

## Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 “El Niño” in southern California

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### Abstract

The relative growth rates of juvenile *Macrocystis pyrifera* in southern California kelp forests were substantially reduced during the El Niño of 1982–1984. The lower growth rates were correlated with increased temperature and decreased nitrogen availability. Fertilization of juvenile plants with slow-release nitrogen-phosphorus fertilizer increased their growth rates to levels previously observed when temperatures were low and nutrient levels were high. The limitation in growth of *M. pyrifera* by levels of available nutrients during El Niño was in contrast to the usual limitation of growth by irradiance during non-El Niño years. Thus, there was a shift in the relative importance of factors controlling growth of juvenile *M. pyrifera* during El Niño.

### Introduction

Growth of juvenile *Macrocystis pyrifera* in coastal kelp forests of southern California is usually limited by irradiance (Dean and Jacobsen, 1984). Irradiance levels in the San Onofre kelp forest from 1979 to 1982 were generally below the saturation level for juvenile kelp growth, and occasionally below the compensation point (Dean and Jacobsen, 1984). Temperature, nitrogen, or correlated factors limited growth only occasionally. However, oceanographic conditions in southern California changed greatly beginning in Fall 1982. An “El Niño” event (i.e., a diminishing of prevailing easterly trade winds in the equatorial Pacific: Cane, 1983) caused a shift in current regimes and an intrusion of offshore surface waters into the coastal southern California region (Fiedler, 1984;

Simpson, 1984). This water mass was characterized by high temperatures and low nutrients (Fiedler, 1984; Simpson, 1984).

Juvenile kelp which recruited during a brief hiatus in the southern California El Niño conditions in spring 1983 grew poorly during the following summer (Dayton and Tegner, 1984; Zimmerman and Robertson, 1985; and own personal observations). The poor growth of juveniles during El Niño was correlated with increased temperatures and reduced nutrient levels. However, it was unclear whether high temperatures, low nutrients, or other factors caused slower growth. Juvenile plants held in a high-light, high-temperature and low-nutrient environment on an offshore platform grew better when fertilized with nitrogen and phosphorus, thereby indicating nutrient limitation under El Niño-like conditions (North *et al.*, 1982). North and Zimmerman (1984) and Zimmerman and Kremer (1984) showed that fertilizing adult plants under high-temperature and low-nutrient conditions enhanced growth. The growth of adult *Macrocystis pyrifera* during El Niño was slowed because of nitrogen starvation and possibly temperature stress (Gerard, 1984; Zimmerman and Robertson, 1985). In this study, we document growth of juvenile kelp during the recent El Niño in relation to previous non-El Niño years and test the hypothesis that the growth of juvenile kelp during El Niño was nutrient-limited.

### Materials and methods

Studies were conducted in the San Mateo kelp (*Macrocystis pyrifera*) forest (33°23'N; 117°36'W) and the San Onofre kelp forest (33°20'N; 117°33'W) in southern California, USA. Detailed descriptions of these kelp forests are given in Dean and Jacobsen (1984) and Dean *et al.* (1984). We examined the growth of juvenile *M. pyrifera* during the summer of 1984 using methods similar to those described by Dean and Jacobsen (1984) and Foster *et al.*

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(1985). Briefly, juvenile plants (approximately 40 cm in height with two fronds) were collected from the San Onofre kelp forest (depth = 13 m) and transplanted to similar depths in the San Mateo kelp (SMK), San Onofre kelp – downcoast (SOKD) and San Onofre kelp – upcoast (SOKU). The stations were the same as those used in previous studies (Dean and Jacobsen, 1984). Plants were attached to PVC racks approximately 1 m above the bottom. All fronds on each plant were measured immediately after transplanting and again after collection after 3 to 6 wk. Irradiance and temperature were measured continuously at 2 m above the bottom at each site. Water samples were taken from 1 m above the bottom for nitrogen analysis ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and  $\text{NH}_4^+$ ) two or more times during each transplant experiment at locations within 50 m of each station. In addition, one blade from each of ten plants remaining from the initial transplant pool and from each of those plants that survived the transplant period was analyzed for tissue-nitrogen. The relative growth rate for each plant was calculated as the natural log of the ratio of total frond lengths at the beginning and end of the transplant period over the elapsed time in days. Growth rates were based on length to avoid exposing plants at the surface, as would be required in weighing. The length of plants was significantly correlated with weight ( $r=0.93$ ,  $P < 0.01$ ,  $N=92$ ), as determined by sampling plants of similar size.

We examined the effect of nutrient availability on growth by fertilizing plants at the SMK station and comparing the growth of fertilized plants to unfertilized controls placed on racks about 15 m away. Muslin mesh bags, measuring 30 cm long  $\times$  4 cm in diameter, were filled with 200 g of Osmocote fertilizer (Sierra Chemical Co., Milpitas, California). The fertilizer was a blend of ammonium nitrate and phosphate salts (26% N and 11% P) which is pelletized and coated with a semipermeable polymer film. The bags of fertilizer were arranged so that one bag surrounded the holdfast of each plant. The bags were attached to the racks with plastic cable ties and were replaced by new bags every 7 to 10 d.

We did not measure nitrogen and phosphorus within the vicinity of the fertilizer during this experiment. However, studies at SOKD showed that during a period when ambient nitrogen levels ( $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ ) were from 1 to 3  $\mu\text{M}$ , total nitrogen levels within several cm of the fertilizer were twenty-fold higher than ambient after 2 d, and were seven to eight times higher than ambient after 7 to 10 d (Table 1). Phosphorus levels were not measured, but we presume that since both nitrogen and phosphorus were coated with a similar semipermeable film, release rates for phosphorus were similar to that of nitrogen, and that phosphorus levels were also elevated in the vicinity of the fertilizer. No increase in nitrogen level over ambient could be detected within 10 m of the fertilizer.

Transplant experiments were conducted from 5 July to 24 July, 1984 and from 24 July to 4 September, 1984. In the first experiment, 20 plants were transplanted to the SMK site. Ten plants (5 on each of two racks) were fer-

**Table 1.** Nitrogen concentrations within several centimeters of bags of fertilizer and at control sites 10 m away, at San Onofre kelp forest; nd: no data

No. of days after initial placement	Replicate No.	Nitrogen concentration ( $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ ; $\mu\text{M l}^{-1}$ ) at:	
		Control	Fertilized
Experiment No. 1 13 July 1981			
7	1	0.6	5.1
	2	0.7	nd
	3	0.6	nd
Experiment No. 2 29 July 1981			
2	1	1.9	28.0
	2	2.9	35.0
10	1	0.8	6.0
	2	0.7	5.7

tilized and 10 plants (placed on another two racks) were unfertilized. In the second experiment, we transplanted 35 plants to SMK. Ten plants were fertilized and the other 25 were unfertilized. In both experiments, racks with fertilized plants were separated from racks with controls by 15 m to prevent drift of fertilizer from the fertilized to control plants. During the second experiment, 25 unfertilized plants were also transplanted to SOKU and SOKD stations.

## Results

Mean relative growth rates of unfertilized juvenile *Macrocystis pyrifera* ranged from 0.012  $\text{d}^{-1}$  in the 5 July experiment to 0.006  $\text{d}^{-1}$  during the 24 July experiment (Table 2). These growth rates correspond to doubling times of 58 and 115 d. During the transplant periods, irradiance levels were high ( $\geq 3.3 \text{ E m}^{-2} \text{ d}^{-1}$ ), temperatures were high (16.7° to 17.9°C) and nitrogen levels at control sites were low ( $< 1.05 \mu\text{M l}^{-1}$ ). The growth rates observed under these conditions were 30 to 60% lower than previously observed at these sites when irradiance levels were similar but temperatures were lower and nitrogen levels higher (Dean and Jacobsen, 1984; and present Fig. 1).

Fertilized plants grew significantly better than unfertilized plants at SMK in 1984 ( $P < 0.05$  for the 5 July transplant and  $P < 0.01$  for the 24 July transplant, Student's *t*-test). The relative growth rates of the fertilized plants were similar to the maximum growth rates observed in previous experiments, when light levels were high, nitrogen levels were high, and temperatures were low (Fig. 1).

Mean tissue-nitrogen levels were slightly higher for fertilized plants than for unfertilized ones at the same site. However, differences in the tissue-nitrogen levels at the end of the experiments were significant in only the longer (6 wk) experiment (Table 3).

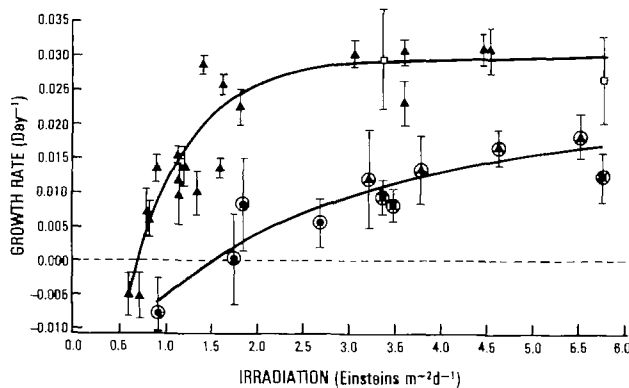
**Table 2.** *Macrocystis pyrifera*. Average relative growth rates ( $\text{day}^{-1} \pm 1 \text{ SE}$ ) of juveniles near fertilized sites (F) and unfertilized control sites (C) in San Mateo (SMK) and San Onofre (SOK) kelp forests. Associated physicochemical measurements are also given. Tissue-nitrogen is average of tissue-N present at beginning of experiment and final tissue-N. SOKD, SOKU: San Onofre kelp – downcoast and upcoast, respectively; nd: no data

Location (treatment)	Growth rate	Tissue-N (%)	Total N ( $\mu\text{g-at l}^{-1}$ )	T ( $^{\circ}\text{C}$ )	Irradiance ( $\text{E m}^{-2} \text{d}^{-1}$ )
5–24 July 1984					
SMK (F)	$0.026 \pm 0.0032$	1.20	nd	16.7*	5.76*
(C)	$0.012 \pm 0.0018$	1.15	1.1	16.7*	5.76*
24 July – 4 Sept. 1984					
SMK (F)	$0.029 \pm 0.0036$	1.03	nd	17.7*	3.37*
(C)	$0.009 \pm 0.0013$	0.90	0.4	17.7*	3.37*
SOKD(C)	$0.008 \pm 0.0012$	1.20	1.0	17.9	3.49
SOKU(C)	$0.006 \pm 0.0014$	1.04	1.1	nd	nd

\* Temperature and irradiance data for both fertilized and control plants were taken at a single location midway between the two treatments

**Table 3.** *Macrocystis pyrifera*. Tissue-nitrogen in plants from fertilized sites (F) and unfertilized control sites (C) at outset of transplant period (initial) and after plants were collected (final). Also given are results of Student's *t*-tests comparing final tissue-nitrogen levels of fertilized and control plants. The *t*-tests were performed on arcsin-transformed data. Percent tissue-nitrogen ( $\pm 1 \text{ SE}$ ) is given for untransformed values in the table

Location (treatment)	Initial N (%)	Final N (%)	<i>t</i>	DF	<i>P</i>
5–24 July 1984					
SMK (F) } (C) }	$1.4 \pm 0.07$	$0.94 \pm 0.05$ $0.85 \pm 0.07$ }	-1.06	18	0.30
24 July – 4 Sept. 1984					
SMK (F) } (C) }	$1.1 \pm 0.03$	$0.96 \pm 0.13$ $0.70 \pm 0.06$ }	-2.78	20	0.01



**Fig. 1.** *Macrocystis pyrifera*. Mean relative growth rates ( $\pm 95\%$  confidence interval) of juveniles transplanted to the San Mateo and San Onofre kelp forests vs mean daily irradiance levels during transplant period. Circled values are for plants that were nutrient-limited,  $\blacktriangle$  = August 1981,  $\bullet$  = September 1982;  $\bullet$  = unfertilized plants in 1984. Others were not nutrient-limited.  $\blacktriangle$  = 1979–1982,  $\square$  = fertilized plants in 1984. Lines were fit by a non-linear curve fitting procedure using the von Bertalanffy equation (see Dean and Jacobsen, 1984)

## Discussion

In a transplant experiment conducted during the initial phases of El Niño in Fall 1982 (Dean and Jacobsen, 1984) and in both the transplantings conducted in 1984, growth rates of juvenile *Macrocystis pyrifera* were below the maximum expected for the given irradiance at all sites (Fig. 1). This is compared to the results obtained prior to El Niño, from 1979 through Summer 1982, when growth rates fit the growth-irradiance curve in all but one of our seven experiments. The one exception occurred during an especially warm period in August 1981. Although irradiance appeared to be limiting more often than nutrients in “normal” years, there was a shift in the relative importance of factors controlling growth during El Niño, and the growth of juveniles became more nutrient-limited.

The results also suggest that there was an interaction between irradiance and nutrient availability in controlling growth. Although we do not have sufficient data on nutrient availability to suggest a formal model of inter-

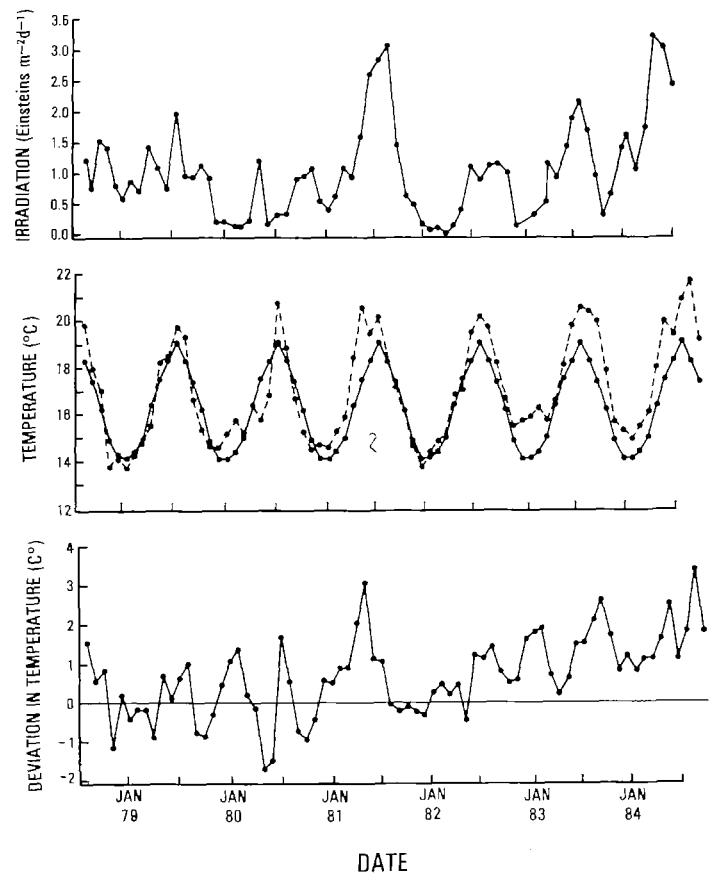
active effects, it appears that both the compensating and saturating irradiance levels increased during periods when nutrients were limiting. Nutrients and irradiance have interactive effects on the growth of juvenile *Macrocystis pyrifera* (Shivji, 1985) and other algae (Lapointe and Tenore, 1981; Rhee and Gotham, 1981) in culture.

Both fertilized and control plants had tissue nitrogen levels near those thought to be critical for maximum growth (Gerard, 1982), and tissue nitrogen levels were higher for fertilized than for control plants in only one of the two experiments. This was probably the result of rapid depletion of tissue-nitrogen surpluses, which can occur within several days (Wheeler and North, 1981). Especially high rates of utilization of nitrogen may have occurred because of the high irradiance levels and high rates of growth. Tissue-nitrogen levels of fertilized plants were probably higher immediately following fertilization, but had declined prior to our sampling 8 to 10 d after the last placement of fertilizer. Tissue-nitrogen levels may also have been low because nitrogen was added in insufficient amounts to allow for accumulation of surplus.

As indicated above, *Macrocystis pyrifera* (especially juveniles) have little capacity to store and later utilize surplus supplies of nitrogen. As a result, *M. pyrifera* appears to need high light and high nutrients almost simultaneously in order to maintain maximum growth rates. This is in contrast to other laminarian algae (e.g. Chapman and Craigie, 1978; Lüning, 1979), that can maintain high rates of growth for several months during periods of high light and low nutrients by mobilizing reserves of nitrogen that were stored when light was low and nitrogen was high. Sufficient nitrogen supplies appear to be generally available in the waters of kelp forests in coastal southern California because of upwelling that occurs on a frequent basis even during the summer and fall months in most years (Dohrman and Palmer, 1981). Nutrient limitation appears to be prevalent only during extreme conditions such as El Niño.

Studies of adult *Macrocystis pyrifera* during the recent El Niño indicated that the growth of mature fronds was slowed and may have been nitrogen-limited (Gerard, 1984; Zimmerman and Robertson, 1985). However, Gerard (1984) attributed poor growth of smaller fronds on these plants to temperature stress. This contrasts with our results, which showed that if sufficient nitrogen and phosphorus were supplied to juvenile plants, growth rates were high even though temperatures were high. However, temperatures in our studies were not as high as observed by Gerard (18° vs 21 °C) and the possibility of temperature stress at higher temperatures cannot be ruled out. It is also possible that there was some interaction between temperature and nitrogen uptake (Lapointe *et al.*, 1984) and that if somewhat lower nitrogen levels were provided, temperature stress or the interactive effects of high temperature and low nutrients may have been more apparent.

It is also possible that phosphorus may have limited growth during El Niño. Juvenile *Macrocystis pyrifera* in culture become phosphorus-limited after 2 wk exposure to



**Fig. 2.** Time histories of irradiance and temperature and deviations from the 56 yr average monthly temperature in southern California from 1978 through 1984. Temperature data are from 9 m below surface at Scripps Institution of Oceanography pier in La Jolla, California. Mean monthly temperatures (dashed line) and the 56 yr monthly mean temperatures (continuous line) are given. Irradiance data are mean monthly values from flat-plate collectors placed on the bottom at SOKD in the San Onofre kelp forest in an area that was cleared of kelp and understory algae

< 1  $\mu\text{M}$  phosphorus, when tissue-phosphorus levels reach 0.2% dry weight (Manley and North, 1984). We did not measure phosphorus in our study, and do not know whether phosphorus levels were below those critical for maximum growth. However, in coastal waters of southern California, phosphorus to nitrogen ratios increase as levels of nitrogen decrease, suggesting that nitrogen becomes limiting before phosphorus (North *et al.*, 1982).

The physicochemical conditions observed in our 1984 experiments were typical of those which prevailed along the southern California coast from Fall 1982 through Fall 1984. Temperatures were higher than normal along the Southern California Bight during 1982 and 1983 (Dayton and Tegner, 1984; Fiedler, 1984), and despite a return to near-normal current regimes in Fall 1983 (Kerr, 1983), temperatures remained high through 1984 (Fig. 2). Based on the generally strong associations between high temperatures and low nutrients (Jackson, 1977; Zimmerman and Kremer, 1984), nutrient levels probably also remained low through 1984. In addition, bottom irradiance-levels

were substantially higher from 1982 through 1984 than in previous years. Average 2 wk irradiance values on the bottom at SOKD were significantly higher during El Niño (October 1982 to December 1984) than during a similar time period (October 1979 to December 1981) before El Niño ( $P < 0.05$ , Student's *t*-test). Thus, the poor summer and fall growth of juvenile *Macrocystis pyrifera* observed at San Onofre and elsewhere (Dayton and Tegner, 1984; Zimmerman and Robertson, 1985) during El Niño was probably due to nutrient limitation. The slower growth of juveniles can affect their competitive ability (Dayton and Tegner, 1984), and subsequent survival (Dean, unpublished data) and presumably, the eventual distributions of adult *M. pyrifera*.

**Acknowledgements.** We thank all those who assisted in field work, especially K. Thies and S. Lagos. L. Deysher provided comments on an earlier draft of the manuscript. Scripps Pier temperature data were kindly provided by G. Andersen of Scripps Institution of Oceanography, La Jolla, California. Temperature and irradiance data from the San Onofre and San Mateo kelp forests were supplied by ECOSystems Management Associates, Inc., Encinitas, California. This project was funded by the Marine Review Committee, Inc., Encinitas, California. However, the Committee does not necessarily agree with the results or conclusions herein.

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Date of final manuscript acceptance: October 25, 1985.

Communicated by J. M. Lawrence, Tampa