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Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California¹

Abstract—Deepened isotherms associated with El Niño resulted in severe nutrient limitation and very low kelp productivity during the last half of 1983. Frond growth rates were so low that terminal blades formed before reaching the surface, eliminating the canopy. Frond initiation rates were also extremely low, resulting in significant reductions in mean plant size. Plants growing above 10 m were more severely affected than plants at 20 m. These results suggest that nutrient pulses associated with internal waves are critical for survival of *Macrocystis pyrifera* in nutritionally marginal habitats in southern California.

El Niño 1983 was one of the strongest such events ever recorded and affected oceanographic conditions and weather patterns throughout the Pacific (Cane 1983; Fiedler 1984). Severe winter storms associated with El Niño hit southern California during 1983 and destroyed many kelp forests along the coast (Dayton and Tegner 1984). Such storm-related plant removals create an opportunity for recruitment of juvenile plants into the cleared areas (Rosenthal et al. 1984; Dayton et al. 1984). However, recruitment of juveniles into open spaces created by the storms was largely unsuccessful during 1983 (Dayton and Tegner 1984). Adult plants that survived the winter storms of 1983 and the newly recruited juveniles were exposed to significantly altered temperatures and patterns of nutrient availability during the rest of the year (Simpson 1984). The normal summer decline in productivity of *Macrocystis pyrifera* is due in large part to decreased nutrient availability

(e.g. North and Zimmerman 1984; Gerard 1982; Jackson 1977). Data on the relationships between water temperature, nutrient availability, and kelp growth rates collected at Santa Catalina Island during 1981 (Zimmerman 1983; Zimmerman and Kremer 1984) provide a basis for evaluating the effects of El Niño on kelp growth rates during 1983.

El Niño thickened the nutrient-poor surface layer in southern California (Simpson 1984). This should have reduced the frequency of nutrient-rich pulses associated with internal wave activity into the kelp forest. Our hypothesis was that growth rates of *M. pyrifera* should have been lower in 1983 than in 1981, a non-El Niño period, and that the effect of El Niño should have been moderated by the depth at which plants grew. We predicted that growth rates and plant sizes should increase with depth, due to increased nutrient availability associated with the pulsing of internal waves (Zimmerman and Kremer 1984).

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Hydrographic conditions and growth of *M. pyrifera* were examined in a kelp forest at the west end of Bird Rock, near the Catalina Marine Science Center (CMSC) at Santa Catalina Island (33°27'N, 118°30'W) from June to December 1983. Because of its location, this kelp forest was protected from the severe winter storms of 1983 and there was still significant surface canopy present in July 1983. Although growth of *M. pyrifera* in this area was nutrient-limited during summer 1981 (Zimmerman 1983), nutrient limitation is not often severe enough to eliminate the surface canopy or cause local extinctions. The principal nutrient source

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Table 1. Fresh weight (g)–length (cm) regressions for *Macrocystis pyrifera* fronds collected at three depths from the study site.

Depth (m)	Relationship	r^2
7	wt = $1.37 \times \text{length} + 47$	0.66
10	wt = $1.57 \times \text{length} + 16$	0.92
20	wt = $1.33 \times \text{length} + 11$	0.98

during summer and fall comes from the propagation of internal waves along the thermocline boundary, bringing cold, nutrient-rich water into the lower regions of the kelp forest (Zimmerman and Kremer 1984).

We made hydrocasts along the 100-m isobath at a station 500 m NE of the kelp forest at approximately weekly intervals. Water samples were collected at 0, 10, 25, 50, and 75 m with 5-liter Niskin bottles fitted with reversing thermometers. Water samples were frozen immediately and autoanalyzed for nitrate, nitrite, silicate, phosphate, and ammonium within a month. Because nitrate is the primary form of nitrogen present in the waters near Santa Catalina Island (Zimmerman and Kremer 1984), we present only the nitrate data here. The full hydrographic data set is available from the Office of the Director, Allan Hancock Foundation, USC. Thermal profiles were obtained from expendable bathythermograph (XBT) recordings at the time of each hydrocast, and sea-surface temperature (SST) was measured daily at the CMSC pier, about 1 km from the kelp forest.

Because of the size and morphological complexity of *M. pyrifera*, direct measurement of total plant growth is complex, but elongation rates of subcanopy fronds and the total number of fronds on each plant provide a good index of plant growth rate. These indices were measured at 2-week intervals from August to December 1983. Three subcanopy fronds on each of 15 plants with 20–30 fronds each at depths of 7, 10, and 20 m (five plants at each depth) were tagged 1 m below the apical tip with a length of plastic flagging tape, and the distance from the tag to the tip of the frond was measured 2 weeks later. The increase in length was used as an index of frond growth. Changes

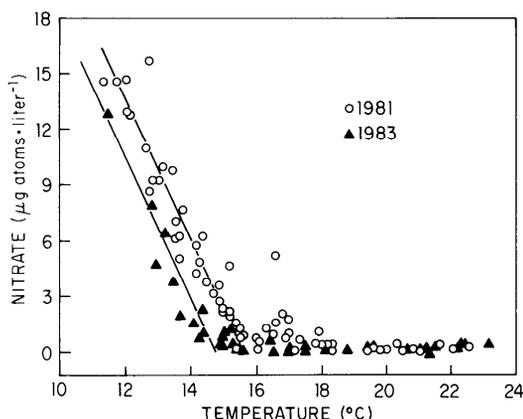


Fig. 1. Scatterplot of the temperature-nitrate relationship during 1981 and 1983. Although there was no difference in slopes for the T - NO_3^- relationship below 15°C between 1981 and 1983, the Y -intercept was significantly lower during 1983.

in plant size were measured by counting the total number of fronds on each plant every 2 weeks.

We converted frond elongation rates to biomass production estimates by using regressions of fresh weight to frond length (Table 1) to assure that any differences in growth rate associated with depth were not due to morphometric differences among the plants growing at different depths (Kain 1982). Three plants were collected from each depth by severing the primary stipe from the holdfast, returned to the CMSC dock, and suspended in the water while the biomass of each frond was weighed to the nearest gram with a triple beam balance and the length was measured to the nearest centimeter with a plastic meter tape. The measurements were completed about 3 h after collection.

In southern California, waters warmer than 15°C are essentially nutrient-depleted (Zimmerman and Kremer 1984; Jackson 1977; Eppley et al. 1979), with nitrate concentrations generally $<0.5 \mu\text{g-atom liter}^{-1}$. This pattern continued through 1983, but water below the 15°C isotherm appeared to be slightly lower in nitrate than in 1981 (Fig. 1). The statistical relationship between nitrate concentration and ambient water temperature below 15°C showed a significant downward shift in the Y -intercept, from $60 \mu\text{g-atoms liter}^{-1} \text{NO}_3^-$ (where $T = 0^\circ\text{C}$) in

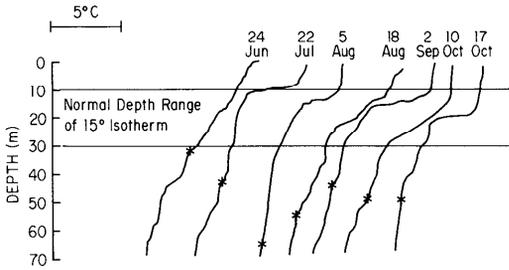


Fig. 2. Temperature profiles of the water column at Santa Catalina Island during 1983 recorded by XBT. The asterisk on each profile indicates the depth of the 15°C isotherm. The depth range of the 15°C isotherm during 1981 is indicated by the horizontal lines at 10 and 30 m. The 5°C bar at the top is a temperature scale indicator for each profile.

1981 to $50 \mu\text{g-atoms liter}^{-1} \text{NO}_3^-$ in 1983 ($P < 0.001$, ANCOVA), but the slope of the temperature-nitrate relationship was unchanged (-3.9 in 1981 to -3.4 in 1983, $P = 0.10$, ANCOVA).

Although the thermocline was not unusually deep in summer 1983, the 15°C isotherm was depressed to about 50 m, more than twice as deep as in 1981 (Fig. 2; Zimmerman and Kremer 1984). This isotherm represents the boundary between the deep, nutrient-rich water and the nutrient-poor surface layer (Fig. 1). Internal wave activity can push these isotherms upward as much as 20 m in 2–3 h (Armstrong and LaFond 1966; Zimmerman and Kremer 1984), and such pulses represent the principal nutrient source for *M. pyrifera* during summer and fall (Zimmerman and Kremer 1984). Depression of the 15°C isotherm to 50 m or more isolated the kelp forest (shallower than 20 m) from these nutrient-rich pulses.

Sea-surface temperatures were slightly warmer during winter 1983 (Fig. 3) but were actually cooler during the spring warming period (May–July 1983) than during 1981. Peak summer temperatures were not unusually high. However, the surface layer cooled more slowly during the fall, resulting in temperature anomalies as high as 3°C above 1981 values during October and November. These trends are consistent with the increased thermal inertia associated with a thickened surface layer, causing a longer warming time from May to June and a long-

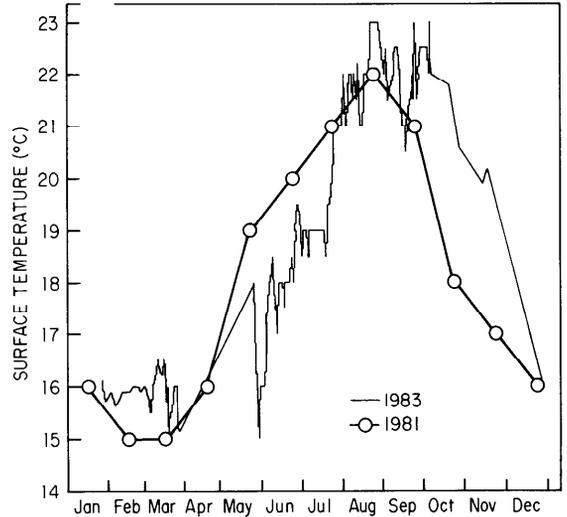


Fig. 3. Annual pattern of sea-surface temperatures taken at the Catalina Marine Science Center pier. The thinner line represents data collected during 1983. The heavier line and open circles represent mean monthly surface temperatures recorded during 1981 by a thermistor about 200 m from the pier. Estimates of daily variability for 1981 are available (Zimmerman and Kremer 1984), but monthly means are plotted here for visual clarity.

er cooling time from September to December. Data from the Scripps Institution of Oceanography pier during 1983 are similar: surface temperatures were elevated during winter and fall 1983, spring and summer temperatures seem to be typical of the 30-year mean (Dayton and Tegner 1984).

These anomalous hydrographic conditions appear to have had a dramatic effect on growth of *M. pyrifera* at Santa Catalina Island. Elongation rates of fronds on plants at 7 m averaged only 3 ± 2 (SE) cm d^{-1} during summer and fall 1983 (Fig. 4A), but $11 \pm 2 \text{ cm d}^{-1}$ for the same period in 1981. When converted to biomass units, the mean growth rate over the entire period of this study was significantly higher at 20 m ($12 \pm 2 \text{ g frond}^{-1} \text{ d}^{-1}$) than at 10 m or 7 m (9 ± 3 and $8 \pm 2 \text{ g frond}^{-1} \text{ d}^{-1}$, ANOVA, $f = 12.358$, $n = 2$ and 160, $P < 0.001$). Plants at 20 m produced an average of 2–4 new fronds every 2 weeks, the shallower plants averaged only 0–2 fronds. Plant size remained constant at 20 m but declined stead-

ily at 10 m and 7 m (Fig. 4C). This was caused principally by differences in rates of frond production. Extremely low rates of frond production were not able to keep up with losses at 7 m and 10 m, and plant sizes declined accordingly. The negative balance was so severe at 7 m that *Macrocystis* was eliminated by the beginning of November.

Individual fronds seemed to survive for 5–6 months, which is normal for *M. pyrifera* (Lobban 1978; North 1971). However, at all three depths fronds formed terminal blades and ceased to grow before they reached the surface. The canopy then disappeared with the loss of the older surface fronds.

Photosynthesis in *M. pyrifera* saturates between 80 and 100 $\mu\text{Einst m}^{-2} \text{s}^{-1}$ (Smith et al. 1983; Wheeler 1978). The light extinction coefficient for the water near our site was calculated from Secchi disk measurements to be 0.1 m. Thus, light levels at 20 m would be adequate to saturate photosynthesis in *M. pyrifera* with a surface irradiance of only 750 $\mu\text{Einst m}^{-2} \text{s}^{-1}$, making it unlikely that light limitation was a significant factor during 1983.

Plant density was visibly reduced on almost every visit, especially at the shallow site. Storm surge, the normal mechanism for plant removal (Dayton and Tegner 1984; Rosenthal et al. 1974), was very low during this period. When adult *M. pyrifera* are removed by winter storms, the entire holdfast is ripped out, leaving a distinctive scar on the rocks; during summer and fall 1983, we saw parts of many holdfasts still attached to the rock substrate, although the primary stipe and upper holdfast were gone.

Growth rates of juvenile *M. pyrifera* recruited in 1983 were also very low. Specific elongation rates of whole juvenile plants measured nearby during August 1983 were about 0.01 d^{-1} . These low growth rates are typical of nutrient-limited conditions and are only 30% of growth rates reported under conditions of nutrient saturation (Dean and Deysher 1984). Although juvenile plants were abundant in cleared areas at Santa Catalina Island during June and July 1983, none survived through the fall.

The deepening of the isotherms associ-

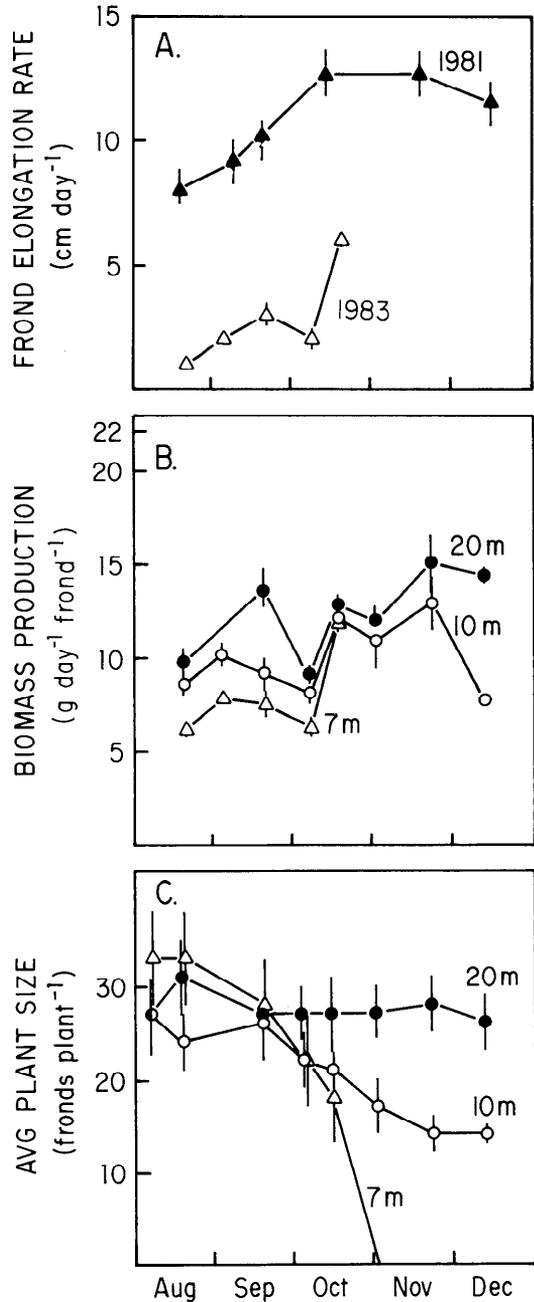


Fig. 4. A. Time series of elongation rates (mean \pm SE) of subcanopy fronds on adult *Macrocystis pyrifera* sporophytes growing at 7 m during summer and fall 1981 and 1983. B. Time series of biomass production estimates (mean \pm SE) calculated from frond elongation rates and weight-length regression data (model 1 regression) for the plants at each depth. C. Time series of mean plant size (mean \pm SE) at 7, 10, and 20 m.

ated with El Niño appeared to reduce the usual input of nutrients during the summer and fall associated with the propagation of internal waves. Dayton and Tegner (1984) noted a similar deepening of the isotherms at Pt. Loma in 1983. Plants at 20 m were probably near the shallow limit for these cold water pulses during 1983, and higher nutrient availability resulted in higher growth rates than that of shallower plants. These episodic pulses are not adequate to prevent nutrient limitation even during non-El Niño summers like that of 1981 (Zimmerman and Kremer 1984; Zimmerman 1983), but they may be important in regulating the summertime extinction of *M. pyrifera* from marginal habitats in southern California.

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