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Effect of Nutrient Availability on *Macrocystis pyrifera* Recruitment and Survival near Its Southern Limit off Baja California

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The effect of nutrient availability on *Macrocystis pyrifera* recruitment and survival of juvenile sporophytes was examined at its southern limit off Baja California, Mexico. Nitrate levels were inversely correlated with water temperature ($r^2 = 0.70$) at the experimental location. Low concentrations of nitrate occurred during most of 1998 (< 3 µM) except in spring (4.8–18.8 µM). Experimental seeding with sporophylls and fertilizing the plants with a slow-release inorganic fertilizer produced successful recruitment when the water temperature was declining (18.7 °C). Survival of transplanted juveniles was significantly higher when fertilized during a period of particularly warm water and low nutrients in 1998 caused by El Niño. Analysis of tissue nitrogen suggests that plants were nutrient-limited during this period, and possibly affected synergistically by temperature stress. The results indicate that nutrients directly affect recruitment and survival of giant kelp at its southern limit, particularly during El Niño conditions.

Introduction

The primary factors controlling growth of *Macrocystis pyrifera* (L.) Agardh sporophytes in southern California are light, temperature, nitrogen concentration, and amount of fouling (Dean and Jacobsen 1984, North *et al.* 1986). Some authors suggest that the decline in juvenile (Wheeler and North 1980) and adult growth (Jackson 1977, Gerard 1982, Zimmerman and Robertson 1985, Zimmerman and Kremer 1986) during summer and autumn results from nitrogen limitation. Dean and Jacobsen (1986) found that growth of juvenile plants under high temperature and low nutrient conditions was enhanced by fertilization, but pointed out that temperatures during the experiment were lower than 18° C and thus stress at higher temperatures cannot be ruled out.

The distribution of *Macrocystis pyrifera* may be also determined by the stress tolerance of gametophytes or small sporophytes. The lack of sporophyte production may be because of high temperatures and low nutrients (Deysher and Dean 1986 a). The addition of extra nutrients to gametophytes in the field in California resulted in increased mean densities of subsequent sporophytes (Deysher and Dean 1986 b), suggesting that nutrients can be an important factor determining recruitment success. Moreover, the reproductive allocation, standing stock, relative nitrogen content, and swimming ability of *M. pyrifera* spores are greater when seawater temperature is low and ambient nitrogen is high (Reed *et al.* 1996). Studies on *Laminaria saccharina* (L.) Lamouroux have demonstrated that N-limited plants are more susceptible to the deleterious effects of high temperature than N-repleted plants, indicating that large-scale declines in algal productivity, such as those that typically occur during El Niños, may result from the interactive effects of nitrogen limitation and heat stress (Gerard 1997).

Knowledge of the boundary conditions for important physico-chemical variables (irradiance, nutrients, temperature, and seston flux) provide a useful index for describing the potential *Macrocystis pyrifera* habitat and allow an assessment of the importance of non-physical environmental factors (biotic) which potentially control the distribution of this species (Deysher and Dean 1986 b). Following the 1982–83 El Niño, *M. pyrifera* forests disappeared at the southern limit of their distribution off southern Baja California and never recovered in the southern-most area from Punta San Pablo to Punta Prieta, a region encompassing 50 km of coast (Hernández-Carmona 1987, Dayton and Tegner 1990). Restoration techniques using transplanted juveniles and fertile sporophylls have demonstrated that *M. pyrifera* can survive in this area (Hernández-Carmona *et al.* 2000), but little is known about the factors controlling its recruitment and survival under natural conditions.

In this study we tested the hypothesis that *Macrocystis pyrifera* recruitment and juvenile survival are limited by low nutrient concentrations, which may be also correlated with high temperatures during summer at the southern limit.

Material and Methods

The experiment was carried out at Isla Asunción (27°6′ N; 114°17′ W) and Punta Prieta (27°1′ N; 114°3′ W), southern Baja California, at 10 m depth (Fig. 1). The two locations are 25 km apart and have similar oceanographic conditions (maximum difference in surface temperature was + 0.5 °C, personal observation), therefore all physical and biological data obtained were pooled and analyzed for the two areas as one. The sporophyll addition or 'seeding experiment' was carried out from April (the usual recruitment time, personal observation) to December 1998. To assess the effect of nutrient availability on *Macrocystis pyrifera* recruitment we used a two-factor orthogonal block design with two levels in each factor, with sporophylls (+/−nutrients) and without sporophylls (+/−nutrients). Four blocks were used with one replicate of each combination of treatment level in each block. Three experimental blocks with the four combinations were set up on Isla Asunción (IA) and one at Punta Prieta (PP). Treatment levels at IA were separated by 10 m under the assumption that this distance was enough to eliminate spores or nutrients traveling from one treatment to another (Deysher and Dean 1986 b). Each combination of treatment levels (i. e. + sporophylls + nutrients) was in a one square meter plot. All understory algae were removed from the plots using a scraper and metallic brush to avoid the effect of competition with understory algae (Hernández Carmona *et al.* 2000). The first treatment-level combination was selected at random and the rest were placed in systematic order to increase the distance between treatments with nutrients and without nutrients.

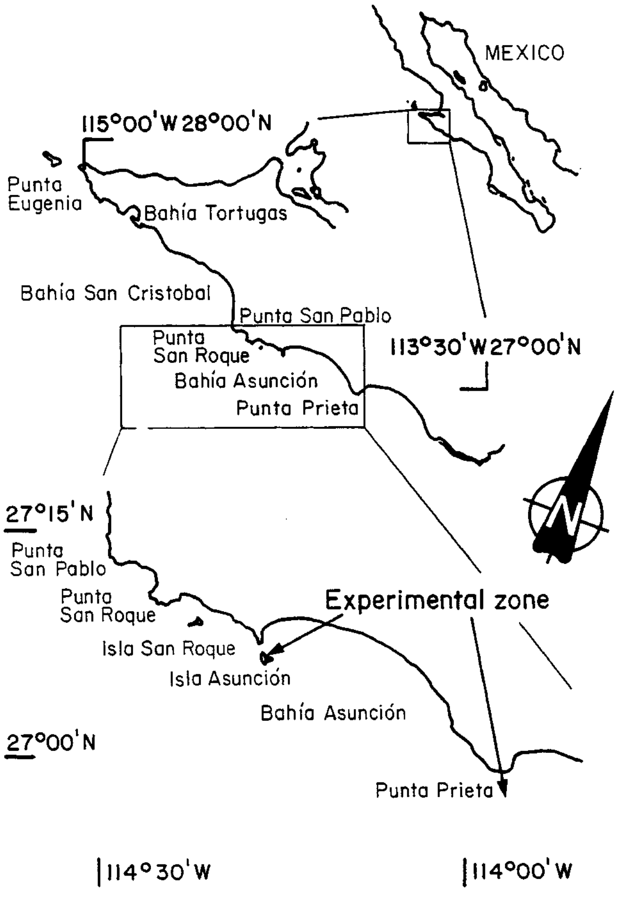

Fig. 1. Experimental area for transplanting *Macrocystis pyrifera* sporophylls and juveniles; Isla Asunción (experimental blocks 1 to 3) and Punta Prieta (experimental block 4).

Macrocystis pyrifera sporophylls were collected from a kelp forest off San Diego, California (686 km north of the study site) from April to August 1998. After the 1997 El Niño this was the closest kelp forest to the study site. From September to December 1998, sporophylls were collected from Punta Eugenia (PE), southern Baja California, after adult *M. pyrifera* returned to this location. The sporophylls were transported in a wet, cool, dark box and transplanted at IA and PP. A concrete base (56 × 36 × 12 cm) with a cage (2.5 cm mesh) was placed in each treatment (Fig. 2). For the treatment with sporophylls, at least 50 reproductive blades per cage were used, and the cages were refilled every month. Pipes made of PVC (15 cm diameter × 40 cm long) were drilled with 48 holes and filled with 8 Kg of slow-release inorganic fertilizer (Multicote®), a blend of ammonium nitrate, phosphate and potassium salts (17% N, 17% P, and 17% K) pelletized and coated with a semipermeable

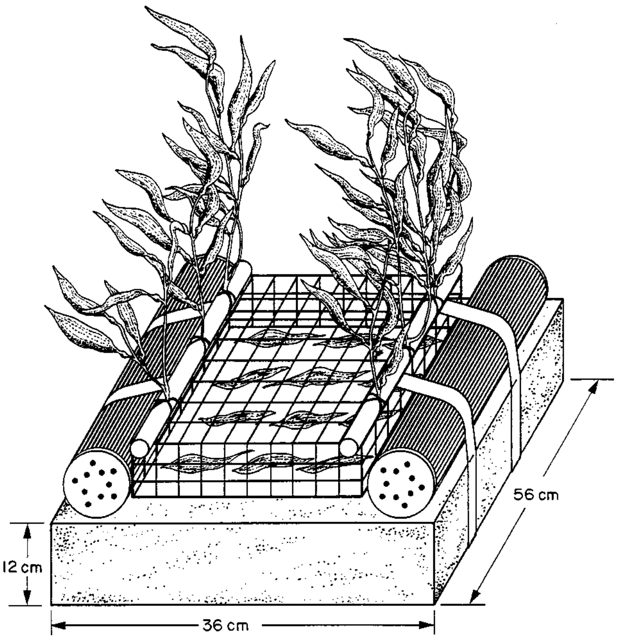

Fig. 2. Concrete base used to seed the experimental area with *M. pyrifera* sporophylls and attach juveniles. Nutrients were supplied from slow release fertilizer introduced in the PVC pipes. Treatments without nutrients were set up without the pipes.

polymer film. To maintain a constant supply of nutrients, two of these pipes were placed at the sides of the cages in the treatments with nutrients and refilled with the fertilizer every month. The number of *M. pyrifera* recruits (plants > 1.5 cm height) was recorded monthly. At this size, *M. pyrifera* recruits were distinguished from *Eisenia arborea* Areschoug by their lighter color and thinner blades.

An experiment examining the effects of nutrients on *Macrocystis pyrifera* juvenile survival was conducted from June to December 1998. Juvenile plants (average 230 cm length) were collected from Bahía Tortugas (84 km from the experimental location). The plants were detached from the bottom by hand and transported in black bags inside a cool box to the experimental sites (IA and PP). The plants were attached to a 2 inch diameter PVC pipe with nylon cord and the pipes were attached to the same cage as was used for the seeding experiment, using plastic cable ties. Two to four plants were transplanted in four plots with nutrients and four plots without nutrients (3 at IA and 1 at PP). A total of 13 plants were in each of the treatments. The number of juvenile survivors were recorded from June (time zero) to December 1998 (162 days). Data was compared using a test of the proportional difference between the survivors in the fertilized versus unfertilized populations (Daniel 1998). Total plant length was measured monthly from the primary basal dichotomy of the stipe to the tip of the apical blade of the longer frond. Average instantaneous relative growth rates (μ) were calculated for each treatment as described by Dean and Jacobsen (1984). The total number of fronds was counted monthly on each of the plants.

Surface water temperature was measured daily with a thermometer at Isla Asunción. The data were averaged and compared with long-term sea surface temperature records from 1989–1996 at the Bahía Asunción pier (Fernando López, Cooperative Leyes de Reforma). Bottom temperature (10 m) was recorded at 4 h intervals with a thermistor attached to the bottom near the transplant area. Temperature anomalies were computed as the numeric difference between the average long-term records (1989–1996) and the 1997 or 1998 records. Nitrate (μM) was determined from bottom seawater samples collected monthly at the fertilized quadrants. The samples were taken in the center of the nitrate source and at one meter from the source in three directions, 120 degrees apart, to detect the nitrate dilution and current direction. Surface and bottom (10 m) samples were taken near the unfertilized quadrants to determine ambient concentrations. The samples were frozen in liquid nitrogen for transportation, and analyzed for nitrate concentration using the cadmium reduction technique (Strickland and Parson 1972). Two laboratories were used to analyze the samples. When results from the two laboratories differed by more than 30%, the data were discarded. By using this criterion, 4 points of 38 observations were removed from analysis. Surface and bottom seawater temperatures were combined into one data set regardless of the date of sampling. Ambient nitrate concentration in water colder than 18.5 °C was greater than 1 μM, and was generally low above 18.5 °C, therefore the analysis of the temperature-nutrient relationship was carried out using two different equations as described by Zimmerman and Kremer (1984). For each equation a linear regression between the temperature and the corresponding nitrate concentrations was made. Least–squares linear regression analysis was used to determine the relation between water temperature and nitrate concentration. For the first equation (cold water), the critical point was determined at x intercept indicating zero nitrate concentration.

Tissue samples of adult *Macrocystis pyrifera* fronds ($n = 3$) from San Roque (March–August 1997 and October 1998), juveniles transplanted at IA (August–December 1998) and juveniles at Punta Eugenia (September–December 1998) were analyzed for total tissue nitrogen (% of the dry weight), using a CHN analyzer. Monthly samples of *Eisenia arborea* plants (25 stipes and blades) from IA (March 1997–December 1998) were also analyzed to compare the variation of tissue nitrogen among these two kelp species living in the same environment. Variation among plants was assessed by analyzing tissue from 4 plants. The standard error was typically lower than 0.07% of the mean. Average tissue nitrogen concentrations were compared within species and years using a t test.

Results

Environmental conditions at Isla Asunción

The minimum bottom seawater temperature during 1998 was recorded in spring (March–June) (13.3–15.7 °C) and increased rapidly during summer, peaking in August at 23 °C. Surface temperatures were similar to bottom temperatures (Fig. 3 a). The average surface temperature from long-term records (1989–1996) ranged from 14.1 to 21.8 °C, therefore the period from July 1997 to August 1998 (Fig. 3 b) reflected El Niño conditions (Wolter and Timlin 1998) with a maximum anomaly of +5.7 °C in August 1997. From September 1998 the trend changed to values slightly lower than average (normal) because of La Niña conditions (Fig. 3 b), starting with an anomaly of −1.3 °C in September.

During 1998, ambient nitrate concentration was low in winter (< 3.5 μM), summer (< 2.6 μM), and autumn (< 0.65 μM), and substantially higher in spring (4.8–18.8 μM) (Fig. 4). Surface and bottom nitrate concentrations were similar. The relationship between nitrate concentration and water temperature was highly significant ($r^2 = 0.70$, $p < 0.1$) with the critical point at 18.5 °C. Nitrate concentration in water colder than 18.5 °C was generally greater than

1.0 μM (Fig. 5). The equation describing this relation was: $[NO_3]$ μM = $55.62 - (2.999 * t)$. At water temperatures above 18.5 °C nitrate was generally lower than 1 μM, and the equation for this part was $[NO_3]$ μM = $1.599 - (0.023 * t)$. The average nitrate concentration in fertilized areas was 25.4 μM (within the range 8.52–49.6 μM) and in all cases the values were higher than in unfertilized areas (Fig. 4). Water samples around the nitrate source indicated that nitrate dispersion occurred towards the north during spring and west during summer (data not presented).

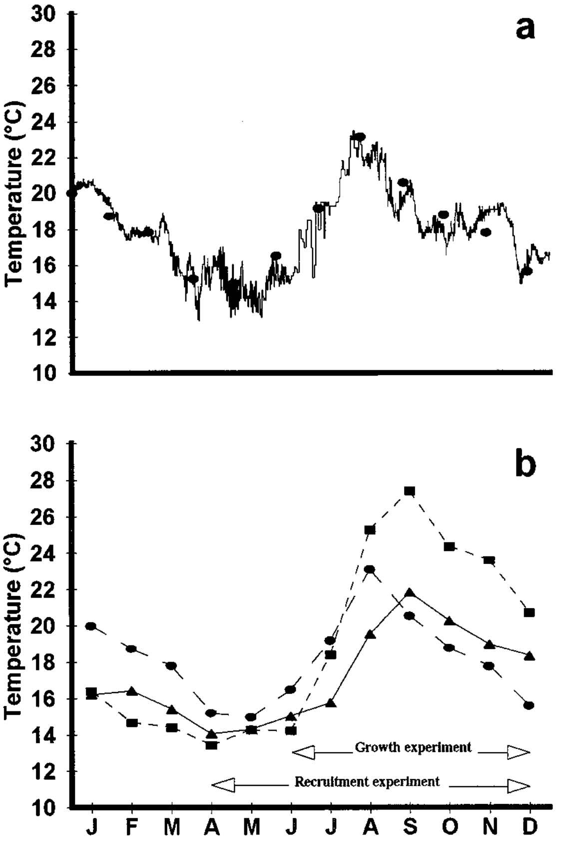

Fig. 3. a) Bottom seawater temperature (10 m deep) at Isla Asunción during 1998. Records were obtained at 4 h intervals with a thermistor (solid line). Monthly average surface temperature in Bahía Asunción, measured with thermometer (●). b) Monthly average surface temperature in Bahía Asunción, measured with thermometer during 1989–1996 (–▲–); El Niño 1997 (---■---) and El Niño-La Niña 1998 (---●---).

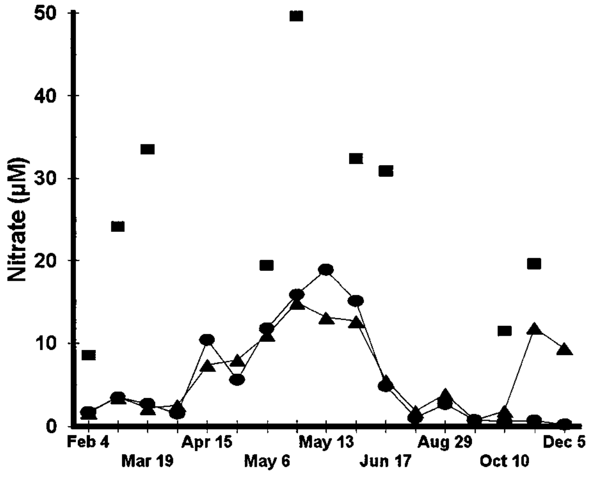

Fig. 4. Nitrate seawater concentration at Isla Asunción during 1998: surface (●), bottom (▲) and bottom (10 m) fertilized area (■).

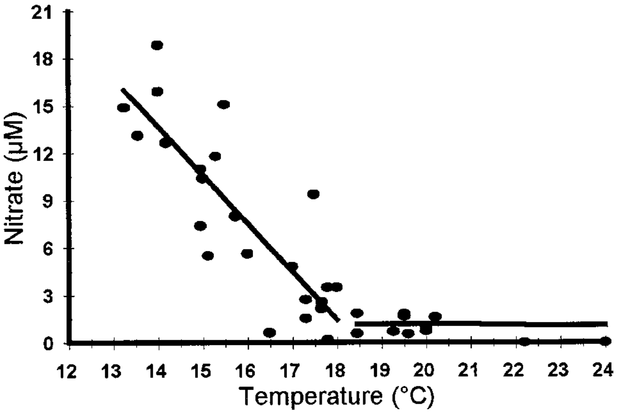

Fig. 5. Nitrate concentration as a function of ambient water temperature. Samples were collected from 4 February to 5 December, 1998 directly by divers. The solid line indicates the least squares regression computed for temperatures below 18.5 °C (critical point): $[NO_3]$ μ g-at $L^{-1} = 55.62 - (2.999 * t)$, and above 18.5 °C: $[NO_3]$ μ g-at $L^{-1} = 1.599 - (0.0233 * t)$.

Total tissue nitrogen concentration

Total tissue nitrogen content in *Eisenia arborea* from IA decreased from July 1997 to October 1998 (Table I). The monthly average in 1998 (1.07%) was significantly lower than 1997 (1.81%) (Student's *t* test, $p < 0.05$). *Macrocystis pyrifera* nitrogen content from San Roque was also high in spring 1997 (2.19%) and declined during summer 1997 to 1.45%, when the plants started to die. A new kelp forest was found at Punta Eugenia in June 1998 and samples from September 1998 showed low tissue nitrogen (0.68%). Tissue nitrogen increased to double this value by December 1998 (1.13%). *Macrocystis pyrifera* started to repopulate San Roque in October 1998 and also had a low tissue nitrate concentration (0.68%). Average (± std) tissue nitrogen in *M. pyrifera* fertilized transplants was 1.24% (± 0.075) (Table I). In September 1998, all plants (10) from three of the unfertilized treatment group were dying and only one piece of the remaining plants could be collected. The nitrogen concentration was very low (0.56%), and because there was no other survival in these three blocks, it was considered the final concentration of this group. In one of the blocks without nutrients, all the plants (3) survived and were growing at a rate similar to the fertilized plants. After analyzing the location of this treatment block, the cur-

Table I. Tissue nitrogen content (%) in *Eisenia arborea* and *Macrocystis pyrifera*, at the southern limit distribution for *M. pyrifera*.

	Eisenia arborea		*Macrocystis pyrifera*				
	Isla Asunción		San Roque		P. Eugenia	Isla Asunción	
						+F	−F
	1997	1998	1997	1998	1998	1998	1998
Mar	1.67	0.96	1.40				
Apr	1.88		2.19				
May	2.09	1.21	1.94				
Jun	1.89	1.26	1.93				
Jul	1.95	1.08	1.91				
Aug		1.07	1.45			1.19	
Sep	1.85	1.02			0.68	1.21	0.56
Oct	1.69	0.88		0.68	0.80		
Nov	1.65				0.96		
Dec	1.59	1.09			1.13	1.33	
Avg	1.81	1.07	1.80	0.68	0.89	1.24	0.56

+F = fertilized transplants; −F= unfertilized transplants.

rent direction, and the tissue nitrogen content of plants in it (0.89 %, data not in table), we concluded that it was ‘contaminated’ by the neighboring fertilized treatments. Because of the random selection, these plants were next to two treatment quadrats with nitrogen fertilization and, given the current direction, those plants were exposed to nitrates from fertilized quadrats (the only quadrat with this particular configuration). Therefore, those plants were not used in our analysis of the effect of nitrogen addition.

Effect of nutrients on *Macrocystis pyrifera* recruitment and juvenile survivorship

No *Macrocystis pyrifera* recruitment occurred in the experimental treatments without sporophylls, either with nutrients (4 blocks) or without nutrients (4 blocks). There was also no recruitment in the treatments with sporophylls and without nutrients, and no recruitment from April to August 1998 in treatments with nutrients and with sporophylls from San Diego. However, after seeding the quadrats with sporophylls from Punta Eugenia in September 1998, recruitment was observed as blade stage plants by October in fertilized treatments in three of the four blocks (two from IA and one from PP). Block 1 (IA) had no plants, block 2 (IA) had 14 plants, block 3 (IA) had 20 plants and block 4 (PP) had 2 plants (because the large number of zeros, the data were not tabulated). The same number of plants was recorded in December. The final average was 8 plants m^{-2}. Therefore, recruitment was observed only in treatments with sporophylls collected from Punta Eugenia and with added nutrients.

In the treatments with transplanted *Macrocystis pyrifera* juveniles, survival was high in three of the four replicates of the fertilized treatment (two from IA and one from PP) (Table II). In September, the only replicate with nutrients added but no surviving *M. pyrifera* had intact kelp holdfast with bite marks, suggesting that mortality was caused by grazers. Average survival was reduced to 92 % in August and 67 % in September. The 8 survivors remained until the end of the experiment in December. In the unfertilized treatments, juvenile *M. pyrifera* survived in only one (at IA) of the 4 replicates. Average survival from September was 25 %. Statistical analysis rejected the hypothesis of equal proportion of survivors (t = 2.33, $p < 0.01$) indicating that the number of survivors was significantly higher in the treatment with nutrients added.

Effect of nutrients on juvenile *Macrocystis pyrifera* growth and frond initiation

The initial average length (± 1 std) of the 13 juvenile plants in the fertilized treatments in June was 220 cm (± 64) and the maximum average length reached at the end of the study by the 8 survivors was 312 cm

Table II. Effect of nutrient availability on survivorship of *Macrocystis pyrifera* transplanted from Bahía Tortugas to Isla Asunción (blocks 1−3) and Punta Prieta (block 4), during 1998 El Niño. Number of plants and final percentage of survivorship (in brackets).

	With nutrients					Without nutrients				
Date	Jun	Aug	Sep	Oct	Dec	Jun	Aug	Sep	Oct	Dec
Time (days)	0	51	101	131	162	0	51	101	131	162
Block										
1	2	2	2	2	2 (100)	3	3	0	0	0 (0)
2	4	4	4	4	4 (100)	3	3	3	3	3 (100)
3	4	4	0	0	0 (0)	3	3	0	0	0 (0)
4	3	2	2	2	2 (66)	4	3	0	0	0 (0)
Average	3.25	3	2	2	2 (66.5)	3.25	3	0.75	0.75	0.75 (25)

Table III. Effect of nutrient availability on average total plant length (cm) and total number of fronds (in brackets) of juvenile *M. pyrifera* sporophytes transplanted from Bahía Tortugas to Isla Asunción (blocks 1−3) and Punta Prieta (block 4), during 1998.

Treatment	June 20	August 11	September 30	October 27	December 4
Fertilized					
Block 1	255.0 ± 65.0 (4)	131.0 ± 45.0 (4)	248.5 ± 31.5 (6)	321.5 ± 38.5 (23)	333 ± 23.0 (23)
Block 2	187.5 ± 15.9 (8)	97.0 ± 28.3 (8)	279.6 ± 75.5 (28)	253.5 ± 65.2 (26)	291 ± 111.8 (26)
Block 3	236.0 ± 132.5 (6)	313.0 ± 21.0 (4)	290.0 ± 126.0 (12)	402.5 ± 97.5 (14)	Not sampled
Block 4	200.0 ± 43.0 (8)	461.3 ± 96.8 (6)	Absent	Absent	Absent
Average	219.6 ± 64.1 (6.5)	250.5 ± 47.7 (5.5)	272.7 ± 77.6 (15.3)	325.8 ± 67.0 (21)	312 ± 67.4 (24.5)
Non-fertilized					
Block 1	257.0 ± 31.6 (6)	325.7 ± 36.6 (6)	Absent	Absent	Absent
Block 2	245.3 ± 23.8 (6)	397.0 ± 71.9 (6)	198 ± 49.4 (10)	373 ± 14.2 (32)	488 ± 106.3 (35)
Block 3	250.0 ± 53.5 (6)	Absent	Absent	Absent	Absent
Block 4	215.5 ± 48.5 (8)	438.0 ± 48.0 (6)	Absent	Absent	Absent
Average	241 ± 39.3 (6.5)	386.9 ± 52.1 (6)	198 ± 49.4 (10)	373 ± 14.2 (32)	488 ± 106.3 (35)

(± 67) (Table III). The maximum growth rate occurred in August−September (2.74 cm day^{-1}, $\mu = 0.013 + 0.013$). The group of transplants had an average of 6.5 fronds when transplanted, and reached an average of 24.5 fronds at the end of the study.

The initial average length of the 13 juvenile plants in the treatments without nutrients was 241 cm (± 39). All plants in three of the four replicates died during August and September and therefore no more measurements were obtained. The average length of the 3 survivors in the remaining block in December was 488 cm (± 106). The maximum growth rate occurred during September−October (5.83 cm day^{-1}, $\mu = 0.022 \pm 0.010$). The average number of fronds per plant increased from 6.5 to 35 (Tab. III). No significant difference was found for average length or growth rate between treatments with nutrients and the three survivors without nutrients. However all survivors in the unfertilized treatment were from the block in which contamination from nearby fertilized treatments was evident

Discussion

Environmental conditions

In the experimental area, water temperature was negatively related to nutrient concentration, following the same trend described by Jackson (1977) and Zimmerman and Kremer (1984). However, the critical point separating low nutrient from high nutrient water, described by Zimmerman and Kremer (1984) at 15.5 °C, occurred at 18.5 °C. Thus, water with temperatures below 18.5 °C had enough nutrients to maintain normal giant kelp growth rates. Water temperature above 18.5 °C was generally lower than 1.0 μM. This temperature appeared to mark the discontinuity between water below and above the thermocline. The annual cycle of low nutrient concentrations most of the year with highs only in spring was similar to that in the coastal area of San Diego (Cairns and Nelson 1970) and the temperature-nitrate relationship described here is characteristic of the southern California Bight (Eppley *et al.* 1979, Zimmerman and Kremer 1984).

Effects of environmental factors during El Niño 1997−98

Nitrogen is the major nutrient required for growth, and the relationship established between tissue nitrogen and growth rates for *Macrocystis pyrifera* can be used to assess the condition of plants in nature with respect to nitrogen nutrition (Wheeler and North 1980). In 1997, *M.* pyrifera tissue nitrogen from San Roque area was rapidly depleted, from 2.29% in April to 1.45% in August. Although still higher than the critical level (1.1%), it may have decreased in September to below the level at which internal nitrogen reserves are depleted, leading to rapid deterioration (Gerard 1982, Dayton and Tegner 1990). In September 1997, water temperature was high (25.3 °C, anomaly +5.7 °C) and nutrients were presumably low (< 1.0 μM), and all kelp forests at the southern end of the distribution disappeared. In this case a synergistic effect of these two environmental factors may have caused the deterioration of the kelp forest in September 1997, because of El Niño (Gerard 1997). Jackson (1977) suggested that canopy growth is supported by translocation of nitrogen from the lower parts of the plant that are bathed in water with higher nitrate. When the lower parts of the plants cannot translocate enough nitrogen to the surface, the canopy dies back. Finally the individuals succumbed probably because they had low nitrogen reserves when high temperature arrived and were unable to maintain positive daily carbon fixation that, in turn, affected their physiological processes (Gerard 1984, Gerard 1997). The fast reduction of tissue nitrogen confirms that *M. pyrifera* does not seem to store nitrogen for more than 30 days (Zimmerman and Kremer 1986) in contrast to *Eisenia arborea* that maintained a nitrogen concentration higher than 1.5% throughout 1997.

Seeding experiment

Recruitment of *Macrocystis pyrifera* was observed only in quadrats to which sporophylls and nutrients were added. The lack of recruitment in areas without added sporophylls suggests a limited availability of spores from natural sources and the lack of a bank of microscopic forms that may survive stressful conditions as proposed for Bahía Tortugas (Ladah *et al.* 2000).

Because of the deterioration of the kelp beds in Baja California after El Niño 1997–98, documented above, the seeding experiment was started in 1998 with sporophylls collected from San Diego, CA. Recruitment never occurred using sporophylls from San Diego, possibly because of the transportation time from collection to seeding was too long (3–4 days) or gametophytes from California may not be adapted to survive at the southern limit with relatively higher temperatures, even with high nutrient concentrations supplied experimentally. The recruitment that occurred in September 1998 resulted from sporophylls from Punta Eugenia whose transportation-seeding time was two days. The sporophylls from Punta Eugenia were seeded in October, when the temperature was declining (19.3 °C bottom) and was slightly below the normal average (anomaly −1.3 °C). According to the temperature-nitrate (T-N) equation described for this area, nitrate concentration was still low (1.1 µM), but the supplied nutrients may have nourished gametophytes that developed into the sporophyte phase. Although the number of recruits was low (average 8 plants m^{-2}), no plants appeared in unfertilized areas, suggesting that recruitment was nutrient limited during that period. In southern California, Deysher and Dean (1986 b) found that fertilization increased sporophyte production even at relatively high temperatures, that natural recruitment occurred at temperatures below 16.3 °C, and the highest temperature at which recruitment occurred was 18.3 °C. In our case, gametophytes seem to withstand higher temperatures when nutrients are high. In California, reproductive allocation and spore standing stocks in *Macrocystis pyrifera* are negatively correlated with seawater temperature and positively correlated with nitrogen content of adult plants and display two peaks of spore production per year (winter and spring), but this pattern is disrupted during El Niño events with warm and poor-nutrient water (Reed *et al.* 1996). Therefore, low temperature may be necessary for recruitment but this is not the only factor. Nutrients also appear to play an important role in the dynamics of *M. pyrifera* populations at their southern limit.

Juvenile transplant experiment

The results of the transplant experiment suggest that fertilization enhanced survival of juvenile *Macrocystis pyrifera*. Even though one treatment without fertilizer was probably contaminated, the statistical difference was highly significant. Although in August 1998, the percentage of survivors was about the same with nutrients and without nutrients (91% and 93%), the plants without nutrients had thinner stipes and heavy incrustations of invertebrates settled on the fronds, and by September 1998 all those plants had died. Survival for plants with nutrients was very high (67%), compared with 10% survival obtained in previous work (Hernández-Carmona *et al.* 2000). The poor survival of juvenile plants without nutrients added was apparently caused by higher than normal temperatures (23.1 °C in August, anomaly of + 3.6 °C), and low nitrogen concentration (1.0 µM), which was below the critical level for *M. pyrifera* to maintain normal growth (Zimmerman and Kremer 1986).

During this experiment, water nitrate concentration was always higher in fertilized areas, indicating the fertilizer system delivered the nutrients selected at levels that were sufficient to maintain high concentrations around the experimental plants. Tissue nitrogen concentration in the fertilized experimental plants was higher (1.24%) than the critical level. Although temperatures were higher than normal from June 1998 (16.4 °C) to August 1998 (23.1 °C) (anomalies from +1.4 to +3.6 °C), they were not as high as in 1997 and survival was enhanced in 1998 by the addition of nutrients. However, there may have been a synergistic effect of high temperature and low nutrients on unfertilized plants, as described by Gerard (1997) for *Laminaria*, but this effect was not evaluated. A similar experiment on juvenile *Macrocystis pyrifera* was carried out by Dean and Jacobsen (1986). However, their experiment was at lower temperatures (16.7–17.9 °C) and the main effect of adding nutrients was a change in growth rate. This same effect (that poor growth of juvenile *M. pyrifera* during the El Niño was probably caused by nutrient limitation) cannot necessarily be expected at the southern limit because of the difference in temperature.

One unfertilized plant sampled in September 1998 had a tissue nitrogen concentration below the critical level (0.56%), indicating it was nutrient depleted. The new kelp forest in Punta Eugenia had a very low nitrogen concentration (0.68%) in September 1998 and the nitrogen-temperature relationship indicated seawater nitrate concentration was also low. However, as the cooler mass of water with higher nutrient concentrations moved into the area in October 1998 (anomaly −1.5 °C), tissue nitrogen concentration increased to 1.13% in December 1998. In comparison, tissue nitrogen in *Eisenia arborea* seemed to decline at a slower rate. After hurricane Linda in September 1997, many *E. arborea* plants were dislodged and washed to the beach, and many of the survivors lost one of their branches. In October 1998, the number of plants was very low (0.06 plants m^{-2}) compared with summer 1997 (3.8 plants m^{-2}) (Hernández *et al.* 2000) and survivors were in a poor condition. Nitrogen reserves were below 1%, but a new generation of *E. arborea* started to repopulate the experimental area in spring 1998.

The three survivors of *Macrocystis* in one block without nutrients were similar in length and number of fronds to the nourished plants, supporting the idea that those plants were supplied with nutrients from neighboring quadrats, and therefore could not be considered as part of the unfertilized treatment. This made growth rates comparison difficult. Average plant length in our fertilized treatments increased only 92 cm in six months ($\mu = 0.002 \pm 0.002$), which was lower than reported by Dean and Jacobsen (1986). The same trend was observed for frond initiation, with an increase from an average of 6.5 to 24.5 fronds (3 fronds per month). This apparent limited growth may have resulted from grazing, probably by fish, which may consume the fronds incidentally as they pick at encrusting organisms (North 1971, Bernstein and Jung 1979). Isolated plants often attract unusually high densities of encrusting organisms and are especially attractive to fish. These may graze the fronds at a rate much higher than the frond growth rate (Dayton and Tegner 1984). Nevertheless, at the end of the experiment the survivors looked healthy and were producing new fronds.

Our results confirm that higher temperature and low nutrients are inversely related (Zimmerman and Kremer 1984) with the nitrate critical point at a higher temperature (18.5 °C) in southern Baja California than in southern California (15.5 °C). During El Niño conditions, *Macrocystis pyrifera* decline was probably caused by the interactive effect of N limitation and heat stress, as described by Gerard (1997) for other species. Fertilization at moderate temperatures (< 23 °C) can enhance recruitment and survival of juvenile stage plants.

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