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Episodic nutrient supply to a kelp forest ecosystem in Southern California

by Richard C. Zimmerman[1] and James N. Kremer[1]

ABSTRACT

Temporal patterns of nutrient input into a Southern California kelp forest were measured using traditional hydrocast sampling coupled with high frequency temperature profiling. Patterns of nutrient input were related to growth rates of *Macrocystis pyrifera* located in an adjacent kelp forest. There were 2 distinct components to the pattern of nutrient availability. The long term, or seasonal, component was consistent with large-scale storm-induced mixing and horizontal advection during winter months. In addition, vertical motions of the thermocline, bringing nutrients into the kelp forest, occurred throughout the year with a frequency of about 2 per day and were strongest during the summer months. Weekly hydrocast sampling methods were inadequate for measuring these episodic events, and high frequency sampling was required to resolve the pattern of nutrient input accurately. Although measurable, nutrient input from vertical thermocline motion was inadequate to sustain maximum growth of *Macrocystis pyrifera* at 10 m depth during the summer months. Thus, the major component of nutrient input came during the winter. These results indicate that nitrate limitation of *M. pyrifera* is a likely cause of reduced summer growth. Further, high frequency sampling is necessary to predict nutrient availability in nearshore ecosystems dominated by benthic macrophytes where the pattern of nutrient input is dominated by episodic events of short duration.

1. Introduction

Transport of nitrate into the euphotic zone appears to be a major factor regulating primary production in Southern California coastal waters (Eppley *et al.,* 1979). The mechanisms of nutrient transport are largely dependent on geographic location within the Southern California Bight, which can create complicated temporal patterns. Local upwelling events (Tont, 1976; Huyer, 1976), horizontal advection of cold, nutrient rich waters of the California current (Jones, 1971), and anthropogenic inputs from coastal runoff and sewage discharges (Eppley *et al.,* 1979) are important sources of nutrients for the Bight.

A previously unevaluated source of nutrients for benthic macroalgal systems may come from the periodic upward vertical movement of the thermocline. Studies by Armstrong and LaFond (1966), Cairns and LaFond (1966), Cairns (1967; 1968), and

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Cairns and Nelson (1970) have shown frequent upward excursions of cold water below the thermocline into the upper 10 m of the water column. These excursions were linked to internal waves and semidiurnal tides and were of short duration, lasting one to several hours. Nutrient concentrations in that cold water can be quite high, and Jackson (1976) suggested that such oscillations may be a significant but difficult to measure source of nutrients for benthic macroalgae, such as the giant kelp, *Macrocystis pyrifera.*

The severe decline and occasional disappearance of *Macrocystis* canopies in Southern California during the late summer and fall is well documented and historically has been attributed to high ambient water temperatures (Clendenning, 1971; Lobban, 1978; McFarland and Prescott, 1959; North, 1971a). However, Jackson (1976) argued that nutrient availability may be important, and noted that the periodic decline in kelp productivity occurs when ambient nutrient concentrations should be lowest. Yet, in previous efforts to understand the growth dynamics of *M. pyrifera,* no strong seasonal pattern of nutrient availability was found when ambient nutrient concentrations were measured at approximately weekly intervals (Gerard, 1976; North, 1971b; Wheeler, 1978; Wheeler and North, 1981). We chose to begin our study on the role of nutrients in regulating the productivity of kelp forests by measuring the exposure of *M. pyrifera* to the nutrient supply more accurately than had been done before, by determining whether there was a strong seasonal pattern in nutrient availability, and whether periods of rapid and slow growth coincided with these variations in nutrient input.

2. Methods

a. Study site. The study site was located near the U.S.C. Catalina Marine Science Center on the leeward side of Santa Catalina Island (Fig. 1). The kelp forest formed a band 50 m wide running parallel to the shoreline in this region. Depths ranged from 3 m on the shoreward edge of the kelp forest to 15 m offshore. Longshore currents were related to the stage of the tide, running toward the east end of the island on falling tides and toward the west end on rising tides. Current speeds were frequently fast enough to hold the kelp canopy below the surface, sometimes forcing it all the way to the bottom.

b. Hydrocasts. Water samples for nutrient analyses were collected using 1.5 l Nansen bottles fitted with protected reversing thermometers. Hydrocasts were performed at 7–10 day intervals from May 1980 to December 1981 at a permanent station (marked "H" in Fig. 1). Sampling depths were determined each time from bathythermograph (B-T) profiles taken immediately before deploying Nansen bottles. If the water column was stratified above 60 m, water samples were taken at the surface, in the middle of the

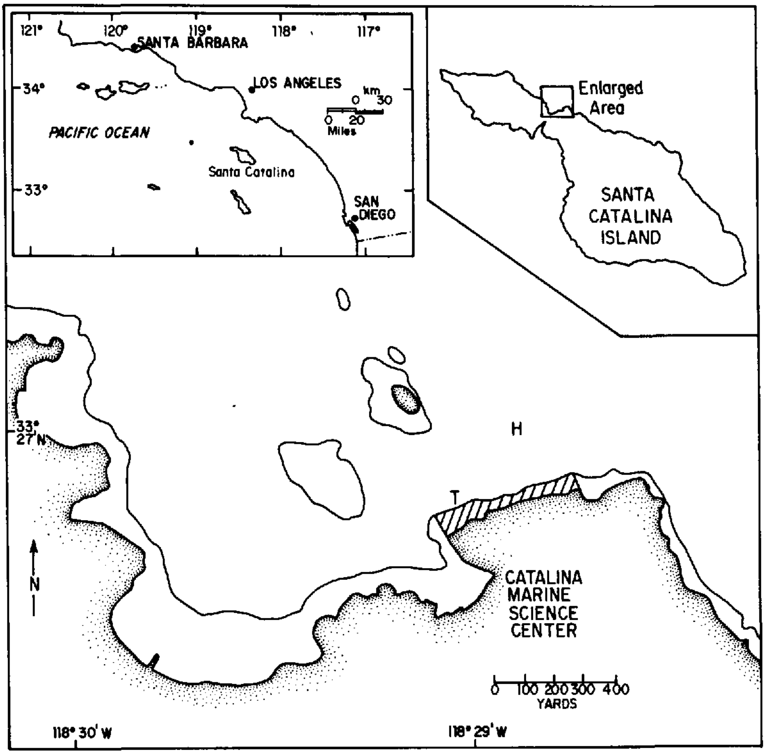

Figure 1. A map of the study site at Santa Catalina Island. "H" marks the location of the hydrocast station. "T" marks the location of the thermistor chain at the seaward edge of the kelp forest, which is indicated by the cross-hatched area. The contour line indicates the position of the 20 m isobath.

mixed layer, at the top of the thermocline, at the bottom of the thermocline and at least 10 m below the thermocline. If the water column was well mixed to 60 m, 5 samples were taken at 15 m intervals from the surface to a depth of 60 m.

Samples were analyzed for ammonium concentration using the indolphenol blue method of Solorzano (1969) scaled down to sample volumes of 5 ml. The remainder of each sample was frozen for not more than a month and analyzed for nitrate concentrations using the cadmium reduction technique (Strickland and Parsons, 1972). Nitrite concentrations of these samples were also measured using methods described by Strickland and Parsons (1972). Least-squares linear regression analysis was used to determine the necessary relationship between water temperature measured by the reversing thermometers and nitrate concentration. This relationship was used to estimate ambient nitrate concentrations from the high frequency temperature profile data.

c. High frequency temperature profiles. A thermistor chain was constructed from armored oceanographic cable and 9 YSI 44033 precision thermistors. The chain was moored to a taut-line buoy located at the seaward edge of the kelp forest (Marked "T" in Fig. 1). Thermistors were located at 2, 4, 6, 8, 10, 12, 15, 17, and 19 m depth (mllw). The cable ran shoreward through the kelp forest and into the laboratory where it was connected to a timed multiplexer, a telethermometer, and a recorder. Thermistors were scanned every 30 min, temperatures were recorded automatically and later digitized to 0.1°C. Two fixed-resistance calibration standards corresponding to 12.2°C and 17.0°C were recorded with every profile. It took approximately 20 sec to scan all 9 thermistors and 2 standards. Thermistor recordings were calibrated frequently to temperatures measured at each thermistor by SCUBA divers using a hand-held reversing thermometer. B-T profiles were used as a second calibration of the thermistor chain.

The average monthly concentration of nitrate available to the kelp forest was calculated using the temperature-nitrate (T-N) regressions derived from the hydrocast data and the high frequency temperature profiles. This computation assumed an 11 m water column divided into 5 homogenous layers, each with a thermistor at its center. The nitrate concentration of each layer was estimated for every 30 min interval using the T-N regression derived from the hydrocast data and the instantaneous temperature values recorded from the corresponding thermistor. Mean nitrate concentration of the water column was estimated by averaging the nitrate concentrations of all 5 layers for each temperature profile recorded. Estimated monthly nitrate concentrations were then calculated as the mean of these half-hourly estimates for the whole water column based on the temperature-nitrate regressions.

d. Kelp growth rates. Frond elongation rates were measured *in situ* each month using a total of 50 subcanopy fronds distributed among 10 plants. A length of plastic flagging tape was tied to each frond 1 m behind the growing tip of the frond. The frond was remeasured from the tip to the tag 2 weeks later, with the increase in length used as a measure of frond growth.

3. Results

a. Hydrocasts. The water column near the study site was usually stratified thermally through the 20 months of this study (Fig. 2), although the thermocline occasionally disappeared during winter. Thermocline depth varied between 5 m and 30 m. The gradient across the thermocline was on the order of 0.3°C m^{-1} during winter and approximately 1°C m^{-1} during summer. Seasonal temperatures above the thermocline ranged from 15°C during winter to 20°C in summer. Temperatures at the bottom of the thermocline were more stable temporally, fluctuating between 12°C and 15°C seasonally.

Nitrate concentrations ranged from undetectable to more than 15 μg-at l^{-1}, frequently within a single hydrocast. Nitrate concentrations frequently varied as much

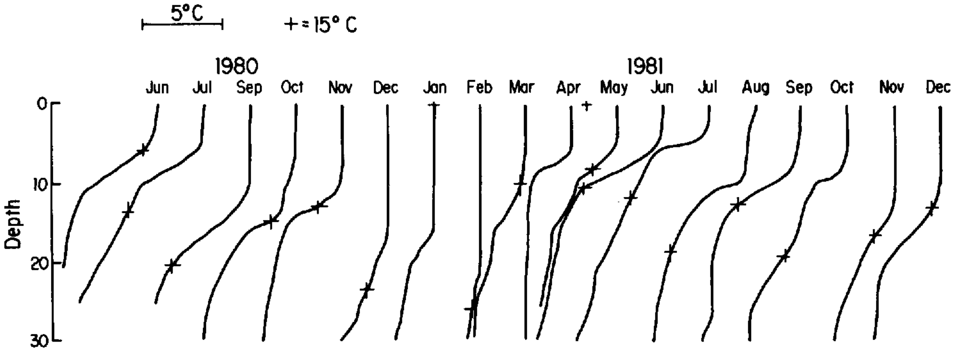

Figure 2. Representative temperature profiles recorded by bathythermograph at Station H between 8 June 1980 and 13 December 1981. The depth of the 15°C isotherm on each profile is indicated by the "+" symbol.

between depths on a single hydrocast as from season to season at the same depth. Surface nitrate values were consistently low, usually less than 0.5 μg-at l^{-1} (Fig. 3). Nitrate concentrations at 10 m were only slightly higher, while they were generally much higher at 20 m. The nitracline was always associated with the thermocline. However, despite typical seasonal changes in thermal structure, no strong seasonal pattern of ambient nitrate concentration availability was evident from the hydrocast data (Fig. 3).

Nitrite and ammonium concentrations were almost always at the lower limits of analytical detection. Nitrite generally increased with depth, but concentrations rarely exceeded 0.5 μg-at l^{-1}. Ammonium never exceeded 0.2 μg-at l^{-1}, and showed no pattern of vertical distribution, even after rainstorms involving terrestrial runoff.

The relationship between nitrate concentration and water temperature was remarkably constant throughout the study (Fig. 4). Nitrate concentrations in water colder than 15.5°C were greater than 1.0 μg-at l^{-1} and were uniformly low above 15.5°C. This temperature appeared to be a discontinuity, with nitrate concentration a constant function of temperature below 15.5°C and above 15.5°C, but with different equations describing the temperature-nitrate relationships (Table 1).

b. High frequency temperature profiles. Thermistor profile data collected between August 1980 and December 1981 showed great temporal variability. Daily temperature range was largest from April to July, while mean monthly water temperatures were highest from July to September and lowest from January to April (Fig. 5). Error bars represent the error mean square or variance for each month. Variances were plotted instead of standard deviations as the large sample size resulted in standard deviations on the order of 0.05°C. They are presented here to provide an indication of the temporal variability and spatial range in thermocline movement. Low temperatures recorded at 2 m depth during June and July 1981 were as low as the lowest

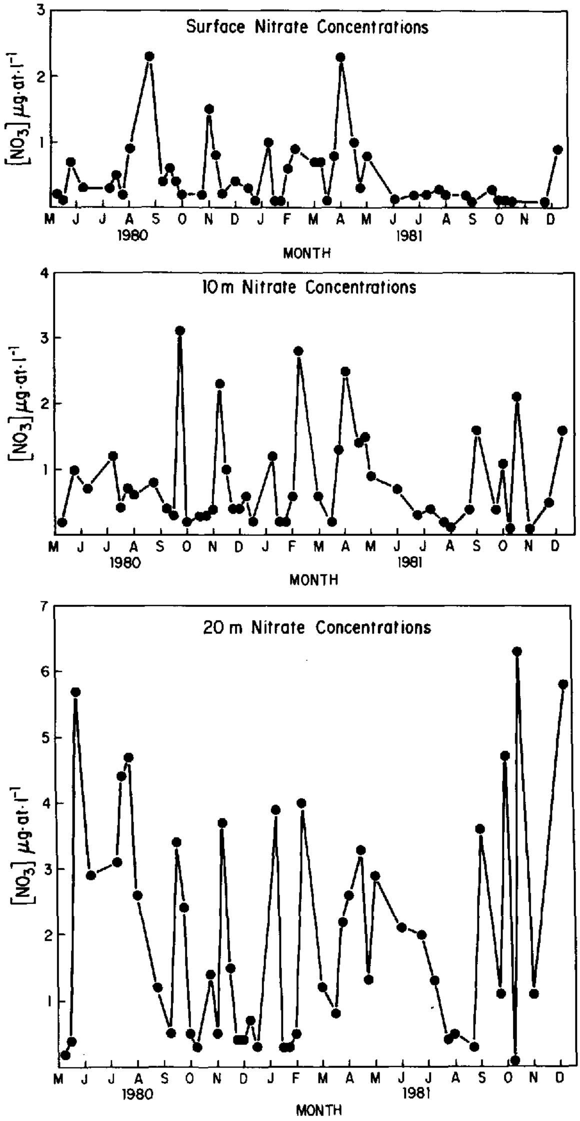

Figure 3. Seasonal nitrate concentrations at 0 m, 10 m, and 20 m based on 7–10 day hydrocast samples.

temperature recorded during the previous winter, although the mean temperature was 6°C higher. Thus there were times during the summer when cold, nutrient-rich water entered shallow regions of the kelp forest. Although the temperature range at each depth was basically the same, variances around the means were quite different, especially during the summer months, indicating that incursions of cold, nitrate-rich

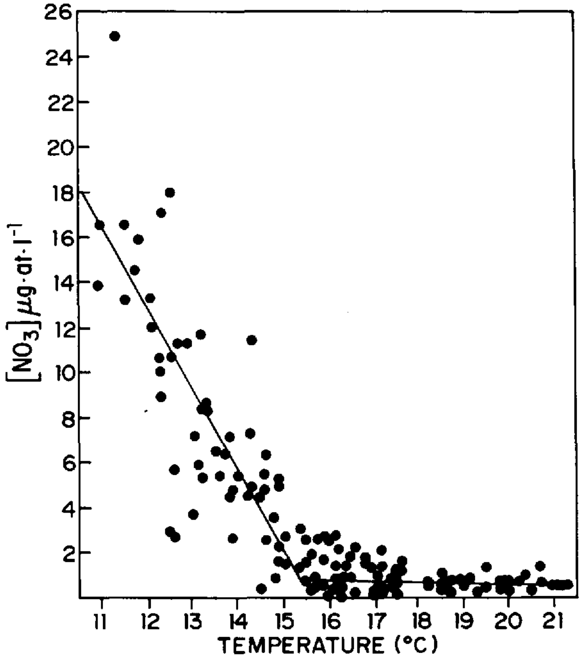

Figure 4. Nitrate concentration as a function of ambient water temperature. Samples were collected from 25 May 1980 to 18 Dec 1981 using Nansen bottles fitted with reversing thermometers. Lines indicate the least squares regression ($P < .01$) for temperatures above ($r^2 = .27$) and below ($r^2 = .81$) the critical 15.5° point.

water were more frequent as depth increased. The source of this cold water was the periodic movement of the thermocline. The amplitude of these periodic motions was greatest during late summer, when thermal stratification was greatest, and smallest during winter (Fig. 6). Spring and fall amplitudes were intermediate with more apparent "noise" in the data during spring. Spectral analysis revealed only one real peak in the variance spectrum of each time series, which corresponded to a period of 12.5 hrs, indicating that these periodic movements were linked to the semidiurnal internal tides during all seasons. Thermocline depths generally became shallower as the tide ebbed and deepened with the rising tide, although the exact magnitude of movement was unpredictable.

When combined with estimates of nitrate concentration based on T-N regressions

Table 1. Regression analysis of temperature-nitrate relationship. "P" is the probability that there was no significant relationship between nitrate concentration and temperature.

Temp range	Slope	Y-intercept	r^2	F_s	P
<15.5°C	−3.866	60.237	.806	70.68	<.001
>15.5°C	−0.131	2.961	.266	11.58	<.01

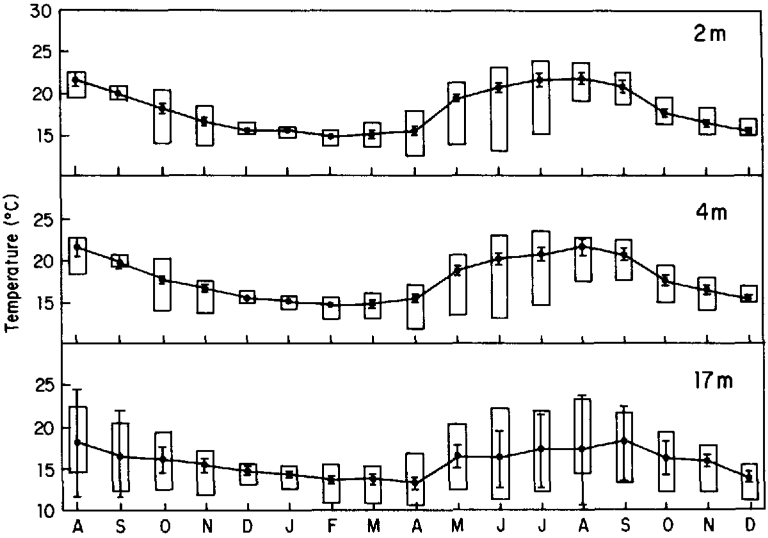

Figure 5. Mean monthly temperatures (± variances) at 2 m, 4 m and 17 m. Boxes indicate range of maximum and minimum temperatures.

from the hydrocast data, the intensive temperature sampling revealed a strong seasonal pattern of nitrate availability that had been undetectable by conventional weekly hydrocasts alone. Nitrate was most abundant from December to April (Fig. 7). Estimated monthly nitrate concentrations (averaged over the upper 11 m) ranged from 2.2 to 9.0 μg-at l^{-1} during that period. Mean nitrate concentrations were less than 2.0 μg-at l^{-1} during the rest of the year, and were frequently less than 1.0 μg-at l^{-1}. Mean nitrate concentrations during the summer months were 5 to 10 times lower than maximum winter values. Because the vast majority of kelp biomass is near the surface, nitrate concentrations were also calculated for a 3 m water column. Although the estimated nitrate concentration was decreased in the smaller water column, the seasonal pattern of availability remained the same.

c. Effect of sampling frequency. By sampling our high frequency data set with different schedules, a significant effect of sampling frequency on the accuracy of the estimates was demonstrated. Reduced sampling frequencies generally underestimated nutrient availability because they missed many of the short pulses of nutrient input. Mean monthly nitrate concentrations were 78% of the best estimate using only a single thermistor profile produced every 7–10 days (Fig. 8). Estimates based on one thermistor profile per month averaged 42% of the best estimate, while high frequency temperature profiles for one day each month averaged 91% of the best estimate.

d. Relationship to kelp growth. A plot of mean frond elongation rates against the most accurate estimate of mean monthly nitrate concentration showed a clear relationship

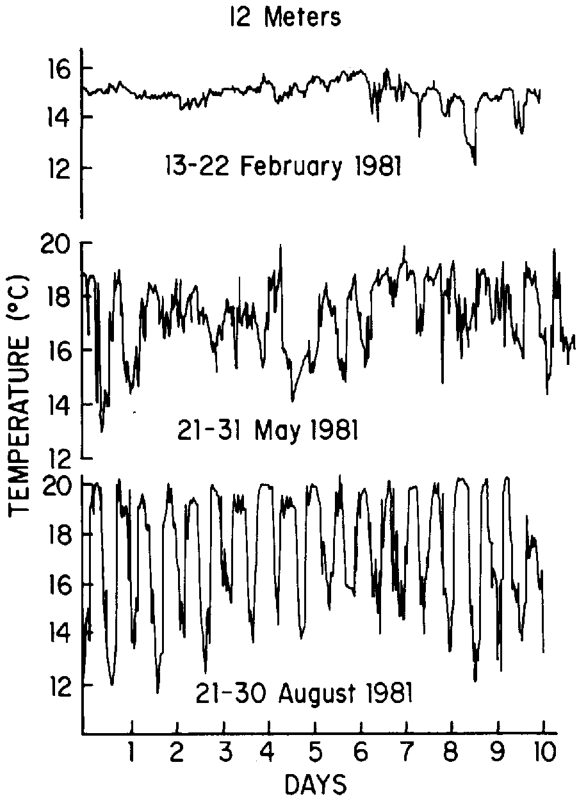

Figure 6. 10 day temperature records from a thermistor at 12 m depth during 13–22 February 1981, 21–30 May 1981, and 21–30 August 1981.

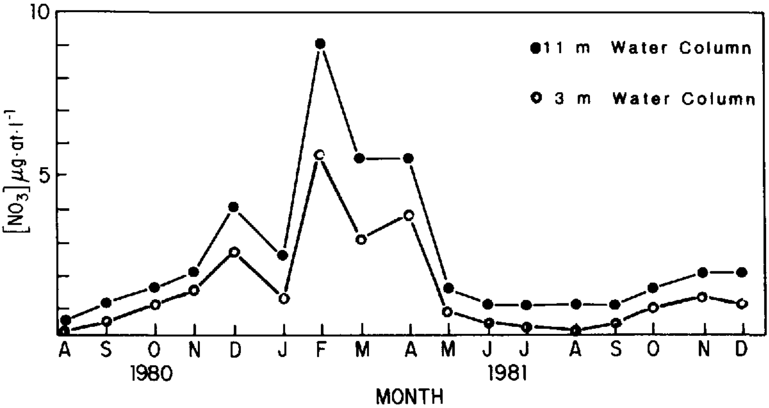

Figure 7. Estimates of mean monthly nitrate concentrations for water columns of 3 m and 11 m. Estimates were calculated from the temperature-nitrate relationships (Table 1) and the high frequency temperature profiles, representing more than 4,500 observations mo^{-1}.

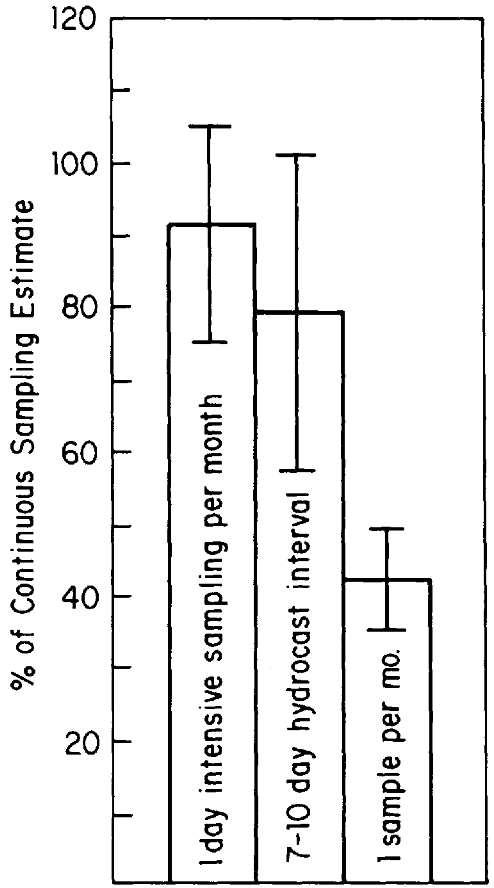

Figure 8. Comparison of the abilities of 3 sampling strategies to predict mean monthly nitrate concentrations for the 11 m water column. Error bars indicate ± 1 S.E. of the mean.

between the 2 variables (Fig. 9). Growth rates were reduced whenever estimated nitrate concentrations dropped below 1.0 μg-at l^{-1}. These growth data are well approximated by the Monod rectangular hyperbola conventionally used to describe the dependence of plant growth on nutrient concentration, although it may be argued that 2 straight lines provide a better fit. The half-saturation constant for growth (K_s) obtained by the linear regression of $[NO_3]$/GROWTH vs. $[NO_3]$ (Dowd and Riggs, 1965) was 0.3 μg-at l^{-1}. While no data were available for very low nitrate concentrations, the data define well the transition and support the extrapolation to the origin.

Dramatically different values of K_s were obtained from the other sampling regimes (Table 2). Conventional sampling provided much lower estimates of K_s, leading to an underestimate of the limiting role of nitrate. However, the magnitude of the maximum growth rate (V_{max}) is relatively insensitive to the different sampling frequencies as all

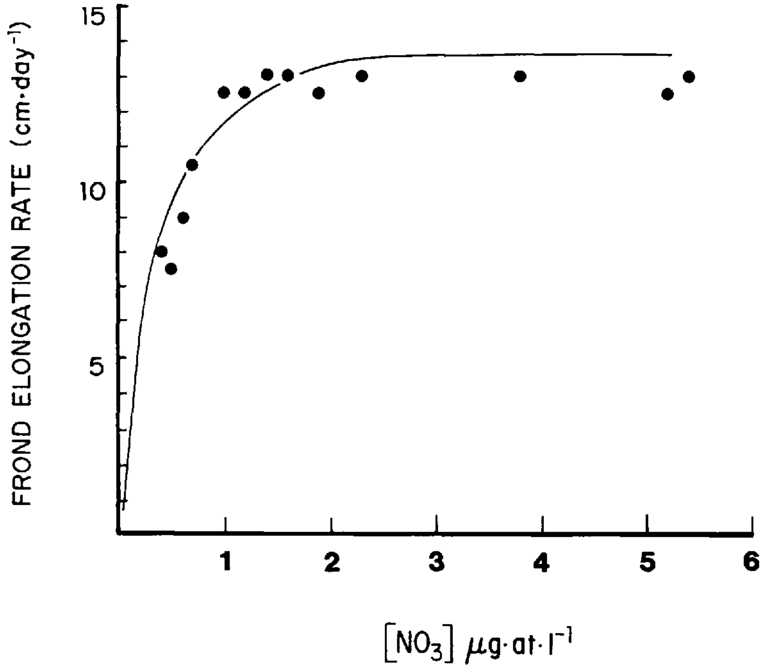

Figure 9. Monthly mean frond elongation rates plotted as a function of estimated nitrate concentration for an 11 m water column (from Fig. 8). The curve was drawn using the kinetic parameters derived from a $[NO_3]$/GROWTH vs. $[NO_3]$ transformation (Table 2).

equations converge at similar asymptotes. Interestingly, the transformed linear coefficients of determination, r^2, remained high regardless of the sampling intensity, but residual sum-of-squares of untransformed data to the Monod curve clearly demonstrate the decreased adequacy of the hyperbolic model due to increased error in estimating nutrient availability from the less intensive nutrient sampling strategies. By all criteria the intensive 1-day per month strategy compared quite favorably, and may provide a viable alternative to continuous sampling in the future.

Table 2. Monod parameters estimated from $[NO_3]$/GROWTH vs. $[NO_3]$ plots using 4 different nutrient sampling strategies. Also listed are the least-squares r^2 for the $[NO_3]$/GROWTH vs. $[NO_3]$ linearization plot and the untransformed residual sum of squares (*SS*) for growth data fit to the Monod curve generated by each strategy.

Method	V_{max}	K_S	r^2	*SS*
High frequency	15.38	.32	.991	12.61
1 day intensive	14.29	.33	.989	23.78
7–10 day interval	14.71	.16	.949	36.06
1 sample per month	13.33	.09	.986	69.41

4. Discussion

The annual cycle of thermocline formation depicted for the study site at Santa Catalina Island was very similar to that for the shallow coastal area off San Diego (Cairns and Nelson, 1970; Winant and Bratkovich, 1981), except that even in winter, a thermocline was usually present in the upper 20–30 m of the water column. This may be due to the protected nature of the leeward side of the island, where the strength of winter storms and prevailing westerly winds is reduced. As a result, the importance of local events on upward mixing of nutrients from deep water may be less than along the mainland, and changes in the vertical structure of the water column may depend more on horizontal advection of cold, nutrient-rich water from other locations.

This study site did not appear to be a location of significant summer upwelling. Temperature profiles collected from August 1980 to December 1981 provided no evidence of a single upwelling event in the traditional sense. Wind induced upwelling occurs in the Southern California Bight on an average of twice a summer, with a maximum surface temperature change of 4.7°C and a mean duration of 11.4 days (Dorman and Palmer, 1981). There were no temperature anomalies of such duration or magnitude during the entire 17 months of this study. The water column was usually stratified thermally, and water temperatures at 2 m depth were never less than 14°C for more than an hour at a time.

The temperature-nitrate relationship described here is characteristic of the Southern California Bight (Eppley. *et al.*, 1979; Zentara and Kamykowski, 1977). The relationship was temporally stable, although there was some noise, which may have been caused by advection of different water parcels into the area at different times of the year. Increased variability in the T-N relationship between 14.5 and 18°C was caused by seasonal variations in the thickness and strength of the thermocline. During summer and fall, these temperatures were within the thermocline, while the same temperature range was well above the thermocline during the winter and spring.

Although the availability of nitrate was clearly seasonal, hourly variability in thermocline depth required a high frequency sampling strategy to detect that pattern. High frequency temperature profiles indicated that *daily* variations in temperature (and therefore nitrate concentrations) at a given depth were frequently as great or greater than mean seasonal variations. This explains the lack of a significant seasonal pattern in nitrate concentration in the upper 20 m of the water column based on the low-frequency hydrocast data alone. Because of this high frequency signal, and because the duration of each pulse was relatively short, even 1 day of intensive sampling each month produced more accurate results than sampling once a day several times each month. Furthermore, frequent sampling throughout 1 day each month is preferable because it minimizes the additional problem of aliasing caused by fluctuations in thermocline depth that are of shorter period than the sampling interval (Platt and Denman, 1975). Sampling over a full tidal cycle but with longer intervals might be adequate since the tidal component was dominant. However, its precise effect was unpredictable, and thus an intensive sampling regime is probably required to assess the real variability.

The high frequency oscillations in thermocline depth observed in this study usually do not result in significant mixing of nutrients upward into the surface layer (Armstrong and LaFond, 1966). In the case of *M. pyrifera*, both mean nitrate concentrations and growth rates were lowest during the months when thermocline movement was greatest. Thus, these incursions were not adequate to prevent nutrient limitation. However, this does not imply that they are unimportant, as recent data on the effects of the 1982–83 El Niño on *M. pyrifera* indicate that such periodic incursions of nutrient-rich water may be necessary for survival during the summer (Zimmerman and Robertson, in prep.).

High frequency temperature profiling clearly improved the estimates of nutrient availability, exhibiting much less "noise" than was encountered in previous studies and allowing much clearer resolution of the nutrient-growth relationship. However, previously studied mainland coastal kelp forests may have received larger nutrient inputs than this kelp forest at Santa Catalina Island such that growth was never really nutrient limited during those studies (Gerard, 1976; Wheeler, 1978; Wheeler and North, 1981). In this study, kelp growth saturated at estimated mean nitrate concentrations above 1.0 μg-at l^{-1}, and nutrient concentrations are generally higher along the mainland than they are in the vicinity of this study site (Eppley *et al.*, 1979; Jackson, 1976; Wheeler, 1978; Wheeler and North, 1981). Future studies of the growth dynamics of *M. pyrifera* must achieve similar resolution of the nutrient signal in order to determine accurately the relationship between kelp growth dynamics and nutrient availability.

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