Survival of Juvenile Giant Kelp: The Effects of Demographic Factors, Competitors, and Grazers

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SURVIVAL OF JUVENILE GIANT KELP: THE EFFECTS OF DEMOGRAPHIC FACTORS, COMPETITORS, AND GRAZERS[1]

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Abstract. Patterns of survival of juvenile giant kelp (*Macrocystis pyrifera*) were examined in relation to grazing by sea urchins, shading by adult kelp, density of recruits, densities of other algal species, and substrate distribution. Survival was poorer in areas where white sea urchins (*Lytechinus anamesus*) were abundant or where there was an overlying canopy of adults. At other sites, the density of recruits explained the greatest proportion of variability in survival, and the proportion of juveniles that survived was negatively correlated with the number of recruits. Potential algal competitors (*Pterygophora californica* and *Cystoseira osmundacea*), red sea urchins (*Strongylocentrotus franciscanus*), and substrate distributions had no significant effect on survival.

The mechanisms of density-dependent survival were similar to "dominance and suppression" models that explain self-thinning in many terrestrial plant populations. In stands where densities of recruits were high, skewed size distributions developed, probably as the result of competition for light. High-density stands had proportionally more small plants than low-density stands, and, during subsequent storms, only the larger plants survived. This led to a more equitable distribution of survivors than would be expected based on the number of recruits.

Intraspecific interactions, both between adults and juveniles and among juveniles of the same cohort, appear to be important structuring forces in most giant kelp populations. This parallels findings in many terrestrial populations. However, in other algal populations, there is little evidence for density-dependent mortality or for the dominance-suppression hypothesis. These differences may relate to competition for light, which is intense in *Macrocystis* forests and many terrestrial populations, but less so in assemblages of other benthic algae.

Key words: density-dependent mortality; dominance; grazing; kelp forests; Macrocystis pyrifera; *self-thinning; size-dependent mortality; suppression.*

INTRODUCTION

Our knowledge of the population biology of plants stems largely from studies in terrestrial habitats, as reviewed by Harper (1977), Antonovics and Levin (1980), and in several recent symposia (Solbrig et al. 1979, Dirzo and Sarukhan 1984, White 1985). The distribution and abundance of terrestrial plants is determined, in part, by disturbances (e.g., grazing, pathogens, storms, and fire) and interspecific competition among plant species, but is also greatly influenced by intraspecific interactions. These factors act together with intrinsic demographic features to provide for selection for competitive ability at the level of the individual.

Several generalities have arisen from these terrestrial studies with regard to plant population dynamics. Seedling or juvenile life stages often provide "bottlenecks" in the life history, and survival in these life stages is disproportionately important to the population in terms of both eventual abundances and selection pressure (Harper 1977, Cook, 1979, Hickman 1979, Werner 1979). Spatial variability in density patterns of newly recruited juveniles results from variability in dispersal, grazing, or "microscale" environmental differences (Harper 1977). In those locales where densities of recruits are high and form monospecific stands, self-thinning occurs. The self-thinning process generally follows the $-3/2$ power law, i.e., a stand develops such that the relationship between the log of the average biomass per individual vs. the log of the number of individuals is described by a linear function with a slope of $-3/2$ (Yoda et al. 1963, White and Harper 1970, and review by Westoby 1984). The underlying mechanism of self-thinning, termed the "dominance and suppression hypothesis," is described as follows (Turner and Rabinowitz 1983, Schmitt et al. 1986, 1987, and references therein): some individuals within a cohort gain an initial size advantage over their neighbors because of genetic differences, timing of recruitment, or differences in microclimate. Initial differences in size are compounded by intraspecific competition for light leading to skewed (often bimodal) size distributions. Small plants are more susceptible to "stress" (e.g., grazing pressure or drought) and eventually die leaving only the larger individuals.

One might expect similar types of interactions to

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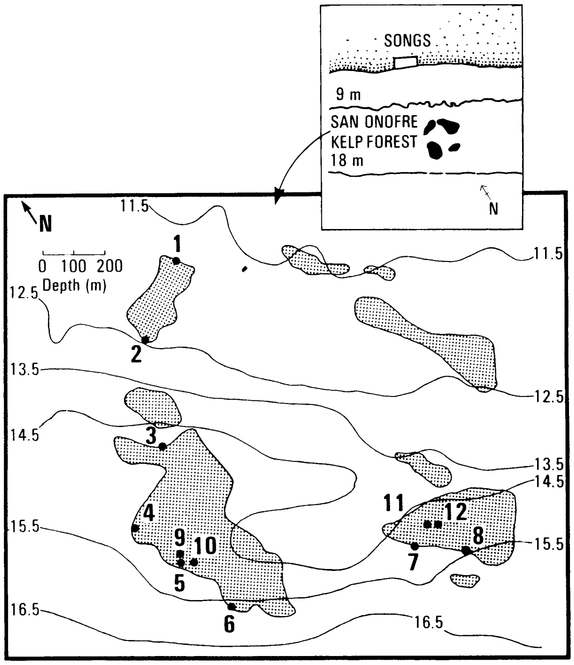

FIG. 1. Map of the San Onofre kelp forest as it appeared in summer 1978 and the position of permanent transects within the kelp forest. Shaded areas are locations of kelp canopy. SONGS is the San Onofre Nuclear Generating Station. Depth contours (in metres) are also given.

determine patterns of distribution and abundance in algal populations. Historically, studies of population dynamics in algal communities have emphasized the role of grazing (Lubchenco and Gaines 1981) or physical disturbance and interspecific interactions (e.g., Dayton 1975, Paine 1979, Sousa 1979, Lubchenco 1980, Kastendiek 1982, Dayton and Tegner 1984, and reviews of kelp forest dynamics by Dayton 1985, Foster and Schiel 1985, Schiel and Foster 1986). Recently however, more attention has been given to demographic characteristics. Survivorship curves have been published for a variety of algal species (Rosenthal et al. 1974, Gunnill 1980, 1986, Coyer and Zaugg-Haglund 1982, Chapman and Goudey 1983, Dayton et al. 1984, Santelices and Ojeda 1984a, Schiel 1985, Chapman 1986), and the importance of density-dependent survival (Black 1974, Schiel and Choat 1980, Chapman and Goudey 1983, Chapman 1984, Schiel 1985) and the effects of age and size on survival (Chapman 1984, 1986, and De Wreede 1986) have been examined. Also, the relevance of the −3/2 power law to algal populations has been explored (Schiel and Choat 1980, Cousens and Hutchings 1983). However, there remains some controversy over the relevance of terrestrial-based models in algal ecology (see, for example, the contrasting views on self-thinning by Schiel and Choat [1980] and Cousens and Hutchings [1983]), and there has been no attempt to integrate demographic studies with those of extrinsic processes (e.g., grazing) in order to assess the relative importance of these factors to the distribution and abundance of algae and to potential selective mechanisms.

Here, we examine factors that determine survival of juvenile *Macrocystis,* the dominant alga in the kelp forests of California. Recruitment of *Macrocystis* in southern California is periodic, with an average frequency of occurrence of once every 3–4 yr (Rosenthal et al. 1974, Dayton et al. 1984). As a result, factors that influence recruitment and survival of early life stages of *Macrocystis* can have impacts on the population that persist for several years. Here, we emphasize the causes of spatial variability in survival of juvenile sporophyte stages of giant kelp, including grazing by sea urchins, the density of canopy-forming adults, substrate distributions, time of recruitment, and the density of recruits. Mechanisms of density-dependent survival are explored in relation to the "dominance and suppression" hypothesis, and the relevance of density dependence in this and other algal assemblages is examined.

MATERIALS AND METHODS

This study was conducted in the San Onofre kelp forest located approximately midway between Los Angeles and San Diego, ≈19 km north of Oceanside, California (33°22′ N, 117°32.5′ W). The kelp forest lies on a low relief patch of cobble extending from 12 to 15 m depths directly offshore from the San Onofre Nuclear Generating Station (Fig. 1). During this study, the generating station discharged heated effluent at a depth of ≈8 m, but had no discernible effect on the kelp populations in the San Onofre kelp forest (T. A. Dean, *personal observation*). Two new generating units were under construction at the time of this study.

The algal community at San Onofre consists of giant kelp (*Macrocystis pyrifera*) with an understory of *Pterygophora californica, Cystoseira osmundacea,* and occasionally *Desmarestia ligulata.* Few other bush-type algae are abundant. Encrusting coralline algae and the red turf *Acrosorium unicinatum* cover much of the hard substratum. There are two major invertebrate grazers of kelp at San Onofre: the white urchin, *Lytechinus anamesus,* and the red urchin, *Strongylocentrotus franciscanus.* The smaller white urchin occasionally grazes adult kelp, but usually feeds on smaller life stages (Dean et al. 1984). Red urchins can form large mobile aggregations or fronts that graze almost all algae in their path. However, during the period of this study they were found only in smaller stationary aggregations that did not actively graze, but apparently subsisted on drift algae (Dean et al. 1984).

In summer 1978, we established 12 transects in the San Onofre kelp forest (Fig. 1). Eleven transects were set up in June and the 12th (Transect 8) was established in August 1978. Each transect was permanently marked with steel reinforcement bars driven into the bottom, and measured 6 m wide by 50 m long. At the start of our study in 1978, the kelp forest consisted of three patches: the southwest, northwest, and southeast. Four transects were positioned in the centers of patches of kelp under heavy canopy, two transects in each of the southeast and southwest quadrants of patches. All other transects were positioned along the edges of the kelp forest such that half of the transect was outside the forest but on areas of hard substratum. For the purposes of the analyses presented here, we divided each transect into two 25 × 6 m segments so that each area sampled would represent a relatively homogeneous environment (with respect to initial adult abundance) and would be equal to every other sampling area in size.

We tagged all kelp plants that were of juvenile size or larger (see definition below) on each transect by driving a steel spike with a numbered plastic tag into the seafloor next to each plant. In addition, we mapped the position of each plant by noting the distance of the plant from the center line, and also from the head, of the transect. Mapping allowed us to identify individual plants in cases where tags were lost and also allowed for evaluation of the dispersion patterns of plants within each transect.

The plants were divided into three size categories, juveniles, subadults, and adults, according to the following criteria. Plants that had split into at least two fronds but were <1 m in height were juveniles. Plants that were taller than 1 m that did not have haptera protruding from above the primary basal dichotomy of the stipe (see Lobban 1978, for a description of plant morphology) were subadults. Plants that had haptera above the primary dichotomy were adults. Size categories were based primarily on morphologies because of the difficulty in measuring adult plants under water. Preliminary observations indicated that adult plants generally had from 6 to 8 fronds, with at least one frond reaching to, or near, the water's surface (i.e., from 12 to 15 m long), and had sporophylls (specialized blades that produce spores).

Surveys of *Macrocystis* were conducted at approximately monthly intervals in 1978, and quarterly thereafter through December 1980. In each survey, we determined the presence or absence of every plant tagged in previous surveys, determined the size classes of survivors, and tagged and mapped any newly recruited plants. Occasionally, surveys were postponed or cancelled because of poor underwater visibility. Densities of the white sea urchin *Lytechinus anamesus* and the two dominant understory algae, *Pterygophora californica* and *Cystoseira osmundacea,* were also determined in each survey. These populations were censused in 10 contiguous 2 × 5 m quadrats along the center line of each transect.

The composition of the substrata within each transect was determined once in December 1979. Substratum types were classified in the following categories: sand, cobbles ≤20 cm in the longest dimension, and cobbles >20 cm. The occurrence of each type was noted at 25-cm intervals along a line down the center line of each transect.

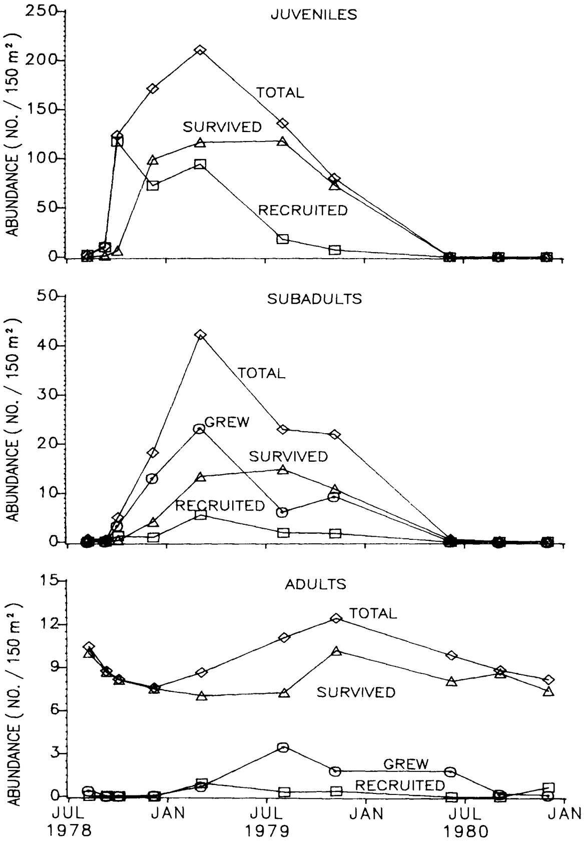

FIG. 2. Mean abundances of juvenile, subadult, and adult *Macrocystis* from 24 transects within the San Onofre kelp forest from 1978 through 1980. Also shown are the numbers of those plants that either were recruited over the previous survey interval, grew from a smaller size class in the previous survey interval, or had survived over the previous survey interval without growing into the next largest size class.

RESULTS

Patterns of recruitment and survival

In Spring 1978, there were virtually no juvenile *Macrocystis* in the San Onofre kelp forest. By July, large numbers of small, single-bladed plants began to appear with densities reaching several hundred plants per square metre on some transects. We did not make regular quantitative estimates of the density of blade stages because of the difficulty in discriminating *Macrocystis* from other laminarian algae when plants are small.

By August 1978, many of these plants had grown to juvenile size (≈40 cm). Newly recruited plants continued to appear through November 1979 (Fig. 2). It was impossible to determine when these plants were initially produced from gametophytes, since gametophyte and early sporophyte stages cannot be identified in situ. We suspect that juveniles tagged in 1978 were produced from gametophytes during a several-week period

TABLE 1. Recruitment, and survival to June 1980, of juvenile *Macrocystis* recruited on each 150-m^2 half of the indicated transects from August 1978 through November 1979.

Transect	Half	Position	Number recruited	Number surviving	% surviving
1	1	outside patch	38	3	8
1	2	edge of patch	76	11	14
2	1	outside patch	107	5	5
2	2	edge of patch	624	15	2
3	1	outside patch	133	10	8
3	2	edge of patch	90	4	4
4	1	outside patch	66	16	24
4	2	edge of patch	7	2	29
5	1	outside patch	560	14	3
5	2	edge of patch	311	4	1
6	1	outside patch	41	4	8
6	2	edge of patch	45	6	13
7	1	outside patch	23	0	0
7	2	edge of patch	250	6	2
8	1	outside patch	33	0	0
8	2	edge of patch	864	12	1
9	1	patch canopy	13	0	0
9	2	patch canopy	31	0	0
10	1	patch canopy	16	0	0
10	2	patch canopy	2	0	0
11	1	patch canopy	932	15	2
11	2	patch canopy	1344	13	1
12	1	patch canopy	1120	3	<1
12	2	patch canopy	1327	2	<1
		Mean =	335.0	6.0	1.8*
		CV =	134.1	93.3	...

* Total surviving/total recruited.

in April–May 1978. A second peak in juvenile recruitment occurred in the March 1979 survey. Most of these plants were probably produced from gametophytes in fall 1978. The lack of visible blade-stage plants (single blades measuring 2–3 cm), in fall 1978, helped confirm that juveniles tagged in spring 1979 were not slow-growing individuals that had recruited in the previous spring. We operationally define "cohorts" of plants as those initially tagged during a given survey. Hereafter, we refer to "recruitment" as the initial appearance of juvenile-stage plants, recognizing that the actual production of sporophytes from gametophytes occurred at some previous time and that the production of juveniles requires the survival of both microscopic sporophytes and visible blade-stage plants.

There was considerable variability in the numbers of juveniles recruited among transects (Table 1). The highest densities of juveniles (>2.4 plants/m^2) were observed on Transects 11 and 12 in October 1978. Little recruitment was observed on Transects 9 and 10 and on outside-patch halves of Transects 7 and 8, where the densities of recruits never exceeded 0.1 plants/m^2. Causes of temporal and spatial patterns in recruitment will be examined in a separate manuscript.

In the months following our initial observations of recruitment, abundance patterns and size distributions of *Macrocystis* within the kelp forest changed dramatically (Fig. 2). These changes were the result of growth, survival, and continued recruitment of juveniles. Occasionally, we found adult or subadult plants that had not been tagged in previous surveys. These were mostly plants that were attached to small cobbles and had apparently recruited elsewhere, and had drifted onto our transects and become lodged there. After November 1979, adult abundances began to decline as mortality of adults outpaced their rate of replacement (Fig. 2). By June 1980, almost all plants recruited in 1978 and 1979 had either died or grown to adult size.

Only a small fraction of those plants initially recruited survived for 2 yr (Fig. 3). Of the >8000 juveniles tagged in 1978 and 1979, only 145 (≈2%) survived until June 1980 (Table 1). There was considerable temporal variability in survival, attributable either to changes in external factors (wave height, irradiance, temperature) over time or to internal developmental processes (changes in size and age of plants) that are dependent on the time of recruitment. It was impossible to segregate these effects and their interactions in a single analysis since not all cohorts were present during each survey. Therefore, we examined the effects of time of initial recruitment and time of year on survival in separate analyses using chi-square statistics. We tested the hypothesis that the proportion of plants that survived was independent of initial time of recruitment (i.e., cohort) by comparing survival of different-aged plants over a given observation interval. The hypothesis that survival was independent of time of year was tested by comparing the proportion of plants surviving over different time intervals, within each cohort. Each of the overall comparisons was followed by single de-

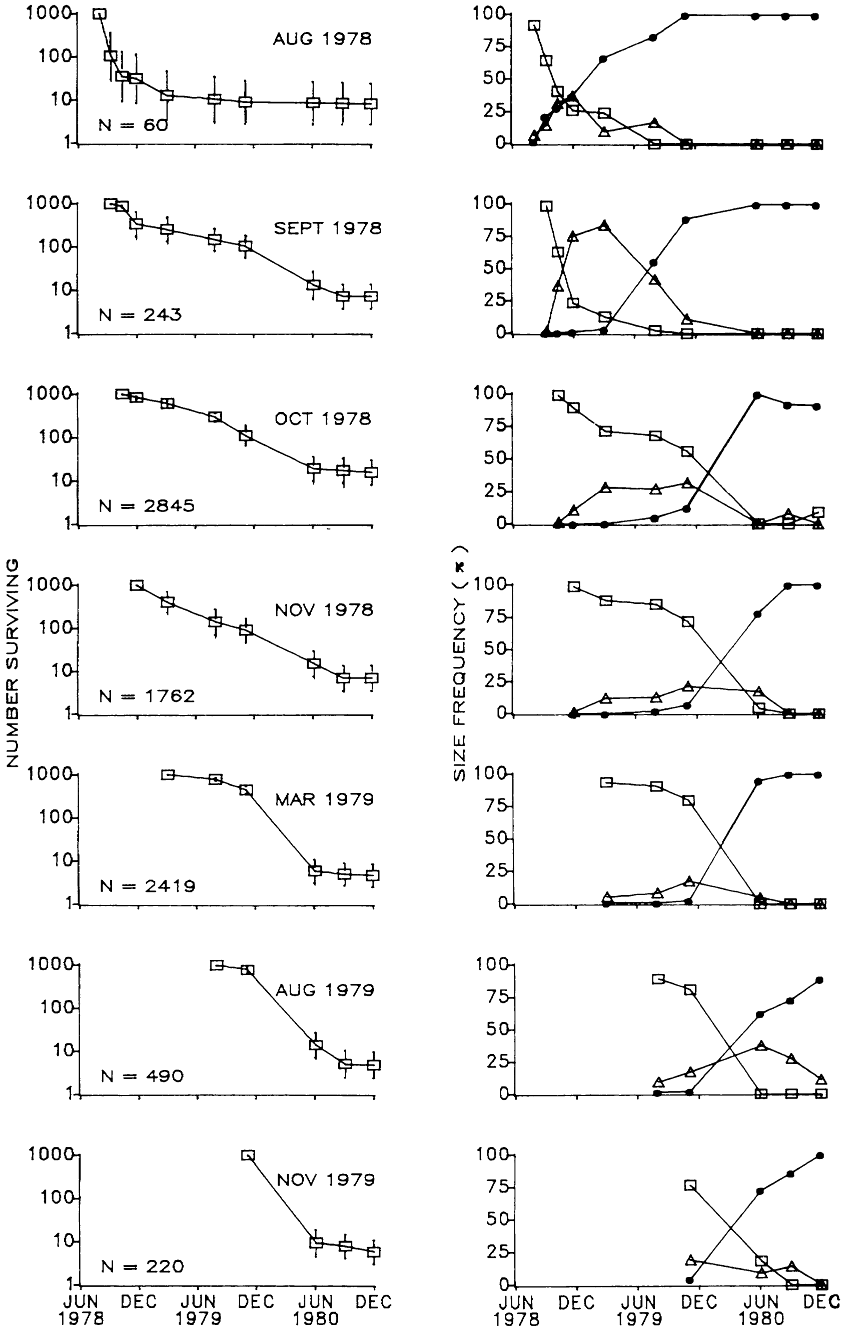

FIG. 3. Survivorship ($\bar{X}$ ±1SE) and size distribution of 7 cohorts of *Macrocystis* recruited on 24 transect halves in the San Onofre kelp forest from August 1978 through December 1979. Size categories are given as juvenile (□), subadult (△), and adult (●). Survivorship data were scaled to produce a hypothetical cohort of 1000 individuals. Actual numbers of plants initially tagged in each cohort are also given.

gree of freedom chi-square tests (Snedecor and Cochran 1967) in order to identify groups among which rates of survival did not differ significantly.

There were significant differences in survival among times within each cohort and among cohorts within each time (Table 2; $P < .05$, chi-square). All cohorts showed an increase in survival after June 1980 when most plants reached adult size. In all cohorts except two (August and September 1978), survival was significantly higher from June 1980 through December 1980 than in all other time intervals ($P < .05$, single df chi-square).

For all cohorts initially tagged after October 1978, survival was significantly lower from November 1979

TABLE 2. Percent survival of juvenile *Macrocystis pyrifera* from different cohorts (i.e., plants recruited at different times) over 5–7 mo intervals between September 1978 and December 1980. N = total number of individuals at risk in each period.

	Cohort (time of recruitment)													
	Aug 1978		Sep 1978		Oct 1978		Dec 1978		Mar 1979		Jul 1979		Nov 1979	
Time interval	%	(N)	%	(N)	%	(N)	%	(N)	%	(N)	%	(N)	%	(N)
Sep 1978–Mar 1979	36	(33)	51	(243)	...		...		...		...		...	
Mar 1979–Nov 1979	17	(12)	22	(124)	19	(2109)	20	(1447)	50	(2419)	...		...	
Nov 1979–Jun 1980	100	(2)	44	(27)	10	(411)	8	(295)	3	(1219)	4	(424)	5	(214)
Jun 1980–Dec 1980	100	(2)	67	(12)	93	(41)	74	(23)	73	(40)	73	(15)	60	(10)

to June 1980 than during all other time intervals (Table 2; $P < .05$, single df chi-square). This was a particularly stormy period, especially compared with the mild winter of 1978–1979, and the high mortality was probably the result of plants being dislodged from the substratum by heavy surge. There was a general tendency for earlier cohorts to exhibit higher survival than later cohorts during the stormy period of November 1979 to June 1980. The oldest plants (the August and September 1978 cohorts) had higher rates of survival than all other cohorts over this time interval ($P < .05$, single df chi-square).

Effects of age and size on survival

The effect of "cohort" or time of recruitment could be attributed either to the effects of increasing size of plants on survival or to some other aspect of age. The average size of plants increased with average age, but the relationship between size and age was a rather loose one. Individual plants of the same age were often quite different sizes. Some plants reached adult size within 6 mo; others remained juveniles (<1 m in height) for over a year (Fig. 3).

We tested the hypothesis that the probability of survival over a given time interval did not differ among plants of different ages (i.e., when they were tagged) or sizes, using linear categorical analyses (Grizzle et al. 1969). The CATMOD procedure of the SAS statistical package (SAS 1985) was employed. Two separate analyses were performed, one for survival over the period from August 1979 to November 1979, and the other from November 1979 to June 1980. In the first analysis, we compared survival among juvenile, subadult, and adult size classes from three cohorts (tagged October 1978, December 1978, and March 1979). The second compared survival among five cohorts initially tagged between October 1978 and November 1979. These intervals and cohorts were selected because they were the only times when all three size classes of plants were present.

Size was more important than age in determining survival. Survival was much higher in the period from August to November 1979 than from November 1979 to June 1980, but in both instances, the survival of adult plants was greater than for subadult and juvenile plants (Table 3).

There was no significant effect of age on survival when ages were summed over all size classes (Table 3). However, the significant interactions between age and size suggest that there were differences in survival among ages within particular size classes, and that in some cases, small plants that were old may have had a lower probability of surviving than small plants that were young. For the period from August to November 1979, younger plants within juvenile and subadult size classes tended to have higher survival than older plants. There were no obvious orderings within a size class with respect to the effects of age on survival in the period from November 1979 to June 1980.

Causes of spatial variability in survival

We also noted considerable spatial variability in survival. The proportion of plants recruited in 1978 and 1979 that survived through June 1980 ranged from 0 to 29% on the various transects (Table 1). Variability in survival was attributable to grazing by white sea urchins, shading by the canopy of adults, and effects of neighboring juveniles. White sea urchins were abundant (>10 urchins/m^2) on the portions of Transects 6, 7, and 8 that were outside of the kelp forest. There were no survivors on the outside portions of Transects 7 and 8, and the only survivors observed on these portions of Transect 6 were in patches where there were few urchins (T. A. Dean, *personal observations*). Our observations, as well as experimental evidence reported elsewhere (Leighton 1971, Dean et al. 1984), leave little doubt that survival was reduced by the grazing activity of *Lytechinus*.

The effect of the presence of canopy of adult *Macrocystis* on the survival of juvenile kelp was tested by comparing the proportion of recruits that survived at canopy, edge, and outside transects using a linear categorical analysis. Transects with high densities of urchins (i.e., those portions of Transects 6, 7, and 8 that were outside of the kelp forest) were eliminated from the analysis. Survival was determined as the proportion of juveniles, recruited between August 1978 and November 1979, that survived until June 1980.

Survival was significantly lower on transects under a canopy of adults than on transects that were positioned either on the edge of the kelp forest or outside of the kelp forest (Table 4). Urchin densities were low

TABLE 3. Percent survival of newly recruited *Macrocystis pyrifera* by age (i.e., cohort) and size, from the periods August 1979 to November 1979 and from November 1979 to June 1980. Also shown are results of categorical analyses testing the equality of survival among ages and size classes.

	Aug 1979 to Nov 1979			Nov 1979 to June 1980		
Cohort	Living	Dead	% surviving	Living	Dead	% surviving
			Adult			
Oct 1978	42	5	89	33	19	63
Dec 1978	13	1	93	11	10	52
Mar 1979	10	7	59	20	13	61
Aug 1979	8	0	...	3	6	33
Nov 1979	...	...	...	6	4	60
			Mean = 80%			Mean = 65%
			Subadult			
Oct 1978	107	139	43	7	123	5
Dec 1978	41	38	52	10	53	16
Mar 1979	110	50	69	15	200	7
Aug 1979	40	6	87	12	61	14
Nov 1979	...	...	...	1	41	2
			Mean = 63%			Mean = 9%
			Juvenile			
Oct 1978	262	356	42	1	228	0.4
Dec 1978	241	282	46	2	209	0.9
Mar 1979	1099	592	65	5	966	0.5
Aug 1979	376	60	86	1	341	0.3
Nov 1979	...	...	...	4	164	2.4
			Mean = 60%			Mean = 0.7%

Categorical analyses

Source	df	χ^2	P	Source	df	χ^2	P
Intercept	1	20.36	<.01	Intercept	1	20.36	<.01
Age	2	0.62	.73	Age	4	2.11	.72
Size	2	16.73	<.01	Size	2	165.91	<.01
Age × size	4	18.21	<.01	Age × size	8	18.50	.02

in all locations used in this analysis (<10 urchins/m^2), and on at least two of the transects (9 and 10) densities of recruits were low, suggesting that the observed effect of canopy cover was unrelated to possible confounding effects of these other factors. Densities of adults did not differ significantly on edge and canopy transects ($t = 0.34$, df $= 14$, $P = .74$), suggesting that canopy effects were due to shading and were not related to the effects of density per se. Even though densities of adults were high, transects on the edge of the kelp forest received considerably more light than in the center because of irradiance that entered the forest obliquely.

In order to examine other possible causes of spatial variability in survival, we performed a multiple regression analysis (Belsley et al. 1980) on the proportion of plants that survived on each transect half in June 1980 vs. the number of juveniles recruited between August 1978 and November 1979, the densities of two potential competitors (*Pterygophora californica* and *Cystoseira osmundacea*), and the proportion of hard substrata on each transect that was cobbles >20 cm in the longest dimension. Canopy transects (9, 10, 11, and 12) and transects with high densities of *Lytechinus* (portions of Transects 6, 7, and 8 that were outside of the kelp forest) were eliminated from the analysis. Densities of *Pterygophora* and *Cystoseira* are mean values of the number of plants >30 cm in height from surveys conducted between August 1978 and November 1979. Mean values for the number of *Macrocystis* recruits, and for densities of *Pterygophora* and *Cystoseira* were log transformed, while values for percent survival and for percent large cobbles were arcsine transformed.

TABLE 4. Percent survival of juvenile *Macrocystis* on transects under a canopy of adult *Macrocystis* in the center of the kelp forest, at the edge of the kelp forest, and outside of the kelp forest. Mean adult densities are given for August 1978.

Location relative to kelp forest	Mean adult density (no./100 m^2)	Mean % survival
Canopy	10.2	0.4
Edge	10.1	8.5
Outside	0.5	9.3

Categorical analysis

Source	df	Chi-square	P
Intercept	1	1880.27	<.01
Location	2	82.74	<.01
	Contrasts		
Canopy vs. edge	1	8.57	<.01
Canopy vs. outside	1	13.98	<.01
Edge vs. outside	1	0.01	.93

TABLE 5. Summary of regression analyses of the arcsine-transformed proportion of plants surviving on each transect in June 1980 vs. the number of plants recruited, the proportion of hard substrate that was cobbles >20 cm in longest dimension, and the densities of *Pterygophora* and *Cystoseira*.

Variable	Parameter estimate	P	Partial coefficient of determination
Intercept	27.49	.18	...
Log$_e$ no. recruited	−4.57	<.01	0.65
Arcsine % cover large rocks	0.17	.15	0.24
Log$_e$ *Pterygophora* density	2.72	.36	0.10
Log$_e$ *Cystoseira* density	0.83	.39	0.09
Overall R^2 = 0.81		N = 13	

In portions of the kelp forest where densities of white urchins were low and where there was not a dense overlying canopy, 65% of the variability in survival among transects could be explained by the density of juveniles (Table 5). There was a significant negative relationship between the density of recruits and the proportion of plants that survived (Fig. 4). There were no significant effects of either density of competitors or substrate composition on survival (Table 5).

Density-dependent survival was also indicated by patterns of dispersion within each transect over time. Dispersion patterns for juvenile plants in each survey and on each half transect were determined using the Clark-Evans index of nonrandomness based on nearest neighbor distances, with a toroidal edge correction (Ripley 1981). Chi-square statistics, as described by Ripley (1981), were used to determine whether dispersion patterns deviated significantly from random.

Prior to the appearance of large numbers of juveniles on transects in fall 1978, plants were generally distributed randomly within transects (Fig. 5). Following recruitment, the dispersion patterns were strongly clumped. As plants were thinned, the degree of clumping decreased, and by June 1980 (when most remaining plants were adults) the dispersion patterns had returned to random on most transects. From this, we infer that mortalities were not random and that plants located within dense patches were more likely to die than those that were more sparsely distributed.

Correlation between size distributions and spatial patterns of survival

Density-dependent survival was correlated with the size distributions of plants prior to the winter storms of 1979. The relationship between density and size was examined by regressing the proportion of survivors in a given size class in November 1979 vs. the number of plants originally recruited. Separate regression analyses were performed for juvenile and adult plants, and for cohorts recruited in 1978 and 1979. Transects with high initial densities of recruits (and low subsequent rates of survival) had proportionally fewer adult plants prior to the 1979 storms than transects with low levels of recruitment (Fig. 6). For plants recruited in 1978, there was a significant negative correlation between the proportion of surviving adult plants on a given transect in November 1979 and the initial density of recruits, and there was a significant positive correlation between the proportion of juveniles and the initial density of recruits. Trends were similar for the 1979 cohorts, but were not significant. The lack of significance in the latter case was due to the small proportion of plants that had grown beyond the juvenile size class. As further evidence of the effect of size on survival, there was a significant positive correlation between the number of adults on transects in November 1979 and the total number of survivors in June 1980 (Fig. 7).

DISCUSSION

Factors affecting survival: comparisons among kelp forests

Spatial patterns of survival of juvenile kelp in the San Onofre kelp forest were primarily determined by intraspecific interactions, both between juveniles and between juveniles and adults. Results from canopy-thinning experiments conducted in the nearby Point Loma kelp forest (Dayton et al. 1984), in central California (Pearse and Hines 1979, Reed and Foster 1984), and in Chile (Santelices and Ojeda 1984*a*) suggest that adult-juvenile interactions are predominant factors in determining the patterns of survival in most *Macrocystis* populations. Intracohort, density-dependent mortality has been less widely studied in algal populations, but some observational evidence (Santelices and Ojeda 1984*a*, *b*) suggests that it, too, may be a common feature in kelp forests over a wide geographical area.

The probable mechanism for both inter- and intracohort, density dependence is intraspecific competition

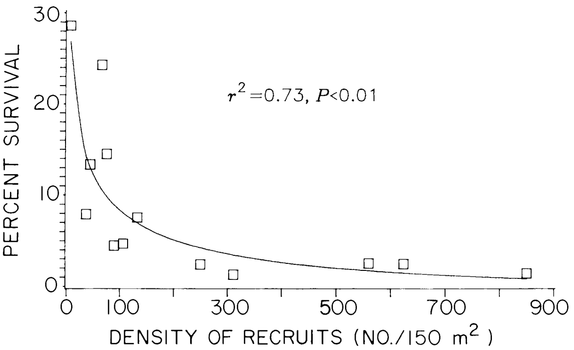

FIG. 4. Percent survival of plants in June 1980 vs. the number of recruits on each 150-m² transect half over the period from August 1978 to November 1979. The curve for the bottom figure was fit using a least squares regression of arcsin (y) = −5.42($\log_e x$) + 41.73.

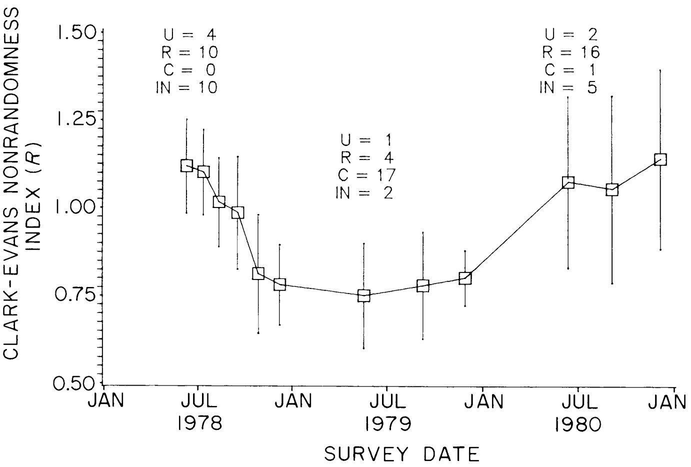

FIG. 5. Changes in dispersion pattern of *Macrocytis* as indicated by the Clark-Evans index, R, over time. Values given are means ±1 SE from 150-m² transect halves where number of recruits was ≥ 6. R values of 1 indicate a random distribution, while values >1 are uniform, and values of <1 are clumped. Also shown are the number of transect halves with random (R), clumped (C), or uniform (U) distributions before recruitment, after recruitment, and after recruits had either died or grown to adult size. "IN" indicates that there were insufficient numbers of plants (<6) on transects to compute meaningful nearest neighbor relationships.

for light. The growth of juvenile *Macrocystis* is generally light limited (Dean and Jacobsen 1984), and significant reductions in light can be attributed to both surface canopies formed by adults and understories formed by dense assemblages of juveniles. Underwater irradiance measurements indicate that dense canopies of adults reduce light on the seafloor by ≈50% at San Onofre (Dean 1985) and up to 90% in other kelp forests (Neushul 1971, Gerard 1984, Reed and Foster 1984, Santelices and Ojeda 1984*a*). Juveniles under a canopy of adults grow more slowly than those in areas that are not under canopy (Neushul 1981, Dean and Jacobsen 1984). Subadult kelp can also provide significant shading of nearby juveniles. In a dense, even-aged stand of juvenile and subadult *Macrocystis* (densities = 18 plants/m²), the trimming of plants >80 cm increased irradiance available to smaller plants by 50% (T. A. Dean, *personal observation*). Reduced irradiance results in reduced growth rate, which, in turn, leads to higher mortality. In this study, smaller, slower growing individuals suffered higher mortality than larger, faster growing individuals, probably because they had poorly developed holdfast structures and were more easily torn loose by waves.

Further manipulative experiments, similar to those proposed by Schiel and Foster (1986), are needed to test this hypothesis. Regardless of the mechanism, it is clear that the effect of intracohort, density-dependent survival was to reduce the differences among transects, with regard to initial densities of recruits. Areas of differing density eventually produced more similar numbers of adults than expected based on a simple ratio of recruits to survivors. Using the equation given in Fig. 4, for example, we estimate that a 10-fold increase in the number of recruits (e.g., from 50 to 500)

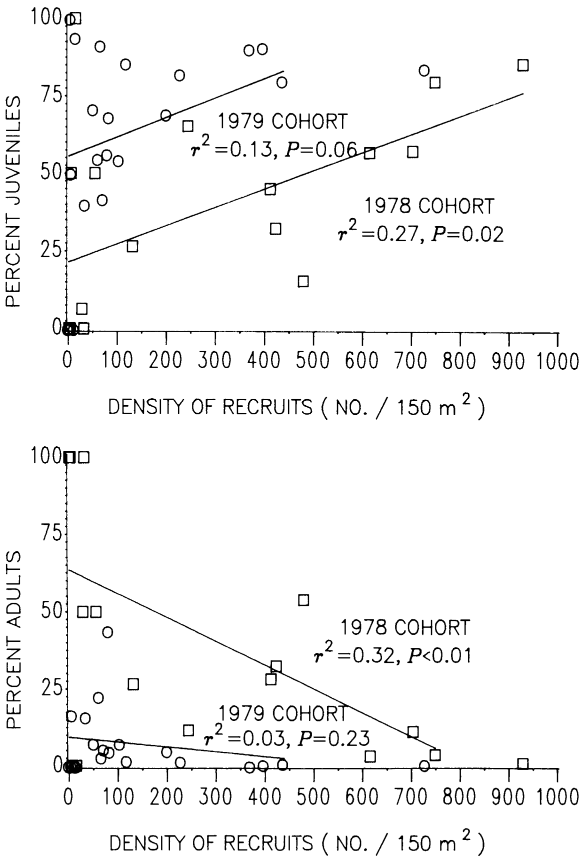

FIG. 6. Relationship between the proportion of surviving plants that were juvenile (top) or adults (bottom) in November 1979 and the number of plants initially recruited on each 150-m² transect half. □ plants recruited between August 1978 and December 1978; ○ plants recruited between March 1979 and November 1979.

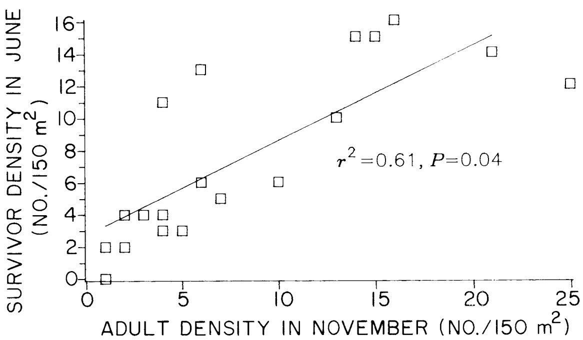

FIG. 7. Relationship between the number of plants recruited on each 150-m^2 transect half in 1978 and 1979 that had reached adult size by November 1979 and the total number of survivors from those cohorts in June 1980.

would result in only a twofold increase in the number of survivors (from 5 to 11).

Some of the spatial variability in survival could also be attributable to grazing by sea urchins. In portions of the kelp forest where white urchins were abundant, both recruitment and survival of juvenile *Macrocystis* were inhibited (Dean et al. 1984, this study). However, *Lytechinus* were not widely distributed and were restricted to the offshore edges of the kelp forest. Red urchins, which sometimes form actively feeding "fronts" (Leighton 1971, Pearse and Hines 1979, Dean et al. 1984, Ebeling et al. 1985, Harrold and Reed 1985) remained in stationary aggregations and did not actively graze kelps during this study (Dean et al. 1984).

Interspecific interactions between understory algae and *Macrocystis* appeared to be less important in determining the spatial patterns of *Macrocystis* survival at San Onofre than elsewhere. We observed no significant negative effects of *Pterygophora* or *Cystoseira* on the survival of juvenile *Macrocystis*. This stands in contrast to results from manipulative experiments conducted in the nearby Point Loma kelp forest in San Diego (Dayton et al. 1984) and in kelp forests in Carmel, California (Reed and Foster 1984), both of which indicated that understory algae had significant negative impacts on the survival of juvenile *Macrocystis*. This difference between kelp forests may have been due to differences in both the density and size of competitors. Densities of *Pterygophora* at Point Loma (Dayton et al. 1984) and Carmel (D. Reed, *personal communication*) were nearly twice those at San Onofre (where we observed a maximum density of 4 plants/m^2), and the plants were nearly twice as large elsewhere as at San Onofre (Dayton et al. 1984, Reed and Foster 1984; T. A. Dean, *personal observation*). These biological differences may ultimately relate to the different substrata present at the various sites. At San Onofre, the primary substratum is cobble as opposed to more consolidated rock reefs elsewhere. The lack of stable substrata at San Onofre might have lead to a higher rate of disturbance there and a less stable assemblage of understory algae. In this respect, the San Onofre kelp forest appears similar to disturbance-dominated systems in central California, such as Piedras Blancas (Dayton et al. 1984) and Sandhill Bluff near Santa Cruz (Cowen et al. 1982, Foster 1983), which are less influenced by competitive interactions among species.

One would ideally like to compare rates of survival in the San Onofre kelp forest with published records from other kelp forests (e.g., Rosenthal et al. 1974, Coyer and Zaugg-Haglund 1982, Dayton et al. 1984). However, quantitative comparisons are difficult because of a lack of replication in most studies and because each study began to follow survivorship from a different point in the plant's life history. The lack of replication is especially problematic since we have demonstrated high spatial and temporal variability within the San Onofre kelp forest, depending, in part, on the number of plants recruited, the timing of recruitment with respect to storms, the density of grazers, and the degree of shading by overlying canopy. Qualitative comparisons of survival in various kelp forests indicate that the survival rates of juvenile sporophytes through the adult stage (a period of 1–1.5 yr, on average) are generally on the order of 1 to 10% (Rosenthal et al. 1974, Dayton et al. 1984, this study). This corresponds to a half-life of ≈2–6 mo. Survivorship curves for visible sporophytes of *Macrocystis* (Rosenthal et al. 1974, Dayton et al. 1984, this study) are generally type III (Deevey 1947), with older (and generally larger) plants having lower mortalities than juvenile plants.

Population dynamics of kelp, other algae, and terrestrial plants

The effects of intraspecific interactions on the population dynamics of plants have been widely studied in terrestrial communities (Harper 1977, Antonovics and Levin 1980, Sarukhan et al. 1984, White 1985). These studies have led to several generalizations with regard to both intra- and intercohort interactions, which are summarized as follows. Intercohort density-dependent mortality occurs as the result of canopy-forming adults shading seedlings that recruit beneath them (Harper 1977, Hibbs 1982). In the absence of canopy, juveniles that recruit undergo density-dependent mortality or "self-thinning." The mechanisms of self-thinning are described by the "dominance-suppression" model (Schmitt et al. 1986, 1987). Large plants shade smaller ones resulting in a skewed size distribution. Mortality is size dependent, and disturbances result in the loss of smaller plants.

The population dynamics in large canopy-forming kelps are largely determined by these same processes, as both intra- and intercohort interactions are prevalent. However, the evidence for conformity to the terrestrial models is less convincing in most other marine algal assemblages. Density-dependent mortality has been observed in even-aged stands of a variety of intertidal and subtidal algae (Black 1974, Schiel and Choat

1980, Chapman and Goudey 1983, Chapman 1984, Schiel 1985), and there is some evidence that self-thinning in algal stands proceeds according to the −3/2 power law (Cousens and Hutchings 1983). However, the mechanisms of density-dependent mortality appear to be quite different from those observed in most terrestrial populations and in populations of *Macrocystis.* There is little evidence for negative effects of density on growth, and in some cases, there have even been positive effects observed (Schiel and Choat 1980, Schiel 1985). Similarly, larger plants do not stunt the growth of smaller neighbors (Schiel 1985) nor do smaller plants suffer higher mortality than larger individuals (Chapman 1984, 1986). Studies by Black (1984) indicate both density-dependent survival and growth in newly recruited stands of the intertidal alga *Egregia menziesii* (*laevigata*), but density dependence was only observed in early stages of cohort development when densities were extremely high, and was attributed to clumps of plants sloughing from rocks rather than from the effects of shading.

We hypothesize that the similarities in dynamics of *Macrocystis* and terrestrial plant populations, and the dissimilarity between these populations and populations of other marine algae, relate to competition for light. The growth and survival of seedlings in most terrestrial populations is light limited (Schmitt et al. 1986, 1987) as is the growth of juvenile *Macrocystis* (Dean and Jacobsen 1984). Density-dependent survival appears to result from size-specific mortality and the indirect effect of shading on growth rate. Such effects may be limited to populations of large canopy-forming kelps in deeper waters since these algae occur where light levels are lower (Dean 1985) and have extensive vertical structure that can shade neighbors. Other algal populations that have been studied with regard to density dependence generally occur in either the intertidal or shallow subtidal (e.g., populations of *Leathonsonia difformis* [Chapman and Goudey 1983], *Egregia menziesii* [Black 1974], *Eklonia radiata* [Schiel and Choat 1980], *Sargassum sinclarii* [Schiel and Choat 1980, Schiel 1985], and *Carpophyllum maschalocarpum* [Schiel 1985]) or comprise morphologically simple plants without a great deal of vertical structure that could cause intense shading (e.g., *Laminaria longicrucis* [Chapman 1984, 1986]). This hypothesis is supported by experiments that have examined the "exception to the rule" in terrestrial plant populations. Turner and Rabinowitz (1983) found no evidence for dominance and suppression in morphologically simple grasses. Also, Schmitt et al. (1987) demonstrated dominance and suppression in dense stands of jewel weed, but suppression was not observed in experimentally thinned plots in which competition for light was reduced.

Terrestrial plant ecologists argue that the self-thinning process results in selection for traits that enhance competitive ability, such as faster growth or larger leaves that may increase interception of light (Schmitt et al. 1987). If our hypothesis regarding the mechanisms of density-dependent survival in marine algal populations is correct, then there should be similar selection among the large canopy-forming kelps. On the other hand, intertidal or shallow subtidal populations of algae, and morphologically simple algae, should respond to different selective pressures such as wave surge or grazing. Some evidence for this comes from studies of defenses of different algal species to grazing (e.g., Steinberg 1985) that suggest that canopy-forming kelp (especially *Macrocystis*) have evolved less sophisticated defenses than other algae.

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