern of juvenile recruitment at each depth (Figure 2). For example, following the 1991-1992 El Niño, a significant, but unsustained, recovery of adult *Macrocystis* occurred first along the 20-m depth transect following a substantial recruitment of juveniles in the spring and summer of 1993. At the 10-m depth, repeated episodes of juvenile recruitment bolstered the

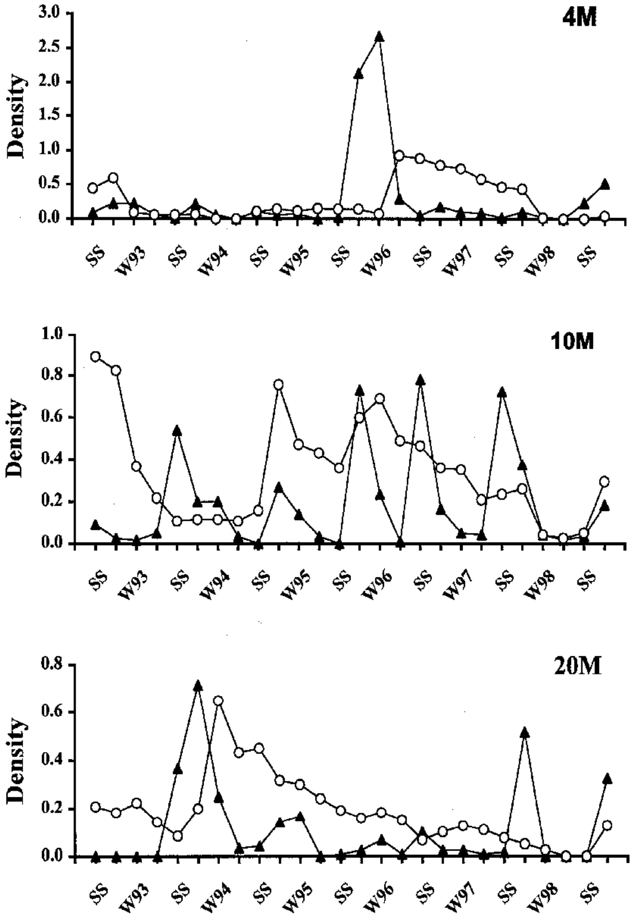

Figure 2. Density m^{-2} of *Macrocystis pyrifera* taller than >1 m (circle) and juveniles <1 m (triangle) along permanent 120 m^2 transects at three depths in quarterly censuses 1992-1998, Catalina Marine Life Refuge, Catalina Island.

density of adult plants, but failed to reverse long-term population losses. By the fall of 1993, adult *Macrocystis* disappeared along the 4-m transect which was now densely populated with low shrubby brown algae. For the next two years, only a few adult *Macrocystis* recruited. In the second half of 1995, a strong influx of juveniles (>2 m^{-2}) elevated densities of adult *Macrocystis* over ten fold, from 0.08 to 0.98 m^{-2}.

At all transect depths, changes in stipe density of adult *Macrocystis* correlated positively with changes in population density of adult plants (r's: 4 m = 0.90, 10 m = 0.87, 20 m = 0.63; N's = 26, P's <0.01), emphasizing the role of recruitment in sustaining biomass. Stipe density at 10 and 20 m was highest in the Summer 1992 census at 12.3 and 4.7 stipes m^{-2}, respectively. Densities of stipes at 4 m peaked in winter 1996 at 9.5 m^{-2} following a strong influx of juveniles in summer and fall 1995. Fluctuations in stipe density and plant size (Figure 3) show the balance between growth and deterioration of surviving plants, influxes of small plants due to recruitment, and loses of plants with storms or other disturbances (e.g., anchor drag). In general, plants tended to be small, averaging less than 25 stipes per plant with a maximum size of 4 to 109 stipes for different census periods. Although individual holdfasts were not routinely inspected, many of the largest *Macrocystis*, including the largest plant observed (109 stipes), consisted of smaller, adjacent plants that had grown together. In the fall of 1995 and spring of 1997, 50 out of 202 holdfasts (~25%) examined had formed from hapteral integration of two to six adjacent plants. Thus, plant size was a somewhat misleading index of individual growth. Holdfasts tended to be larger (more stipes) at depth (ANOVA, df =2, N = 24, p = 0.009), but differences were slight. Mean plant size (±SD) over all census periods at 4-m, 10-m, and 20-m depth were 8.0 ± 4.7, 10.7 ± 4.2, and 10.7 ± 6.5 stipes plant^{-1}, respectively. Correlations between the size and density of plants at different depths were small and not statistically significant (at 4 m, r = 0.39; 10 m, r = 0.11; 20 m, r = -0.06; N's = 26, P's >0.05). At 20 m depth, from the fall of 1993 into early 1997 mean plant size and density showed a typical pattern of succession in which density declined (from 0.65 to 0.08 plants m^{-2}) as surviving plants tended to increase in size (from 4.2 ± 4.1 to 20.3 ± 17.2 mean ± SD stipes plant $^{-1}$). During the 1991-1992 and 1997-1998 El Niños, however, population density and mean size declined at all depths.

Rates of frond elongation (RFE) for *Macrocystis pyrifera* measured along the 10-m transect correlated positively with temporal changes in plant density and stipe density (r's at 10 m = 0.56 and 0.58; r's over all depths = 0.70 and 0.62 respectively, N's = 21, P's <0.01) and lacked a conspicuous seasonal pattern. RFE varied significantly over a relatively narrow range of mean ocean temperatures in each season whereas in different seasons similar rates occurred over a relatively broad range of temperatures (Figure 4). Rates within each season tended to be highest for the lowest mean temperatures and tended to increase as the variance in temperature increased to include colder water (Figure 5). For example, during the winter, when ocean temperatures at the study site exhibited the lowest daily averages, and least amount of spatial and temporal variance, rates of frond elongation increased substantially as exposure to cold water,

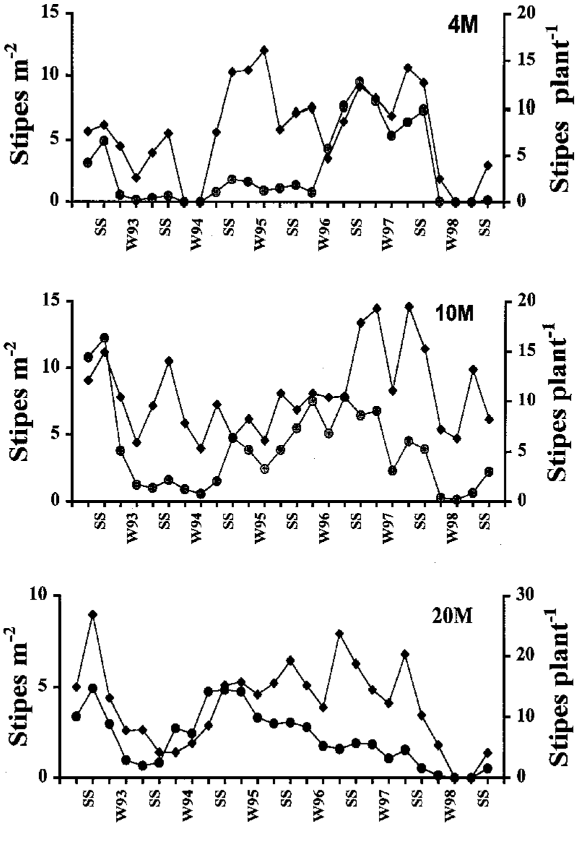

Figure 3. Density of stipes (circle) and mean plant size (diamond) of *Macrocystis pyrifera* along permanent 120 m^2 transects at three depths in quarterly censuses 1992-1998, Catalina Marine Life Refuge, Catalina Island. At: 4 m, r = 0.50; 10 m, r = 0.51; 20 m r = 0.48; N's = 24, P's ~ 0.01.

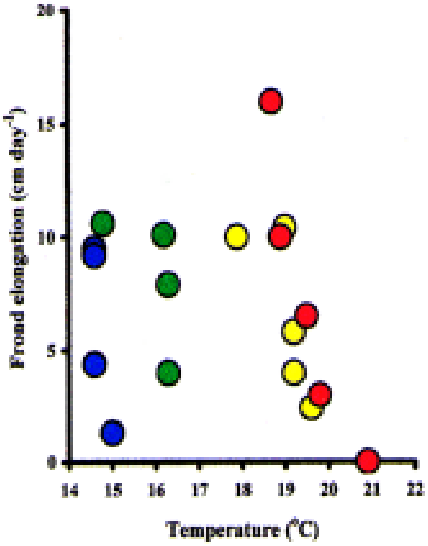

Figure 4. Mean rate of frond elongation of *Macrocystis pyrifera* growing at 10 m depth as a function of mean ocean temperature during a growth window (10 to 14 days over which rates of frond elongation were measured plus 30 days prior to the date of initial tagging). Symbols: Winter = blue; Spring = green; Summer = yellow; Fall = red. Catalina Marine Life Refuge, Catalina Island.

particularly 13.0 to 13.9°C, increased (Figure 5). For most of the year, ocean temperatures were more variable than in winter depending on the depth and strength of the thermocline. The highest RFE's in spring, summer, and fall growth experiments were associated with ocean temperature distributions that brought the greatest exposure to water $\leq$16°C and least exposure to water $\geq$20°C. RFE showed a significant negative correlation with increasing temperature in summer and fall when plants were regularly exposed to ocean temperatures of $\geq$20°C ($r = -0.773$, $N = 10$, $P < 0.01$). The rate for fall 1997 was recorded as zero due to the absence of kelp and healthy (dividing) meristems along the 10-m transect.

Sea Urchins

Distribution patterns for the three most abundant species of sea urchin in monitoring area, *Strongylocentrotus purpuratus* and *S. franciscanus*, and *Centrostephanus coronatus*, varied significantly and consistently with depth and location throughout five years of monitoring (Figures 6 A and B). The number of sea urchins in some 20 m^2 segments varied by only a few individuals between successive censuses. Such consistent counts suggested that urchins in the refuge area were generally sedentary.

Between 1992 and 1995, population densities of *Strongylocentrotus purpuratus* declined by ~70%. Changes in the abundance of *S. franciscanus* over this same period were smaller ~35%. Diseased individuals and empty tests of these species were common, especially during episodes of warm water. In contrast, by 1998 densities of *Centrostephanus coronatus*, a species with tropical affinities, almost tripled within the monitoring area (Figure 6C). Out of 31 *Centrostephanus* collected in February 1994 by thoroughly searching 1 m^2 quadrats at 4-m to 10-m depth, 3% were very small individuals (test diameter <20 mm). The presence of these smaller juveniles suggested recent recruitment.

DISCUSSION

Fluctuations in the growth of *Macrocystis pyrifera* between 1992 and 1997 occurred over a broad range of ambient temperatures from 14.6° to 18.9°C with no consistent relation to mean ambient temperature or season. With the exception of spring 1992 and fall 1996, RFE's were within the range described for this location by Zimmerman and Kremer (1986) as nitrogen limited (RFE's <12 cm day$^{-1)}$ at [NO$_3$] <1– 2 micro g-atoms liter^{-1}). Nutrient availability, which is generally related to the introduction of cold nutrient-rich waters of the California Current, is governed by a complicated flow regime (Hickey 1992). At Catalina, the primary temporal inputs of nitrate are large-scale storm-induced mixing, horizontal advection of different water masses, and vertical movements of the thermocline associated with internal waves and daily tidal forcing (Zimmerman and Kremer 1984). Tidal introduction of cold water is especially

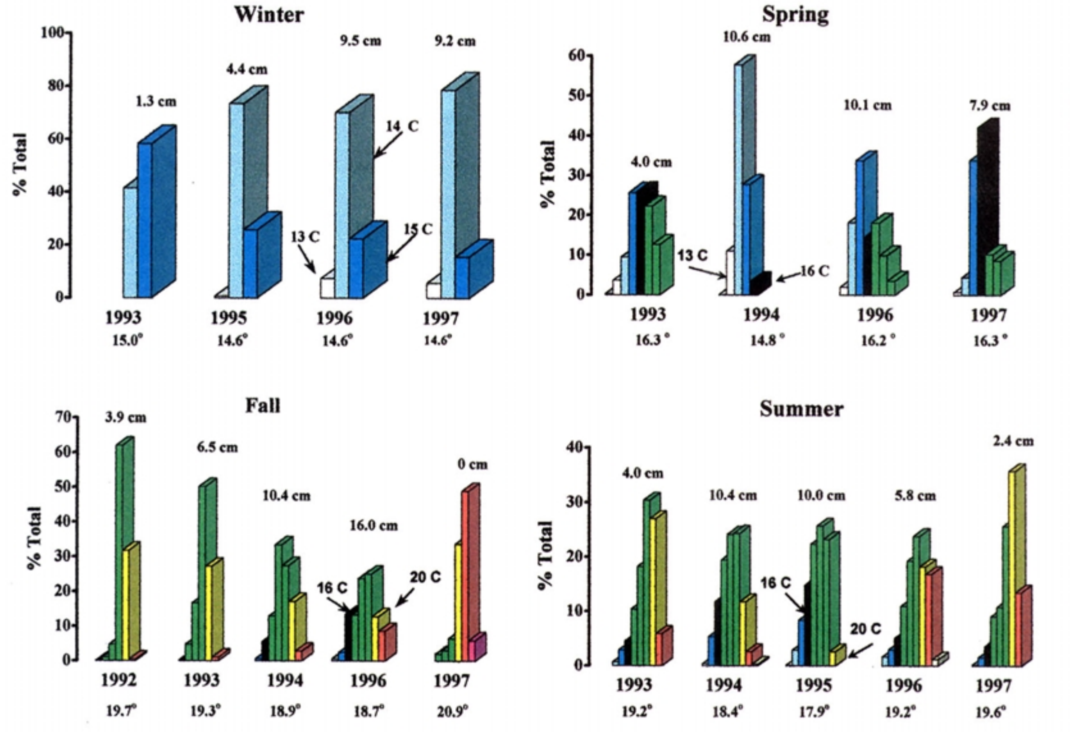

Figure 5. Mean rate of frond elongation per day of *Macrocystis pyrifera* at 10 m depth as a function of the distribution of ocean temperatures. For each season, the frequency of ocean temperatures and mean ocean temperature (°C) during the growth window (one month prior to and during the period when rates of frond elongation were measured) and mean rate of frond elongation per day are given. Each colored bar represents an interval of 1° Celsius. For clarity, symbols: 13°C = white; 16 °C = black; 20°C = yellow. Catalina Marine Life Refuge, Catalina Island.

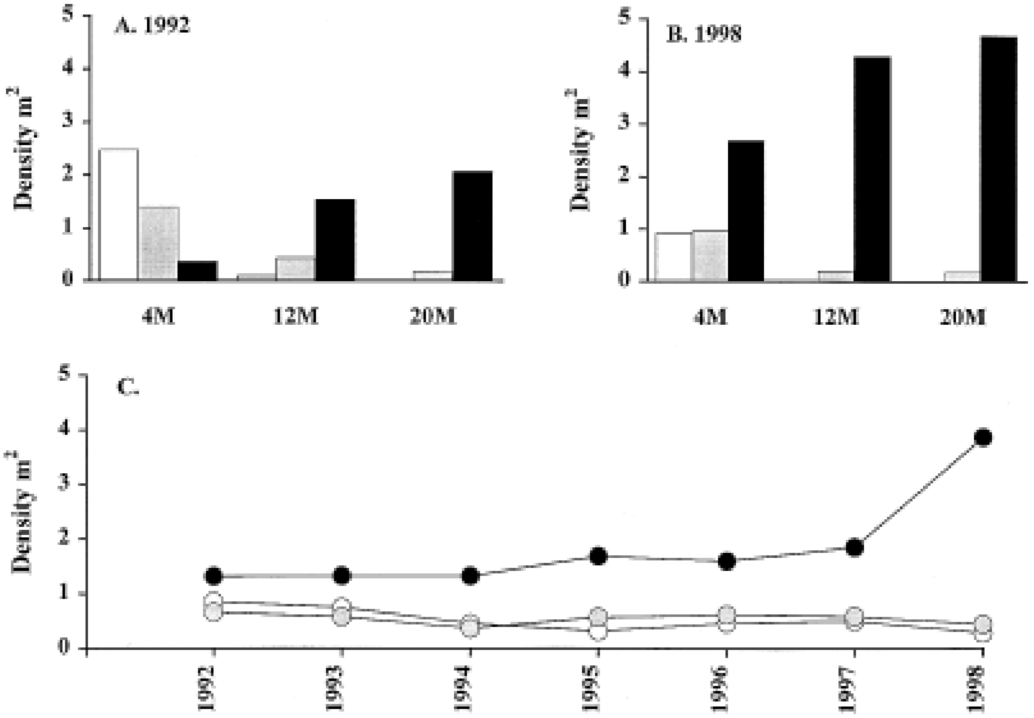

Figure 6. Densities m^{-2} for three species of sea urchins along permanent 120 m^2 transects at 4 m, 10 m, and 20 m depth in August (A and B) showing stable depth distribution. C. Fluctuations in the abundance of sea urchins summed for all transects at quarterly censuses from 1992 to 1998. Symbols: *Strongylocentrotus purpuratus* = white; *Strongylocentrotus franciscanus* = gray: *Centrostephanus coronatus* = black. Catalina Marine Life Refuge, Catalina Island.

important in summer and fall when surface waters are essentially nutrient-depleted. Runoff from storms may also be an important source of nutrients at the site, but sewage discharge is probably not.

In different seasons, similar RFE's were obtained for different mean ocean temperatures and thermal distributions. The greatest percentage of annual ocean temperatures above 20-m depth at the monitoring site were 15° to 19°C. Over this range, the kinetic effects of increasing temperature and day length may affect RFE positively at least up to 17° to 18°C; whereas the limiting effects of nutrient-depletion, especially >16°C, is difficult to predict due to advection of different water parcels and variation in the strength and thickness of the thermocline in the area at different times of the year (Zimmerman and Kremer 1984). Lower RFE's with increasing exposure to water above ≥20°C were expected and likely due to a combination of nutrient starvation and carbon limitation (Gerard 1984). When episodes of warm water were prolonged as occurred at Catalina in 1992 and 1997, densities of giant kelp declined rapidly. Unexpectedly, and in marked contrast to seasonal RFE's measured by Zimmerman and Kremer (1986) at this site in 1980-1981, the lowest RFE measured (when dividing meristems were present) occurred in winter, not summer (Figures 4 and 5). Water <15°C usually has sufficient nitrogen to support rapid kelp growth (see Figure 4 in Zimmerman and Kremer 1984), but during El Niños, nitrogen-temperature relations near the monitoring site show a significant downward shift (Zimmerman and Robertson 1985; J. Kremer, pers. comm. 1993). Thus, thermal anomalies such as El Niño lead to the diminishment of kelp forests not only by intensifying stressful conditions in summer (high temperatures, low nutrients) but also by limiting production during winter and spring.

Significant correlations between growth rates and fluctuations in plant and stipe density indicated that growth dynamics were an important influence in maintaining *Macrocystis pyrifera* at this site. They reinforce Tegner et al.'s (1997) suggestion that stipe density is a useful index of environmental carrying capacity for giant kelp. In this study, fluctuations in stipe density and RFE did not correlate significantly with the number of stipes per plant. Thus, fluctuations in plant size may not be a reliable index of growth in all situations, especially in cases where holdfasts used to identify individuals consist of more than one plant. At Catalina, it remains whether recruitment of new individuals and intermittent periods of climate favorable to growth can balance recurrent episodes of low nutrients and thermal stress.

Unlike many kelp forest areas around the Channel Islands, urchin-dominated areas are relatively rare around Catalina Island (J. Engle, pers. comm. 1994; Chess and Hobson 1997). Relatively low densities and an apparent die-off of *Strongylocentrotus purpuratus* and *S. franciscanus* within the monitoring area suggest that grazing on giant kelp by these two species was not a significant variable. Large increases in the abundance of *Centrostephanus coronatus*, a species with tropical affinities (Family Diadematidae), is a more ominous warning of changes in community structure. *Centrostephanus* is highly mobile at night. Individuals could have emerged from deep rock shelters or migrated into the monitoring area from adjacent areas or deeper water. Chess and Hobson (1997) interpreted variable transect counts at another densely populated area on the lee side of Catalina as indicative of this species' potential for long-term changes in distribution. The presence of juveniles in quadrat samples and diver awareness of smaller individuals during transect counts, however, suggest that recent recruitment contributed to density increases. Little is known about this species' interactions with giant kelp.

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