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TEMPORAL AND SPATIAL PATTERNS OF DISTURBANCE AND RECOVERY IN A KELP FOREST COMMUNITY[1]

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Abstract. This paper addresses questions of community and patch stability as defined by the population biology of dominant plants in the context of different areas within a large kelp forest. We ask (1) "Do large-scale episodic events override biological mechanisms as major community structuring processes?", (2) "Are different local areas characterized by different processes?", and (3) "How persistent are the patches or biological structure over decadal and local spatial scales?" We evaluate these questions with regard to the effects of various types of disturbance for as much as three decades on the populations of several species of kelp in the large kelp forest off Point Loma, San Diego, California. The most sensitive population factors we studied include recruitment, density, and survivorship. Patch stability was evaluated with regard to the persistence of patches already well established in 1971–1972. The study sites offer a cross-shore transect through the central part of a large kelp forest at depths of 8, 12, 15, 18, and 21 m; two additional sites at the north and south ends of the forest offer a longshore transect along the 18-m contour.

There were marked differences among the decades with regard to the intensity of the disturbances. Compared with the 1980s, the two preceding decades were relatively benign. The 1980s had two extreme disturbance events: the 1982–1984 El Niño-Southern Oscillation (ENSO) was the most severe El Niño event in the last century, which included very warm, nutrient-depleted water, and a short but intense storm in January 1988 appeared to have been the most severe in perhaps 200 yr. The storm changed age-specific kelp mortality patterns and caused the first large-scale understory mortality in several decades. By sweeping away drift algae it caused intense local urchin grazing. The storm was followed by a strong La Niña event marked by cool, nutrient-rich water in 1988–1989.

Differences in kelp recruitment and survivorship in different areas of the kelp forest are influenced by gradients in longshore currents, temperature, light, wave energy, floc, planktonic propagules, and physical disturbance. The areas are characterized by different plant population patterns and the effects of several species of herbivores. The massive disturbances of the 1980s obliterated much of the structure in the kelp forest. Certainly the disturbances caused many lag effects including outbreaks of understory algae such as *Desmarestia ligulata,* intraspecific competition, changes in grazing patterns, etc., which in turn resulted in between-area variation in recovery rates. However, in all cases this variation was overshadowed by the overwhelming competitive dominance of *Macrocystis pyrifera.* Most of the understory patches on the transect lines, some of which had persisted for 7 yr, died out by the end of 1990.

The population biology of *Macrocystis* was remarkably similar in most areas, as the cohort longevity and survivorship curves were very similar, and the plant and stipe densities tended to level off in only a few years. Thus large-scale episodic events such as El Niños, La Niñas, and rare storms exert dramatic impacts, but small-scale responses such as density-vague recruitment (neither density dependent nor density independent) and survival allow prompt recovery, often to preexisting patterns. The one exception was the southern site, which was marked by sea urchin grazing and poor kelp recruitment through the latter half of the 1980s, but a recent sea urchin disease event has led to kelp recruitment in fall 1991. A seeming paradox to the observed *Macrocystis* dominance is that in almost all areas, some understory patches of old plants have persisted through the 1980s.

Key words: canopy; competition; El Niño; grazing; kelp cohort; kelp community; patch dynamics; recruitment; scale; stability; storms; succession; survivorship; understory.

INTRODUCTION

The proper scaling of questions and methods is fundamental to science, but only recently has it received much explicit recognition in ecology (Wiens 1989). It is becoming recognized that different research scales result in definition of different ecological patterns. Usu-

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ally apparent unpredictability at smaller scales blends into more robust general patterns at larger scales. As time scales increase, time lags and rare events become more conspicuous and important (Platt and Denman 1975, Jassby and Powell 1990), but few ecologists have adequate data for such spectral analyses. Ricklefs (1987) demonstrated that terrestrial community structure and patterns of species diversity represent large-scale specific histories, dispersal patterns, geographic dispersal and history, and local processes such as predation, competitive exclusion, and stochastic variation. Finally, this mosaic is superimposed over physical processes that influence the biota in many ways. Haury et al. (1978) made similar arguments for zooplankton data, and Bernal (1981) applied spectral analyses to California Cooperative Oceanic Fisheries Investigations data and described long-period fluctuations relating to flow patterns in the California Current. The implication is that most natural communities exist in a nonequilibrium condition and that their structure is determined by an array of historical events as well as physical and biological processes.

Here we consider the importance of historical, physical, and biological events impacting different areas within a large Southern California kelp forest. Specifically we address the questions: "Do large-scale episodic events override biological or equilibrium mechanisms as major structuring processes of the community?", "Are different areas characterized by different processes?", and "How persistent are the patches or biological structure over decadal and local spatial scales?" To evaluate these questions in an evolutionary context, it is necessary to define demographic and life history patterns as well as persistence of biological structure in different areas of the community.

All natural communities are exposed to many types of disturbance; the effects of disturbances depend upon their temporal and spatial scales and the magnitudes of the disruption (e.g., Highsmith et al. 1980, Sutherland 1981, Peterson 1984, Sousa 1984, Connell and Keough 1985). In addition, most communities and their component populations exist along environmental gradients. Most marine research dealing with gradients has focused on zonation; in contrast, it is the continuum across such gradients that occupies much terrestrial interest. Kelp communities reflect many types of disturbance from storms and grazing (Chapman and Johnson 1990), as well as at least some zonation across depth gradients (Dayton 1975*b*, Schiel and Foster 1986), but it is unknown how such gradients affect disturbance and/or recovery. The effects of storms depend upon their frequency and magnitude as well as the depth (Seymour et al. 1989). The persistence of disturbance effects on kelp forests varies on local and regional scales (Dayton 1975*a*, 1985*a*, Schiel and Foster 1986, Harrold and Pearse 1987, Tegner and Dayton 1987, Witman 1987, Johnson and Mann 1988, Kennelly 1989). Some sea urchin barrens in Alaska appear very persistent (Simenstad et al. 1978), while extensive sea urchin barren grounds off Nova Scotia, which seemed to exhibit a high degree of stability for at least a decade (Mann 1977, Chapman 1986), suffered mass sea urchin mortalities with subsequent kelp recovery (Miller and Colodey 1983, Scheibling and Stephenson 1984, Johnson and Mann 1988, Elner and Vadas 1990). Shorter term reverses in kelp forest community structure have been documented at Naples Reef near Santa Barbara (Ebeling et al. 1985). The ubiquity of such disturbances emphasizes the importance of understanding the mechanisms responsible for stability and succession.

This work was done in the Point Loma kelp forest off San Diego, California (Fig. 1A). Research dating from the mid 1950s offers a valuable historical perspective and much of our original work was predicated on earlier studies by Neushul (e.g., 1959), Pearse et al. (1970), and especially Wheeler North (e.g., North and Hubbs 1968, North 1971), who laid much of the foundation for subsequent kelp forest research. It is one of the largest giant kelp forests in the world, with cross-shore and longshore gradients in the physical and biological landscapes. This productive community is dominated by the giant kelp, *Macrocystis pyrifera,* but also includes a variety of understory algae (Turner et al. 1968). While our variance data are inadequate for spectral analyses, we have 8–20 yr records of densities of *Macrocystis* and some understory species. During this period there have been major disturbances, including the largest El Niño-Southern Oscillation (ENSO) event ever recorded, and what coastal engineers estimated to have been a once-in-200-yr storm (Dayton et al. 1989). We have study sites in different areas of the kelp forest, and we attempt to focus on scale patterns within a kelp forest large enough to encompass gradients in important factors such as depth, light, nutrients, wave energy, current speed, planktonic propagules, epifaunal animals, and flow. That is, within the Point Loma kelp habitat we focus on differences between local areas; within given areas there are specific sites for various observations and experiments. We hope to blend natural history and environmental determinism into an understanding of some of the larger scale patterns characterizing this kelp community. We pick kelp recruitment and survivorship as sensitive and important indicators of population biology, and ask whether there is coherence between the temporal and spatial patterns exhibited by *Macrocystis pyrifera,* the most conspicuous species and competitive dominant of several species of kelps (North 1971, Dayton et al. 1984), in different areas of the Point Loma kelp forest.

The importance of storm disturbance is determined by the area actually cleared of plants by being entangled or dislodged. In most cases at Point Loma the understory species are much less affected by storms (Dayton et al. 1984). Perhaps the most generally important source of disturbance in kelp forests worldwide is sea urchin grazing (reviewed by Dayton 1985*a*, *b*, Chapman 1986, Harrold and Pearse 1987). For this reason an important second-order result of storms is the effect on drift algae, the major source of food for sea urchins (Ebeling et al. 1985, Harrold and Reed 1985). The history and consequences of storms, El Niños, and sea urchin grazing at Point Loma have been reviewed by Tegner and Dayton (1987). Subsequent to this review Point Loma experienced an extremely severe storm in January 1988 (Seymour et al. 1989, Dayton et al. 1989). Not only did this storm devastate all species of algae, it had massive effects on the substratum. This paper will discuss the scaling and population consequences of these and other disturbances across both cross-shore and longshore gradients within the large Point Loma kelp forest.

Here we focus on kelp density, recruitment, and survivorship as influenced by several physical and biological phenomena that limit the carrying capacity or the maximum number of individuals persisting under the conditions characteristic of particular areas of the kelp forest. Estimates of relative distribution and abundance of species define among-area patterns. Foster (1990) pointed out the paucity of studies that have quantitatively assessed the abundance of kelps and associated species along the complete depth gradient over which they occur. A life table would offer the most complete description of the local population dynamics of the species in each habitat. Unfortunately it is essentially impossible to quantify birth rate. Each kelp plant produces many millions of spores, and it is extremely difficult to quantify the survivorship of the early stages because of the difficulty in identifying and counting these small and densely packed individuals. As a compromise we have evaluated the survivorship of arbitrarily defined adult *Macrocystis* plants.

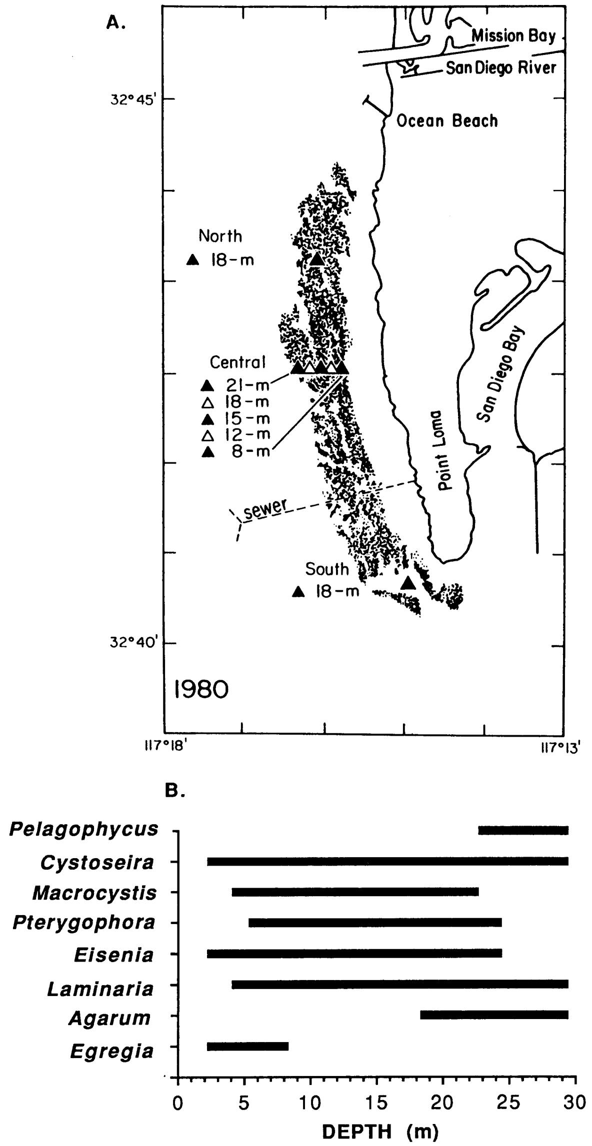

FIG. 1. (A) Map of the Point Loma kelp forest and location of the study sites. The stippling represents the *Macrocystis* canopy in December 1980; there is considerable temporal variation. The 18-m North site was at the northern end of the forest when it was established in 1983. (B) Depth zones of maximum abundance of the major algal species in the central Point Loma kelp forest.

SITE AND SPECIES DESCRIPTIONS

Like any other natural habitat, all kelp forests are different from each other, but the Point Loma kelp forest (Fig. 1A) is representative of Southern California hard-bottom habitats and has been studied for many years. The kelps grow on a broad, rocky shelf which is rather flat in most areas, but has some reefs and boulder piles, as well as sand-filled channels. It is bounded on the north by a sandy bottom and the mouth of Mission Bay, from which sand is occasionally dredged. To the south it is bounded by the opening of the large San Diego Bay. The bottom in the northern area of the kelp forest is exposed to shifting sand and in the southern area to floc, presumably from the bay. The Point Loma *Macrocystis* canopy is generally ≈8–10 km long and 1 km wide, large enough to modify its environment. Jackson and Winant (1983) showed that the current velocities within the forest are about one-third of those along the outer edge, and that the transition occurs within 100 m. As most of an energetic longshore current encountering a kelp stand will flow around it, the longshore ends and outer edge are exposed to a different environment than are sites within the forest. This has important implications for the distribution of nutrients, planktonic food, and larvae (Jackson 1983). The offshore and inshore edges are in ≈24 and 7 m depths with obvious implications for the light and wave action regimes (Jackson 1987, Seymour et al. 1989).

Kelps occur from the intertidal to a depth of ≈30 m, and the species composition of the kelps changes across this gradient (Fig. 1B). In the shallow (0–6 m) zone the feather boa kelp *Egregia menziesii* and the understory kelps *Laminaria farlowii* and *Eisenia ar-*

borea grow on boulders and areas of relief above a generally sandy bottom. The sea grass *Phyllospadix* spp. grows from the base of the rocks into the sand. Giant kelp *Macrocystis* grows from ≈6–24 m depth; this area also includes patches of the understory *Pterygophora californica, Eisenia, Laminaria,* and the fucoid *Cystoseira osmundacea.* Plants in deeper areas (>24 m) are predominantly prostrate *L. farlowii, Agarum fimbriatum,* and *Cystoseira. Desmarestia ligulata* is widely abundant after disturbances and some plants persist in deeper water.

Pterygophora californica is perhaps the understory species most able to colonize new habitats. It disperses well and has high recruitment rates (Reed et al. 1988), and once established, individuals can be very long lived (Dayton 1985*a,* Hymanson et al. 1990). *Eisenia arborea* is a stipitate kelp similar in appearance to *Pterygophora* when they grow together. *Eisenia* has an interesting distribution pattern with patchy but often dense populations in- and offshore of the *Macrocystis* forest. Within the forest it seems most abundant on reef tops or other areas exposed to heavy surge. *Eisenia* also occurs in high densities on the offshore banks, where it has been collected from 60 m (Lissner and Dorsey 1986). *Laminaria farlowii* is a prostrate kelp, individuals of which may be >2 m long in areas with low surge, and which may form thick patches covering as much as 100 m^2.

Our study sites (Fig. 1A) were placed to offer a cross-shore transect through the central part of the forest and representative 18-m sites at the north and south edges of the forest. The 15-m central site is the original site reported in Dayton et al. (1984); work here was initiated in 1971. We have continued to monitor the 100 × 4 m transect established in 1971 and two 50 × 4 m transects established in 1981. Transects (100 × 4 m) were also established at 12 and 18 m depths in 1972 at sites that represented the inner and outer edges of the forest at the same latitude as the 15-m site. The species assemblages in each of the cross-shore areas are different (Fig. 1B, Tables 1 and 2). Concurrent with the onset of the ENSO in 1983, new transects were established at the same 12-, 15-, and 18-m sites studied in the 1970s. The 10-m designation in Dayton et al. (1984), should have been recorded as 12 m. In addition, two new sites were initiated at a depth of 18 m at the north and south ends of the kelp forest. The 18-m North site is exposed to relatively clean water as well as the nutrient-rich longshore currents. In contrast, 18 m South appears consistently stressed by poor light penetration, a high rate of sedimentation, and grazing by sea urchins (P. K. Dayton et al., *personal observations* 1983–1991). Finally, some observations will be reported from sites at 8 and 21 m in the center of the forest. The density/depth data (as well as the clearings at 8, 12, 15, 18, and 21 m, see *Materials and methods: Clearings*) come from areas chosen for homogeneous flat substratum biasing against *Eisenia,* which tends to be more common on vertical relief. The issue of line and time bias is discussed in the *Results* section, but we picked habitats as similar to each other as possible; the data do not represent random samples of general areas within the kelp forest.

Distinct patches dominated by particular species (Dayton et al. 1984) are widespread. The distributions of kelp species and distinct patches were determined in a systematic survey in 1991 (Tables 1 and 2). Persistence of established patches was evaluated by monitoring boundaries marked in 1970–1972 (Dayton et al. 1984); this was done only at 15 m. However, individual *Pterygophora* and *Eisenia* can be aged, and we found patches composed of plants >8 yr old in all areas in 1991. This implies that patch persistence is general.

MATERIALS AND METHODS

Temperature and nutrients

Macrocystis growth depends upon an ambient nitrate concentration >1 μmol/L (Jackson 1977, Gerard 1982, Zimmerman and Kremer 1984). *Macrocystis* adults can use internal nitrogen reserves for growth over a period of 2–4 wk (Gerard 1982) once nutrients become limiting. Fortunately there is a strong inverse relationship between temperature and nitrate in which there is negligible nitrate above 16°C (Jackson 1977, Gerard 1982, Zimmerman and Kremer 1984). This well-documented threshold relationship between temperature and nitrate allows us to use temperature as a surrogate for nitrogen availability or stress. Thus, we have maintained continuous bottom temperature recordings at each site as an indication of nitrate availability, which might affect gametophyte reproduction and growth as well as sporophyte growth (Deysher and Dean 1986). In situ bottom temperatures were collected with recording Ryan Thermographs deployed for 3 mo at a time. Each thermograph was calibrated at the beginning and end of each deployment. Temperatures were determined every 3 h from the continuous records, adjusted for the calibration, and averaged by month. Our sea surface temperature records are from the pier at Scripps Institution of Oceanography ≈9 km to the north. Temperature recordings made on most dives verify that the surface temperatures from the Scripps pier are usually the same and always within 2°C of those at Point Loma.

Kelp density

There are three distinct meanings of recruitment as used in this paper. First is the germination or recruitment to the benthos of the zoospores as they settle and grow into gametophytes. Second is sporophyte germination or recruitment when the fertilized egg starts growing into a tiny sporophyte; when we can see that it has appeared as a small blade we refer to that as sporophyte recruitment. Third, unless otherwise spec-

TABLE 1. Densities (individuals/m^2) of algae in the Point Loma kelp forest across the depth gradient, summer 1991. A minimum of 10 50 × 2 m transects at each depth was used to determine the densities with sites haphazardly chosen throughout the bed.

Species	Depth (m) 8	12	15	18	21	24
Macrocystis pyrifera	0.21	0.28	0.35	0.34	0.17	0.05
Laminaria farlowii	1.40	1.47	0.37	0.07	0.20	0.28
Pterygophora californica	0.98	1.32	0.84	0.05	0.11	0.11
Eisenia arborea	0.06	0.01	0.05	0.00	0.01	0.02
Agarum fimbriatum	0.00	0.00	0.00	0.00	0.05	0.16
Pelagophycus porra	0.00	0.00	0.00	0.00	0.00	0.09
Egregia menziesii	0.03	0.00	0.00	0.00	0.00	0.00
Cystoseira osmundacea	0.18	0.70	0.00	0.00	0.11	0.13

ified, we employ the fisheries use of the term as recruitment into a particular size or year class, in our case the four-stipe stage that we arbitrarily refer to as an "adult" plant.

Four parallel 25-m lead lines were installed in an offshore–onshore direction at each site. The spacing of the lines forms a square 25 m wide, so we can test for directional differences within or between the 25 × 4 m quadrats. The plants were mapped quarterly within 2 m to each side of the lines, a total of 400 m^2 per site, from spring 1983 through fall 1990. All *Macrocystis* with at least four stipes were mapped, as were the understory species when possible. The maps were updated each visit to evaluate survivorship and growth. Percent cover of understories not counted was estimated quarterly. Maximum densities were not recorded because there were a few periods in which the *Macrocystis* were so dense that the sampling itself would have caused many mortalities from entanglement with the divers. For this reason the peaks in these figures should be used to approximate when the peaks occurred and represent minimum densities at the actual peaks. We sampled episodic recruitment events (usually of *Desmarestia*) with shorter 5, 10, or 20 × 2 m transects. The distribution of *Macrocystis* was not uniform along the transects at each site and this pattern appeared to persist through time. To examine this within-site variation further over time, a nonparametric Friedman's two-way ANOVA was performed on the data collected along the four 100 × 4 m transects at each site.

Survivorship of kelp stages

Survivorship of kelps is difficult to measure because the very young stages suffer the highest mortality, which can occur in a patchy manner. Our earlier work (Dayton et al. 1984) measured cohort survival in three preadult size classes. New kelp sporophytes may occur in very high densities before they are large enough to be identified; a cohort of 1543 of these was mapped. Of these, the first size class to 5 cm tall had 19% survivorship. The 5 cm to 1.5 m size class had 86% survivorship, with 17% of the original cohort attaining 1.5 m. The 1.5 m high to 4-stipe size class had 14% survivorship or ≈2% of the original cohort. To simplify monitoring in this study, an adult *Macrocystis* was arbitrarily defined as one having differentiated four stipes; the rationale for this definition is that the fronds of most such plants approached or reached the surface and, when healthy, such plants begin to differentiate sporophylls. Under exceptional conditions the sporophylls of such young plants may have some fertile sori, but most plants do not actually become fertile until the 16-stipe stage. In this study we focused on the actual survivorship of adults (4-stipe stage and above). In comparison, Dean et al. (1989) monitored survivorship of much younger plants <1 m long. We (Dayton et al. 1984) found that such plants have very much lower survivorship than 4-stipe plants. We emphasize that we recognize the importance of germination events (Deysher and Dean 1986) and we did monitor sporophyte recruitment. We found in the 1980s that every

TABLE 2. Abundance of kelp patches in 50 × 2 m transects at various depths across the depth gradient, summer 1991. Data are mean numbers of patches and mean patch length (in metres) in each transect. Patch length was determined by point-intercepts along the transect line. A minimum of 10 50 × 2 m transects was conducted at each depth.

Depth (m)	*Macrocystis pyrifera* No.	*Macrocystis pyrifera* Length	*Laminaria farlowii* No.	*Laminaria farlowii* Length	*Pterygophora californica* No.	*Pterygophora californica* Length	*Eisenia arborea* No.	*Eisenia arborea* Length
8	1.7	5.24	1.0	5.50	0.6	10.08	0.2	2.00
12	1.0	2.64	1.0	2.80	1.7	4.16	0.0	
15	0.7	4.00	1.1	4.41	2.6	4.46	0.0	
18	1.6	9.19	0.1	3.00	0.2	2.50	0.0	
21	0.4	20.50	0.2	4.00	0.2	3.50	0.0	
23	0.3	1.60	0.1	3.50	0.1	4.50	0.0	

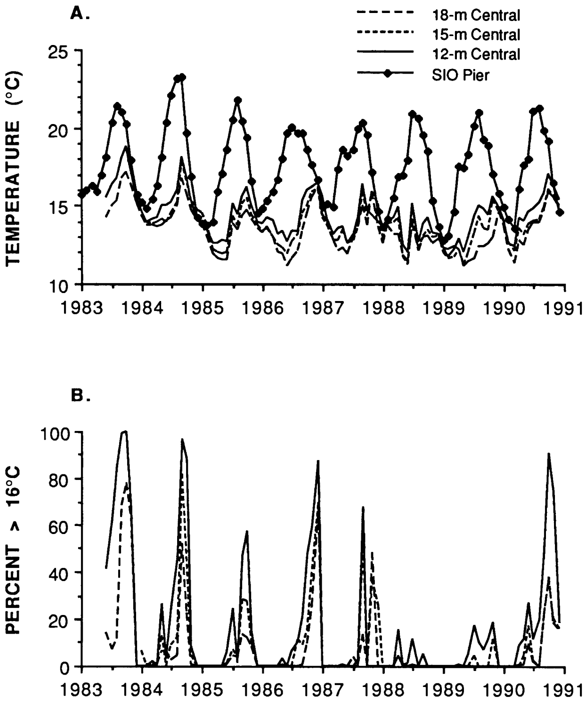

FIG. 2. (A) In situ bottom temperatures from 12, 15, and 18 m depths in the center of the Point Loma kelp forest and the surface temperature from the Scripps Institution of Oceanography (SIO) pier, ≈9 km to the north, 1983–1990. (B) Percent of the observations (8 per day) each month in which bottom temperatures were above the 16°C nutrient threshold (NO_3 concentration is negligible at temperatures higher than this) at the same three sites in the center of the forest.

release in *Macrocystis* canopy cover was followed by a strong recruitment event. Temperature and water transparency factors may have fine-turned these responses, but did not much influence sporophyte recruitment. The survivorship data we present, however, describe survivorship of plants after they reach the 4-stipe stage.

Patch surveys

To better determine species and understory patch distributions, a series of haphazard surveys was conducted across the depth gradient at six locations in the Point Loma kelp forest, north and south of the central study sites. A minimum of 10 50 × 2 m transects was counted per depth during summer 1991. Distinct patches of predominantly one species (Dayton et al. 1984) were recorded as point intercepts on the transects.

Macrocystis–Pterygophora *interactions*

Macrocystis is known to dominate *Pterygophora* in competition for light (Pearse and Hines 1979, Dayton et al. 1984), yet patches of *Pterygophora* are common (Table 2). We evaluated the amount of "head start" that a *Pterygophora* patch needs to become established. A 20 × 20 m square 10 m east of the transect lines at the 12-m site was marked in a mixed stand of kelps on a relatively flat sandstone pavement in October 1984. *Macrocystis* were removed by clipping the stipes at the apex of the holdfast to minimize disturbance to the *Pterygophora.* Fifty *Pterygophora* were tagged in the center of the clearing, an additional 50 in the reduced light environment within 2.5 m of the southern edge of the clearing, and 50 more in a mixed stand of *Macrocystis* and *Pterygophora* along transect line A. *Macrocystis* recruits and immigrants (drifters on rocks) were removed from the clearing monthly. After 1 yr, the *Pterygophora* were harvested and assessed for growth (stipe elongation), sporophyll mass, and the presence of sori.

Clearings

In 1987, 20 × 20 m clearings with a 5-m buffer zone were established in early spring at 8, 12, 15, 18, and 21 m near the established transect lines (plus two new sites at 8 and 21 m) in the center of the forest. With the exception of encrusting coralline algae, all macroalgae and sea urchins were removed to compare subsequent algal recruitment, growth, and reproduction across a depth gradient. Most of these data will be presented in a later paper, but some mortality results are relevant here.

RESULTS

Temperature

Fig. 2A records 7 yr of temperature data from the surface at Scripps Institution of Oceanography and bottom sites representing three depths in the center of the forest. The water column is generally isothermal for a period each winter. A thermocline develops in the late winter/early spring and becomes quite pronounced by midsummer. The lowest bottom temperatures occur during the spring when most juvenile recruitment is observed, and the surface temperatures are warmest in late summer when canopy diebacks often occur. Bottom temperatures rise during the late summer/fall as the surface temperature drops; winter storm mixing eventually eliminates the differential. A cross-shore temperature gradient is also apparent in Fig. 2. Finally, the El Niño years of 1983 and 1984 are strikingly warmer than the subsequent period; the cold years of 1988–1989 represent La Niña conditions (Kerr 1988).

Because of the importance of nitrate concentration to recruitment and growth of kelps and the inverse relationship between nitrate concentration and temperature (Jackson 1977, Gerard 1982, Zimmerman and Kremer 1984), temperature differences between sites imply important between-area differences to kelp populations. Monthly averages of eight values per day of bottom temperatures for the three central sites (Fig. 2) were compared for the period of fall 1983 through spring 1990 using Friedman's two-way ANOVA.

Rankings were considered ties unless the temperature differential was >0.3°C. The results showed significant ($.05 > P > .025$) differences between sites, and an a posteriori test (Nemenyi 1963) indicated that 12 m was significantly warmer than 15 m, which was significantly warmer than the 18-m Central site. Perusal of Fig. 2 indicates that these depth-related temperature differences are not constant; during some quarters temperatures are similar across the forest, and in others, the differences suggest significant differences in nitrate availability for kelp growth. A similar analysis for the three edge-of-the-forest sites indicated that the 18-m North site was significantly warmer than 18-m Central and 18-m South; the latter two sites were not different (Tegner and Dayton 1991). The implications to different areas of the kelp forest of temperatures exceeding the 16°C threshold for the availability of nitrate are suggested in Fig. 2B.

Patterns of abundance in different areas of the kelp forest

A) *Macrocystis.*—The distribution of adult *Macrocystis* along the transects within each site through time was examined with a nonparametric Friedman's two-way ANOVA performed on the data collected along the four 25 × 4 m transects at each site. Results of this analysis show that significant differences ($P < .01$) between transects do exist at all sites, and that *Macrocystis* do vary significantly ($P < .01$) from year to year. This implies that there are microhabitat differences within each site. However, trends in numbers between transects appear consistent through time at each site (Fig. 3). In other words, although microhabitat effects do exist at all sites, the patterns within each remain consistent over time. This implies that the numbers of adult *Macrocystis* along the four transect lines at each site changed through time in concert. The relative density differences between lines generally persisted through time, implying that the microhabitats and the original pattern of recruitment were very important in determining patterns of distribution and abundance. We also compared the number of *Macrocystis* along each line from 1983 through 1987 with the patterns of distribution after the 1988 storm. It appears that the plants generally recruited along the lines in the same patterns before and after the storm, further suggesting that recruitment was not random and emphasizing the importance of local microhabitats to the distribution of *Macrocystis* (Reed 1990*a*).

Fig. 4 plots up to 20 yr of density data for adult *Macrocystis* at three depths in the center of the forest. All of the 15-m data in this figure come from the original 100-m transect; the 12- and 18-m data come from the 100-m transects of the 1970s and the four 25-m transects from 1983 onwards. Notice the much higher densities in shallow water. Fig. 3 presents densities on the individual transects and Fig. 5 presents cohort densities for all five sites (both the 25-m transect) through the 1980s. Notice the higher shallow water densities and the mortality following the January 1988 storm (Seymour et al. 1989). In the 1970s the 12-m Central site had two very strong kelp recruitment episodes, with the giant kelp population subsequently being eliminated by sea urchin grazing (Dayton et al. 1984). By 1983 the red sea urchin (*Strongylocentrotus franciscanus*) had been functionally eliminated from this site by an unregulated fishery (Tegner and Dayton 1991). The *Macrocystis* density rebounded twice from the ENSO event and slowly declined from ≈1.8 to 0.3 plants/m^2; the latter value probably approximates the carrying capacity for adult plants (Fig. 5).

The major peak at 15 m in 1975 (Fig. 4) was a response to the loss of almost all the canopy following a storm that killed a cohort of 6–8 yr old plants. Density leveled off at 0.08–0.10 plants/m^2, whereas the density after the 1983 ENSO event declined from ≈0.5 to a little over 0.2 plants/m^2 (Fig. 5). The post-ENSO peak at 15 m was muted despite continuous strong recruitment because the plants were extremely stressed by El Niño conditions, usually before they became adults; then as they grew the self-thinning was faster and more effective, such that peak high densities of adults did not occur.

The population at the 18-m Central site showed more stable patterns, which leveled off with a carrying capacity during the 1970s between 0.05 and 0.15 (Fig. 4), while the asymptote in the 1980s was ≈0.13 plants/m^2 (Fig. 5), perhaps a little higher than the 1970s, but not remarkably so. The North and South sites also are 18 m deep, and during the 1980s, the North densities never really leveled off, but stayed above ≈0.15 plants/m^2 (Fig. 5). The southern site averaged about 0.13 plants/m^2, but here there was tremendous grazing-related variability in survivorship. Most mortality of pre-ENSO plants resulted from El Niño, although a few of these plants were killed by amphipods in 1985–1986 (18-m South, Fig. 5; Tegner and Dayton 1987). In no case were there enough pre-ENSO plants to suppress recruitment. These data emphasize spatial differences in the kelp forest; recruitment rate and carrying capacity both decline with depth. The only difference between the decades was at the 15-m site.

Stipe density may be a more meaningful measure of carrying capacity than plant density. Fig. 6 shows a sharply increasing number of stipes per plant at the deeper depths, while the actual stipe density curve leveled off at 4–6 stipes/m^2 between 1986 and 1987. Comparable data were collected only twice at 15 m in the 1970s. In 1976 a mature stand of plants had a mean of 5.8 stipes/m^2. Later, in 1979, the mean was 1.0 stipes/m^2, but in this case the plants were becoming senile and losing stipes while still maintaining a sufficient surface canopy to inhibit recruitment.

B) *Pterygophora.*—Tables 1 and 2 show the *Pterygophora californica* densities and mean patch sizes, respectively, at various depths. *Pterygophora* recruited

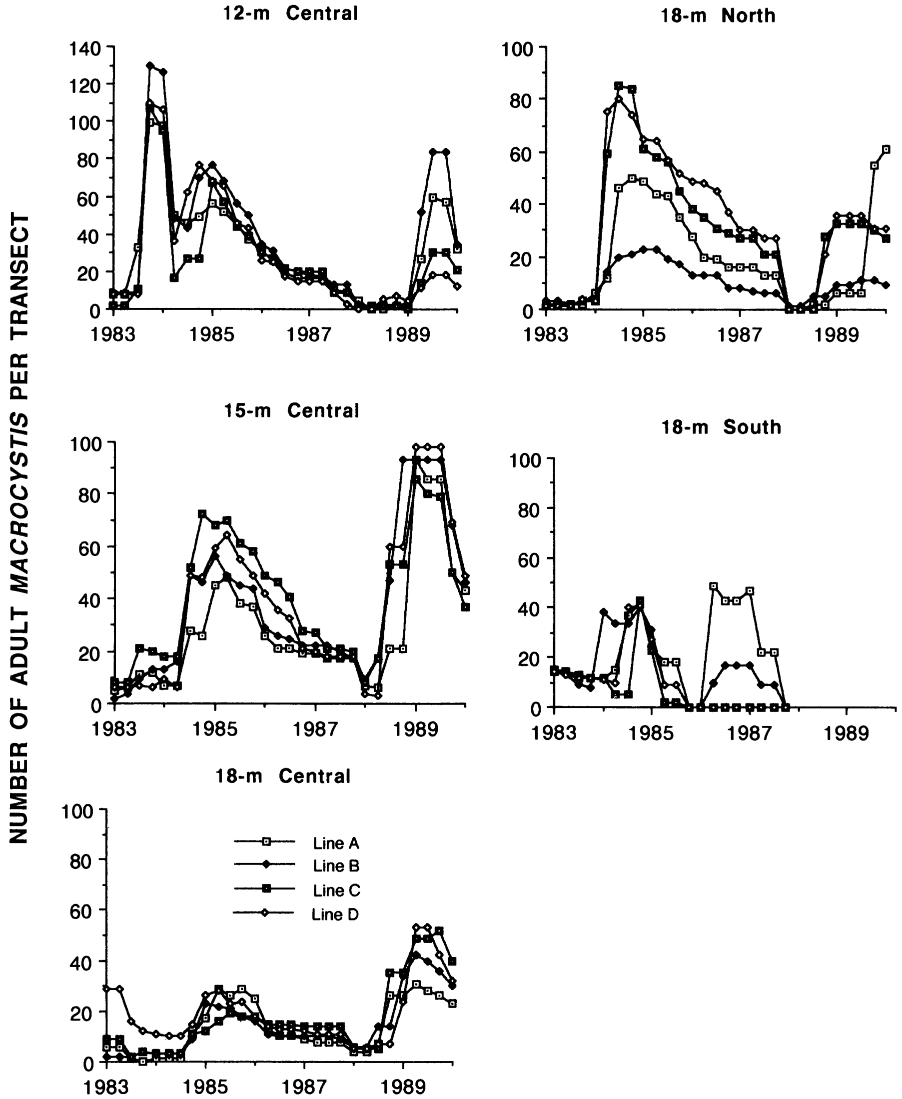

FIG. 3. Number of adult *Macrocystis* per 25 × 4 m transect at each site from 1983–1990. While there was significant variability in density among the four transect lines at each site, the trends were similar in each case. Note the change in scale among the graphs.

at all our study areas after both the ENSO disturbances and the January 1988 storm, but only the two shallowest sites were densely colonized (Figs. 7 and 8). The other transects generally showed a remarkable long-term constancy in the period between the 1982–1984 ENSO and the 1988 storm. The 18-m South site differed because *Pterygophora* recruitment followed the loss of the *Macrocystis* canopy to amphipod grazing in 1986 (Fig. 9). There was also a decline of *Pterygophora* at 18-m North, apparently due to the dense *Macrocystis* canopy (Fig. 9). We know from a *Macrocystis* thinning experiment discussed later that the 12-m *Pterygophora* decline resulted from competition with *Macrocystis*.

Most of the *Macrocystis* and *Pterygophora* at our sites were scoured off the substratum at 8- and 12-m Central by the 1988 storm. This intense storm stripped most of the coralline algae and in some areas as much as a centimetre of sandstone from the bottom. *Pterygophora* quickly recovered at the 12- and 15-m sites (Figs. 7 and 9). The *Pterygophora* along the ENSO transect lines at 15 m eventually were eliminated by competition with *Macrocystis*. However, most of the original *Pterygophora* patches on the 1971 line have persisted through September 1991. *Pterygophora* densities at 12 m showed significant decline by summer 1991. Scattered young patches of understory kelps could still be discerned for many months after the storm, but many such patches disappeared beneath the unusually dense *Macrocystis* canopy. The unusually good growth conditions of 1988–1989 resulted in scramble com-

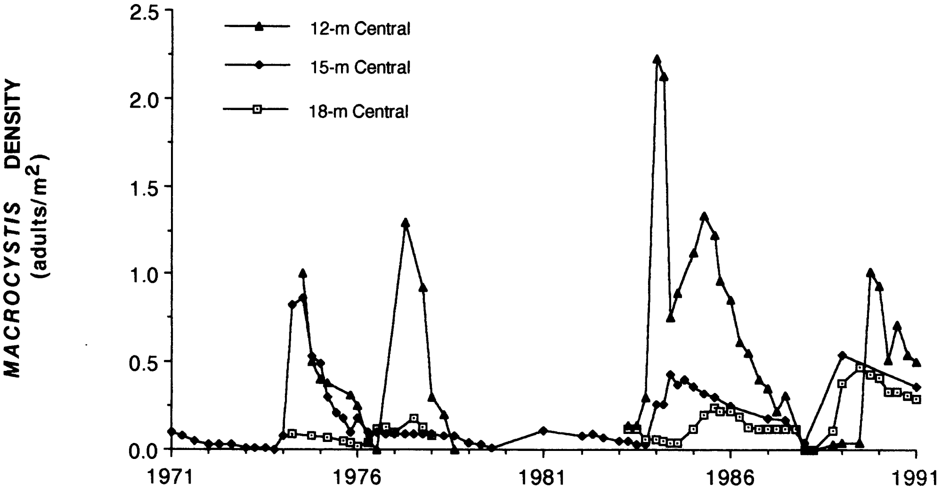

FIG. 4. *Macrocystis* density at three sites in the center of the Point Loma kelp forest, 1971–1990. No data were collected at 12- and 18-m Central from 1978 through 1983. See *Results: Patterns of abundance . . . : Macrocystis* for an explanation of the different transect lines from which the data came.

petition convincingly won by *Macrocystis* (Figs. 5 and 9). In contrast, at 15 m the patches already well established and marked in 1972 were not destroyed by the storm, as a few battered individuals in each patch survived to reproduce, and all *Laminaria* and *Pterygophora/Eisenia* patches persisted through July 1991, often immediately beside *Macrocystis.* Thus the storm erased many but not all understory patches. Those observed to persist did so largely as a result of adult survivorship and post-storm recruitment, because in most cases the bottom below was sandblasted, thus vastly reducing the density of gametophytes. Within 4 mo of the storm there was heavy recruitment.

C) *Eisenia.*—Tables 1 and 2 give densities and patch sizes of *Eisenia arborea* at various depths. Distinct patches of *Eisenia* do occur but are rare. Unlike *Pterygophora, Eisenia* has low recruitment after massive perturbations and seems to grow much more slowly. Both *Eisenia* and *Pterygophora* were remarkably resistant to death during the ENSO disturbances, and in deeper areas, to the 1988 storm.

D) *Laminaria* and *Cystoseira.*—Tables 1 and 2 give densities and patch sizes of these low-lying canopy species. *Cystoseira* tends to occur in the same canopy guild with *Laminaria* but does not have much canopy at Point Loma. As expected for understory species, *Laminaria* and especially *Cystoseira* have higher densities in and offshore of the *Macrocystis* canopy than within the forest, where their distribution is very patchy. These data parallel the percentage cover data from each study site (Fig. 8).

Although formal population work was not done in the present study, there was massive post-ENSO *Laminaria* recruitment at 15-m and 18-m North, which was quickly reduced to an asymptote of ≈5% cover in the face of thick *Pterygophora* and *Macrocystis* canopies (Figs. 8 and 9). The *Laminaria* at the 12-m site did not have a post-ENSO burst, perhaps because of the *Desmarestia* in 1983 (see *Section E: Desmarestia*), but has continued at about the same 5% cover. The 18-m Central site maintained 15–20% cover of *Laminaria* until the 1988 storm, after which this kelp recovered quickly and continued to persist at about the same 15–20% cover until 1990, when it underwent a sharp decline. We saw little evidence of recruitment at the 18-m Central site, and it seems that *Laminaria* in deep water has good survivorship. The *Laminaria* at 18-m South was eliminated by amphipod and urchin grazing in mid-1986 (Tegner and Dayton 1987). By July 1990, *Laminaria* cover at all sites was much lower than the apparent carrying capacities observed in 1986–1987 (Fig. 8), probably because of intense competition with the unusually dense *Macrocystis* canopy.

An unusual grazing event affected the *Laminaria* population at 18-m Central. Sea hares, both the large *Aplysia vaccaria* and the more common *A. californica,* were often seen (at densities up to 0.08 individuals/m^2) at this site in 1984, the last year of the ENSO (also see Reed 1990*b*). Previously we had never seen either in the deeper kelp forest, nor have we afterwards. *Aplysia vaccaria* was thought to feed exclusively on the shallow-water kelp *Egregia* (Morris et al. 1980), but we observed them feeding on *Laminaria* blades. The characteristic radular bite patterns on the blades indicated that *Aplysia* grazing was responsible for patches of heavily grazed blades and denuded stipes, and a large increase in the *Laminaria* contribution to the drift. Feeding observations and examination of the drift showed that the sea hares also fed occasionally on *Macrocystis* sporophylls, *Pterygophora, Agarum,* and *Cystoseira,* but only the *Laminaria* population was significantly affected. *Laminaria* percent cover declined

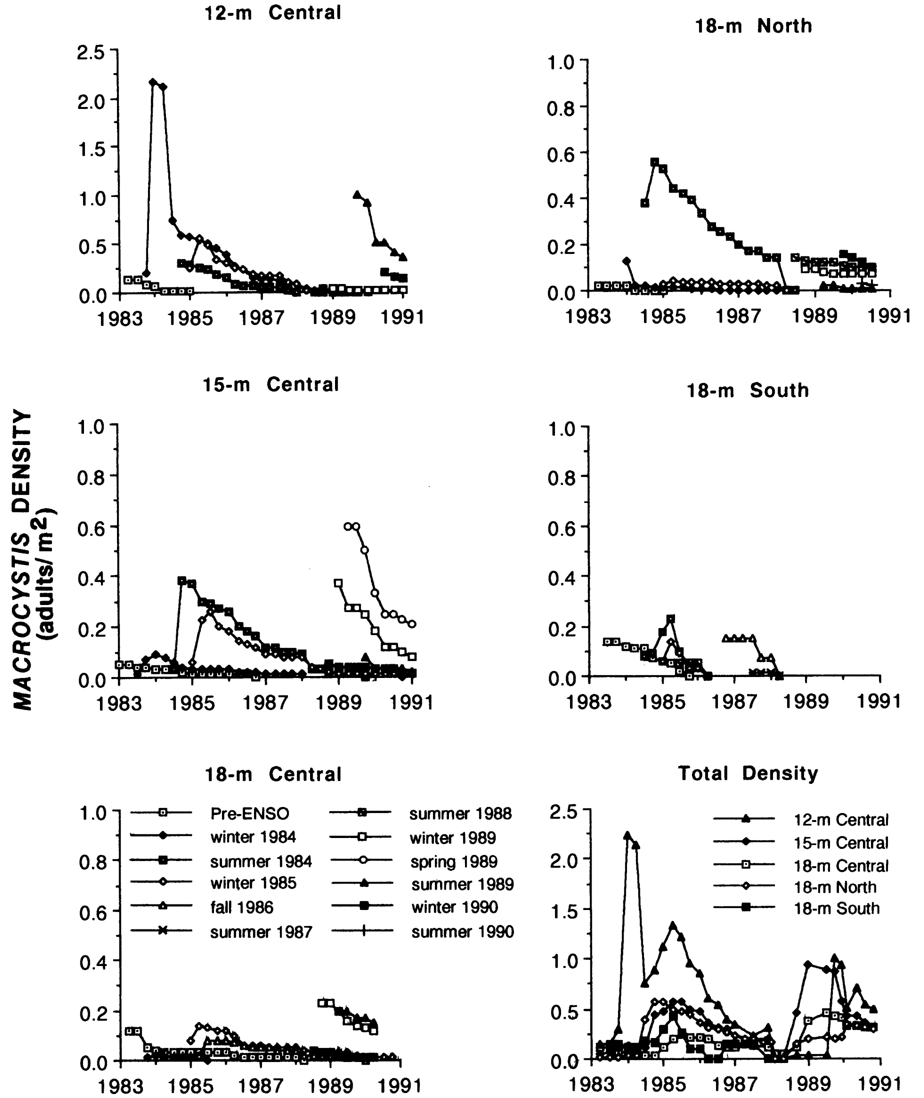

FIG. 5. Density of *Macrocystis* cohorts by site and total density (all cohorts summed) compared among five sites in the Point Loma kelp forest, 1983–1990. ENSO = El Niño-Southern Oscillation. Note the different scale for the 12 m depth and the total density data.

on the transects, but observations of tagged plants indicated that even heavily grazed (no blade remaining) plants showed rapid regrowth. Thus *Laminaria* maintained its patch boundaries through several waves of *Aplysia* grazing during summer 1984.

E) *Desmarestia.*—The pre-ENSO distribution of *Desmarestia ligulata* var. *ligulata* and *D. ligulata* var. *firma* (Chapman 1972) appeared restricted to isolated patches cleared by storms or where sea urchins had been removed. This pattern of small patches was much changed during the 1980s. During the ENSO there was widespread, massive recruitment of *Desmarestia* at several sites, which persisted much longer than normal. There was again massive recruitment following the 1988 storm, which in some areas formed canopies sufficiently dense to obscure the substratum over several hectares. In these cases the *Desmarestia* patches had distinct borders and appeared in areas of the most severe disturbance where there was little or no surviving *Macrocystis* canopy. These patches following the ENSO and the storm were unusual because they persisted through the winter and in some cases through the next year as well (Fig. 10).

To evaluate the effect of *Desmarestia* on the recruitment and species composition of other algae, we established two 20 × 2 m transects through the 1988 *Desmarestia* patch at the 15-m site where we recorded frond morphs, turf abundance, and kelp and *Desmarestia* biomass. In addition we evaluated the densities and the mean lengths of *Desmarestia* fronds in and outside the *Desmarestia* patch and the persistence of the border of the patch itself. In some cases frond lengths

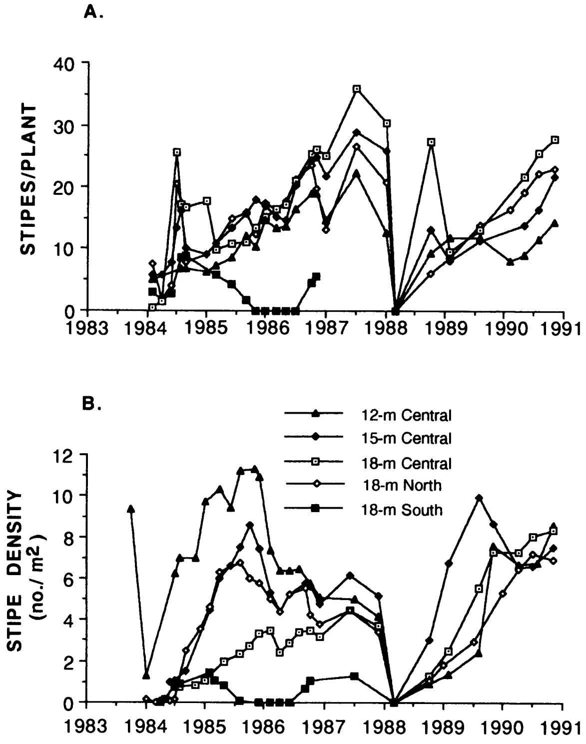

FIG. 6. (A) Changes in the mean number of stipes per *Macrocystis* plant. The anomalous peak of the 18-m Central plants in late 1988 reflects storm survival of these deep-water plants. (B) *Macrocystis* stipe density.

inside the canopy approached 4 m! The plants persisting inside the patch became thick and dark, and many appeared senescent with *Chlorocytrium,* an epiphytic green alga that is common on spent *Pterygophora* and *Eisenia* sporophylls; this apparent senescence was about the same within and outside the *Macrocystis* canopy. Relative biomass composition data gathered inside, at the edge, and outside the *Desmarestia* canopy indicate an inverse relationship between *Desmarestia* and kelp biomass (Fig. 11). The kelps had almost no recruitment inside the 15-m *Desmarestia* patch up to January 1990, 2 yr after the storm. This contrasts with the massive recruitment of all kelps seen in areas not dominated by *Desmarestia* (Figs. 7–9), and also with 12-m and 18-m North (Fig. 10), where kelp recruitment followed the disappearance of the *Desmarestia* in 1989.

Patterns of Macrocystis *survivorship in different areas of the kelp forest*

The *Macrocystis* density and survivorship data (Figs. 4, 5 and 12) are based on adults, arbitrarily defined as having four stipes, and do not reflect infant and juvenile survivorship. We followed individual cohorts through time to evaluate differences in survivorship in different areas of the kelp forest. The spring of 1983 had a brief upwelling period (Fiedler 1984) when cool, presumably nutrient-rich water entered the kelp forest. This and the extraordinary amount of open space created by the storms resulted in strong recruitment of juvenile sporophytes during late spring 1983 (Dayton and Tegner 1984). The warm summer–fall El Niño waters (ENSO physical conditions are reviewed in Tegner and Dayton 1987) delayed recruitment of adult plants in 1983. However, the continued release from canopy competition for light and the breakup of the ENSO watermass, allowing cooler, nutrient-rich water to return, led to more recruitment events in fall 1984 and winter 1985. The January 1988 storm eliminated much of the *Macrocystis* and understory (Seymour et al. 1989). The following patterns were observed in different areas of the kelp forest.

The 12-m site.—Only 34% of adult plants survived the ENSO storms of 1982–1983, and only 33% of these survived the nutrient-poor water in 1983 (Fig. 5). The dense sporophyte recruitment following the 1983 spring

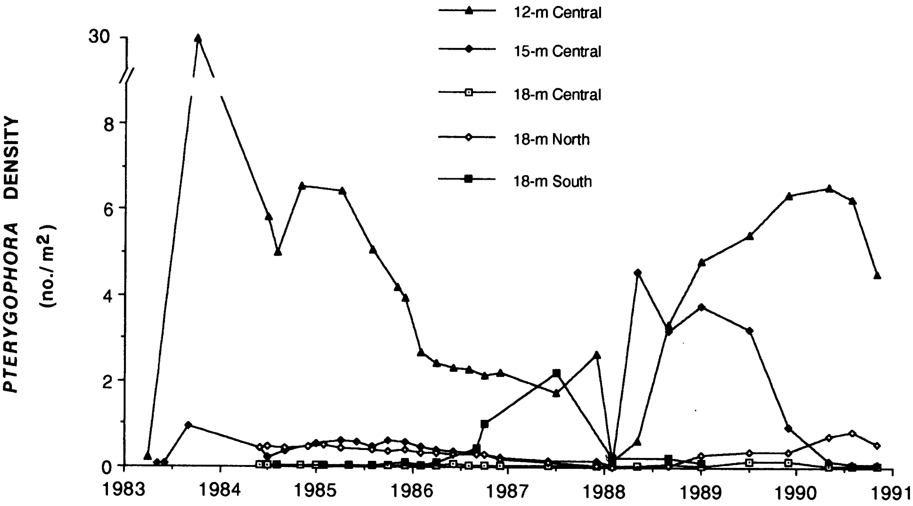

FIG. 7. Density of *Pterygophora* at five sites in the Point Loma kelp forest, 1983–1990.

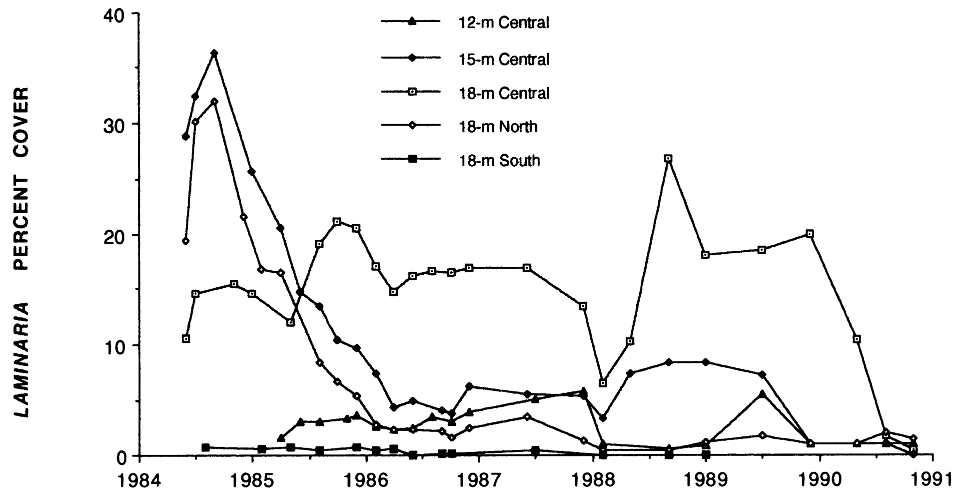

FIG. 8. Percent cover of *Laminaria* at five sites in the Point Loma kelp forest, 1984–1990.

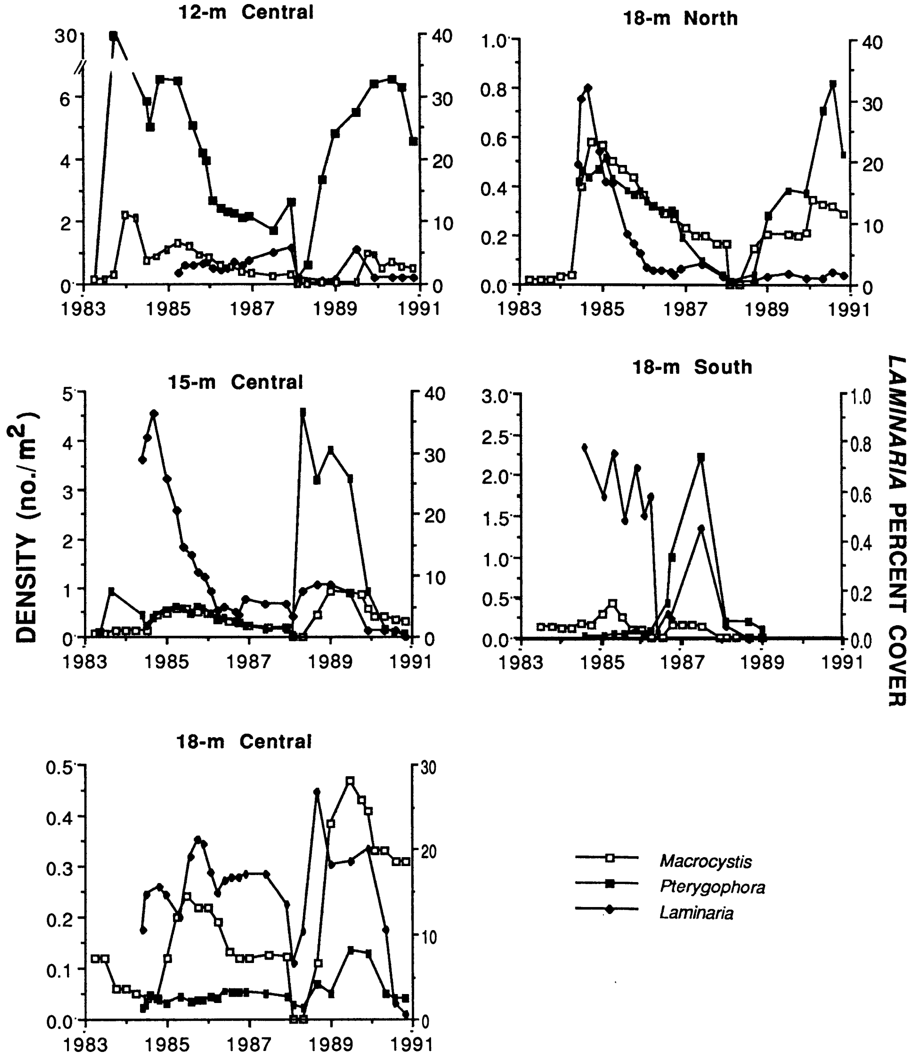

FIG. 9. Comparison of the densities of *Macrocystis* and *Pterygophora* and the percent cover of *Laminaria* at five sites in the Point Loma kelp forest. Note change in scales between sites.

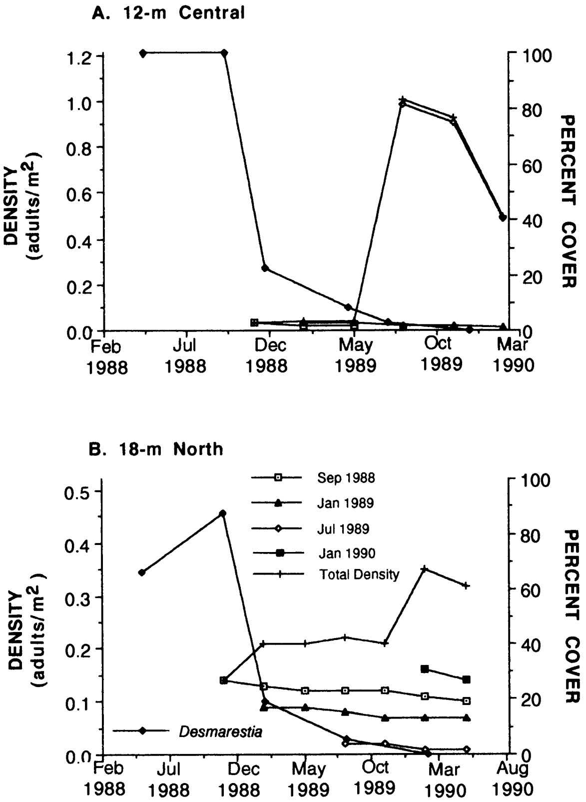

FIG. 10. The relationship between *Desmarestia* percent cover and density of cohorts of *Macrocystis* adults after the 1988 storm at (A) 12-m Central and (B) 18-m North.

upwelling resulted in high densities of new adult plants in fall 1983. Throughout the ENSO period there was continuous dense sporophyte recruitment of *Laminaria, Pterygophora,* and *Macrocystis,* all of which was obscured by very thick growth of *Desmarestia* in 1983. Of the initial 1983 cohort, 60% died within 9 mo of reaching adulthood, but some persisted until 1988 (Fig. 12). In this case none was observed to become reproductive in 1983 or 1984. Two of the 12-m transects did not have any adult recruitment in late 1984, but there was recruitment the next winter associated with the return of cool water. Eventually the survivorship of these cohorts blurred into each other and the l_x curves were very similar. There were no more recruitment events before 1988.

The January 1988 storm resulted in 100% mortality of most *Macrocystis* cohorts; only three adults survived. Sporophyte recruitment following the storm was very slow, apparently because of the presence of another dense *Desmarestia* recruitment (Fig. 10). The few *Macrocystis* plants that managed to overgrow the *Desmarestia* became adults in September 1988, but died by mid-1989 (Fig. 12). By March 1988, *Desmarestia* completely covered all the transect lines and maintained this cover until December 1988, when it dropped to 20%. A few *Macrocystis* soon became adults, resulting in a January 1989 cohort (Figs. 5 and 12). Only after the *Desmarestia* cover receded were there signs of dense recruitment and growth of juvenile kelps (Fig. 10); the *Desmarestia* cover fell to 10% while the young *Macrocystis* and *Pterygophora* grew rapidly. By early summer 1989, the dense *Macrocystis* sporophyte recruitment grew into a jungle of 2- and 4-stipe plants. After these plants underwent self-thinning, a much smaller spring 1990 cohort appeared. Eighteen months after the storm, the *Macrocystis* densities were higher than at any other site (> 1.0 plants/m²); however, these *Macrocystis* were a year behind those in non-*Desmarestia* areas. Self-thinning subsequently resulted in the *Macrocystis* densities falling to <0.5 plants/m².

The 15-m site. —These transects lost 47% of the adult plants in the ENSO storms, and of the survivors, 58%

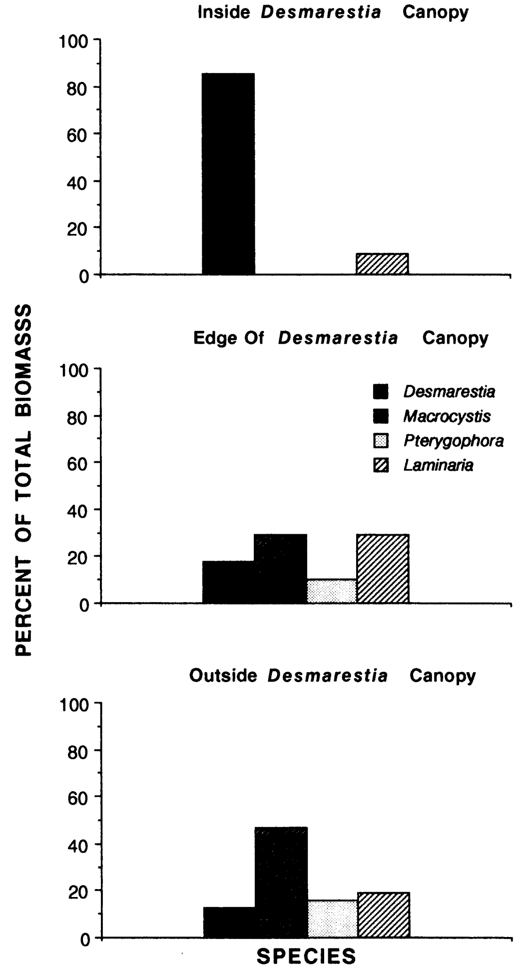

FIG. 11. Biomass composition data as a function of the relationship with the *Desmarestia* canopy. The canopy was defined as that area occupied by *Desmarestia* below which the substratum was not visible. Biomass was sampled in five 1/16 m² quadrats in each grouping. The total biomass values were 832 g for inside the *Desmarestia* canopy, 1374 g for the edge grouping, and 439 g for outside the canopy.

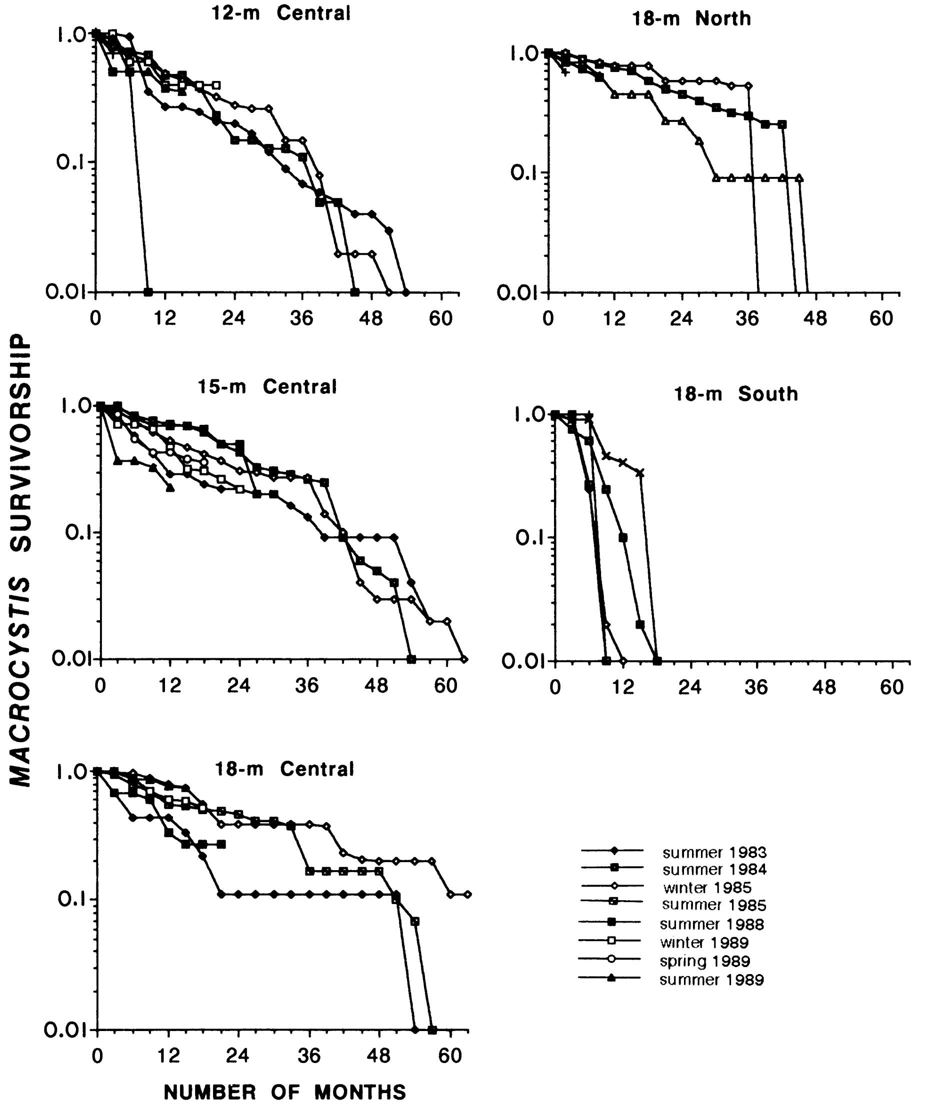

FIG. 12. *Macrocystis* cohort survivorship at five sites in the Point Loma kelp forest, 1983–1990. Key indicates starting time of cohorts. Survivorship was tracked through 1990.

were lost during the following summer. Nevertheless, some of these survived through 1986 (Fig. 5). The sporophyte germination that followed the ENSO storms resulted in a 1983 cohort that declined but did not disappear during the rest of the ENSO (Fig. 12). The 1984 summer adult recruitment resulted in a very distinct cohort, which was joined by another strong adult recruitment that appeared in winter 1984–1985. By early 1985 the pre-ENSO adult plants, suffering from nutrient-poor water, had poorly developed canopies and their sporophylls appeared sterile. Minor storms during the winter of 1985–1986 dislodged one plant, which then entangled and killed most of the other plants along one transect line. This canopy gap resulted in several patches of germinating kelps, but they were heavily shaded by the surrounding plants and none recruited as adults. In general the 15-m site had somewhat better ENSO survivorship than the 12-m site.

Twenty-one battered *Macrocystis* survived the 1988 storm at 15 m, but only one (from the winter 1985 cohort) survived through April 1990 (Figs. 5 and 12). Many of these post-storm mortalities were older plants with sea urchin cavities in the holdfasts. While a dense patch of *Desmarestia* developed in a nearby area where all the *Macrocystis* were killed by the storm, the transects themselves with their thin canopy of surviving kelps did not develop a *Desmarestia* swarm. *Macrocystis* germinated immediately after the storm and this resulted in a May 1988 cohort (Fig. 5) that had 59% survivorship through April 1990, but dropped to 20% survival by October 1990 (Fig. 12). The mortality resulted from self-thinning (Dayton et al. 1984). This cohort was able to become well established and seems to have resulted in lower survivorship of subsequent cohorts. This is the only site where a May 1988 cohort appeared. *Macrocystis* densities peaked at 0.91

plants/m^2 15 mo after the storm (Figs. 4 and 5). As at the 12-m site, the third cohort after the storm (spring 1989) was the largest, and self-thinning accounted for the high mortality.

The 18-m Central site.—Of the existing adults in 1982, 87% survived the ENSO storms but 61% of these died in the presence of the warm, nutrient-poor waters of the 1983 summer–fall (Fig. 5). The presence of this canopy and an extremely dense cover of the small understory alga, *Dictyopteris undulata* (which ranged up to 85% cover in 1984), probably affected subsequent recruitment of juvenile kelps. However, there was strong 1983 *Macrocystis* recruitment which did not grow well but did result in an identifiable cohort that persisted in the face of canopy competition and the 1984 ENSO summer (Fig. 12). The winter 1985 cohort thrived in the cool water of early 1985 and formed a thick canopy by 1986. The survivorship of the spring 1985 and fall 1983 cohorts was similar to that of other cohorts in other sites; however, the winter 1985 cohort had much better survivorship than is usually observed. The understory consisted mostly of *Laminaria,* which persisted until 1990 (Figs. 7–9).

Twenty-two (51%) pre-storm *Macrocystis* (1 from spring 1983, 14 from summer 1984, and 7 from summer 1985 cohorts) survived the 1988 storm at 18-m Central and all of these survived until November 1989; by August 1990 all but 5 had died (Fig. 12). All deaths were associated with heavy sea urchin grazing in the holdfasts, which apparently led to structural failure. No *Desmarestia* recruitment was observed along the transects at 18-m Central, and there was prompt post-storm recruitment of *Macrocystis.* These plants grew more slowly at 18 m than those at 15 m, and the adult cohort did not appear until September 1988. A spring/summer sporophyte recruitment resulted in another adult cohort in January 1989. *Macrocystis* densities peaked 21 mo after the 1988 storm, but were still only 40% as high as densities in shallower sites (Fig. 5).

The 18-m North site.—The pre-ENSO plants suffered 40% mortality in the 1982–1983 storms, and another 22% of the survivors died in summer–fall 1983. After the ENSO several of the transects were covered with extremely dense growth of *Dictyopteris, Desmarestia,* and especially *Acrosorium uncinatum.* This latter red alga, which previously had not been seen in our study areas, acquired up to 44% cover during summer 1984. There was strong 1983 *Macrocystis* sporophyte germination, but none survived the effects of canopy competition and El Niño water conditions to become adults. Winter and summer 1984 cohort survivorship curves were similar and relatively high (Fig. 12), but most of the plants represented the summer rather than the winter 1984 cohort (Fig. 5). The *Macrocystis* dominance became particularly strong, and by 1986–1987 the canopy shading was so effective that the understory cover approached zero (Fig. 9). Even though the *Macrocystis* densities were low, the stipe density was high (Fig. 6). A few metres to the south there was a large (at least 2000 m^2) patch of understory kelps composed of a mixed stand of *Laminaria* and *Pterygophora.* Almost all of these old understory plants were eliminated by the January 1988 storm.

None of these healthy *Macrocystis* survived the 1988 storm (Fig. 5), in contrast to the 18-m Central site where there was reasonable survivorship. Immediately following the storm there was intense *Desmarestia* recruitment (again contrasting with 18-m Central) which maintained heavy cover until December 1989 (Fig. 10). However, there was no delay in the appearance of the first post-storm cohort relative to 18-m Central, where there was no *Desmarestia.* Subsequent *Macrocystis* cohorts appeared in January 1989, July 1989, and January 1990. The January 1990 cohort appeared only on one line adjacent to a dense *Macrocystis* stand. Survivorship of the post-storm cohorts is remarkably high, possibly because the cohorts were never very dense, having recruited through a *Desmarestia* canopy (Dean et al. 1989).

The 18-m South site.—The South site differed from the other sites. Before the ENSO the study site had a healthy *Macrocystis* population, 41% of which was lost to the storms, while 20% of the survivors were lost during the 1983 summer. Unlike most other areas, however, many of the older plants that survived 1983 persisted through 1985. During the ENSO there was heavy cover of *Desmarestia* and *Acrosorium.* While most of the *Macrocystis* cohorts seen elsewhere did recruit along these transects, their survivorship was much lower (Figs. 5 and 12). In fall 1984, the drag from large clumps of drifting *Desmarestia* (single plants weighed up to 727 g) observed wrapped around individual *Macrocystis* plants likely contributed to the latter's mortality.

A surviving patch of older plants can inhibit *Macrocystis* recovery. When no *Macrocystis* canopy developed at the 18-m South site in spring 1984, a period of intense canopy development in nearby areas of the same depth, we investigated the population structure. Correlation of holdfast dimensions with known-age plants (P. K. Dayton et al., *unpublished data*) indicate that holdfast volumes (Ghelardi 1971) can be used as a rough proxy for age structure. Under a medium-density canopy ≈250 m from 18-m South, the holdfast volume (excluding one older individual) was 666 ± 533 cm^3 ($\bar{X} \pm 1$ SD, $N = 45$), while the volume was $18\,157 \pm 9663$ cm^3 ($N = 45$) at the 18-m South site. Clearly the first site was dominated by post-ENSO plants, whereas the age structure at 18-m South was a mixture of young and old plants. The single ENSO survivor at the first site had not interfered with the growth of subsequent cohorts, and young plants that had not been stressed by the ENSO storms were the source of the canopy.

The surviving pre-ENSO plants and the heavy 1984 recruitment were eliminated by an outbreak of amphipod grazing (Tegner and Dayton 1987). The transects at this site are on a homogeneous flat substratum, but the site itself is not homogeneous with respect to the kelps because the area to the south of the site has been involved in very dynamic cycles of kelp recruitment and heavy grazing by sea urchins. The few 1984 plants surviving the amphipods in the southern part of the study site continued to have the canopy grazed by amphipods while sea urchins invaded from the south. Most of the plants in the study site were dead by fall 1985, and all were dead by spring 1986. Almost all of these mortalities resulted from amphipod and sea urchin grazing; the winter 1985–1986 storms accounted for the rest. Water conditions at this site, however, were generally poor for kelp growth. The plants always appeared stressed: they seemed bleached of pigments, fragile, and they were rarely, if ever, reproductive. The remaining understory plants also appeared stressed. In this particular area of the kelp forest the stress probably results from unfavorable water tidally flushed from the adjacent San Diego Bay.

Still another factor inhibiting the development of the kelp canopy was heavy recruitment of *Desmarestia ligulata,* which appeared in very large, dense patches in 1983 and 1986. Storms in 1985/1986 swept away much of the sediment, leading to *Desmarestia* recruitment. There was strong fall 1986 sporophyte germination of *Macrocystis,* after the *Desmarestia* died back. There was also a modest 1987 germination which was starting to produce patches of adult plants in areas not yet cleared by the invading sea urchins. Almost all of the surviving plants were eliminated by the January 1988 storm; the few survivors were dead by late summer 1988, at which time the entire area became a sea urchin barren (sensu Lawrence 1975). One of the two urchin species died of an unknown disease by April 1991 and a massive kelp recruitment event was underway in September 1991.

Canopy relationships

While all three species generally have massive sporophyte germination following a disturbance of the surface canopy, *Macrocystis* usually dominates *Laminaria* and *Pterygophora* in the competition for light (Pearse and Hines 1979, McPeak 1981, Dayton et al. 1984, Reed and Foster 1984). The shaded understory may persist without growth or reproduction, but eventually die unless canopy gaps occur. Alternatively, if there are sufficient disturbances to the surface canopy, the *Pterygophora* and *Laminaria* may persist and develop sufficient canopy to inhibit further *Macrocystis* recruitment (Dayton et al. 1984, Reed and Foster 1984).

Pterygophora, rare at 12 m in the 1970s, had a density of 0.2 plants/m^2 in April 1983. Intense sporophyte germination facilitated by the ENSO storms led to a peak of over 30 individuals/m^2 in September 1983, which then declined as the *Macrocystis* developed (Figs. 7 and 9). The El Niño of 1982–1984 destroyed the *Macrocystis* canopy three times in this area in a 2-yr period. The canopy was first lost during the storms of winter 1983, reformed during the spring upwelling, then was lost during the warm summer–fall of 1983, reformed again during the winter of 1984, only to be lost again during the warm summer of 1984. The 12-m site suffered the highest *Macrocystis* mortality (Dayton and Tegner 1984) and the highest bottom temperatures (Fig. 2). By fall 1984, the influence of adult *Macrocystis* was negligible; only one pre-El Niño plant persisted. But despite all the disturbances and a dense population of *Pterygophora, Macrocystis* continued to recruit in high numbers. By 1986 the *Pterygophora* was much reduced and there was a complete *Macrocystis* canopy that did not completely eliminate the *Pterygophora,* although it was clear that at 12 m scramble competition was always won by *Macrocystis.* The post-1988 storm pattern was similar to the post-ENSO pattern.

We did a *Macrocystis* canopy removal experiment to test the effects of the *Macrocystis* canopy on *Pterygophora* growth (stipe elongation) and reproductive effort (sporophyll mass and presence of sori). As the size of this plot and the effort required to maintain it did not allow independent replications of the experiment, the data are presented as means and standard errors (Table 3). Freed from competition, the *Pterygophora* flourished. There are huge differences in each category between the clearing, the intermediate light environment, and the canopy areas, especially considering that the amphipod infestation of spring and summer 1985 minimized the *Macrocystis* canopy effect. The results suggest nonlethal physiological stress with the potential for important demographic consequences via much reduced fecundity. With regard to *Pterygophora* resistance to *Macrocystis* invasion, ≈2.5 yr of repeated disturbance (including 9 mo of total giant kelp removal after the natural disturbances) were required for the *Pterygophora* canopy to become sufficiently dense to inhibit further giant kelp recruitment.

At the 15-m site there was a pronounced release of *Laminaria* after the ENSO, but it declined steadily through the mid-1980s as first *Pterygophora* and then *Macrocystis* took over the canopy. *Pterygophora* recovered after the storm and persisted until June 1990, when it died as *Macrocystis* began to exert its dominance (Fig. 9). Within 4–8 mo following the 1988 storm at all sites except 18-m South, *Pterygophora* regained pre-storm densities and often exceeded them. The *Pterygophora* recovery was much faster at 18-m North and 15-m Central compared with the 12- and 18-m Central sites. The canopies at the three 18-m sites each had prompt *Laminaria* recovery following the ENSO. At the 18-m North site the *Macrocystis* and *Pterygophora* recovered quickly. At the 18-m North site the *Pterygophora* persisted and the *Laminaria* crashed, whereas at the 18-m Central site the *Laminaria* persisted. The *Macrocystis* never recovered at the stressed 18-m South site and the understory canopies responded differently.

TABLE 3. *Macrocystis pyrifera* effects on the growth (measured as stipe elongation) and reproduction of *Pterygophora californica* at 12 m depth. These parameters were compared in the center of a 20 × 20 m *Macrocystis* clearing, in the reduced light environment within 2.5 m of the south edge of the clearing, and underneath the *Macrocystis* canopy. Fifty plants were tagged per treatment.

Treatment	Growth (cm) ($\bar{X}$ ± 1 SE)	Sporophyll mass (g) ($\bar{X}$ ± 1 SE)	Presence of sori (% of plants)
Clearing	11.3 ± 1.3	163.8 ± 21.5	83
Intermediate (south edge)	9.0 ± 0.6	63.6 ± 10.6	25
Under *Macrocystis* canopy	3.8 ± 0.4	9.8 ± 1.9	0

The 1988 storm

A) *Survival and recovery of young kelps across a depth gradient.*—The 1988 storm produced interesting data on storm resistance of tagged young kelps. Five large clearings across the depth gradient had uniformly 8–10 mo old plants before the storm. While not all the species were present at all sites (*Eisenia* was absent from 12 and 21 m and *Agarum* had recruited only at 18 and 21 m) and the *Pterygophora* data were somewhat compromised because of tag loss, there was a strong depth dependence of survivorship for both *Macrocystis* and the understory species (Fig. 13). With the exception of 8 m, there was a steady increase in the survival of tagged *Macrocystis* from 12% at 12 m to 48% at 21 m. There was a major increase in understory survival between 12 and 15 m. *Eisenia* and *Laminaria* both exhibited 92% survivorship at 15 m with slight subsequent declines with depth. As both the 18- and 21-m sites appeared to suffer from wave-propelled projectile damage (Dayton et al. 1989), this decline is probably not a biological trait.

B) *Regrowth of storm-damaged* Macrocystis *holdfasts.*—The storm of January 1988 was followed by very cold (Fig. 2), relatively clear water and virtually no *Macrocystis* canopy. Holdfasts of very badly damaged plants appeared to be responding to these optimal conditions with the initiation of new frond growth. While we have observed frond initiation from bare holdfasts in Chile (Dayton 1985*b*) and the Big Sur coast in Central California (both situations were in shallow, high-nutrient environments), we had never before seen this in Southern California. The mixed-age *Macrocystis* plants on the transect lines were graded as to the severity of storm damage and their progress followed. There were 331 mapped plants in December 1987 and 53% of these were killed outright by the January storm (Table 4). By October 1988 only 12% of the plants mapped the previous December were still alive, and 71% of the plants alive after the storm had since died. Of the 84 plants (25%) that had all their stipes ripped off at the holdfast, 8 (9.5%) were still alive by fall 1988. Seven percent or 22 of the plants survived the storm with 1–3 battered stipes remaining, and 5 (23%) of these survived through the fall. Of those 20 plants in which the stipes were ripped off at least 2 m above the holdfast, 11 (55%) survived through the fall. Of those 28 plants that survived the storm with little apparent water column damage, only 54% survived through fall 1988. Similar to the pattern observed after the storm, survival into the fall increased with depth in

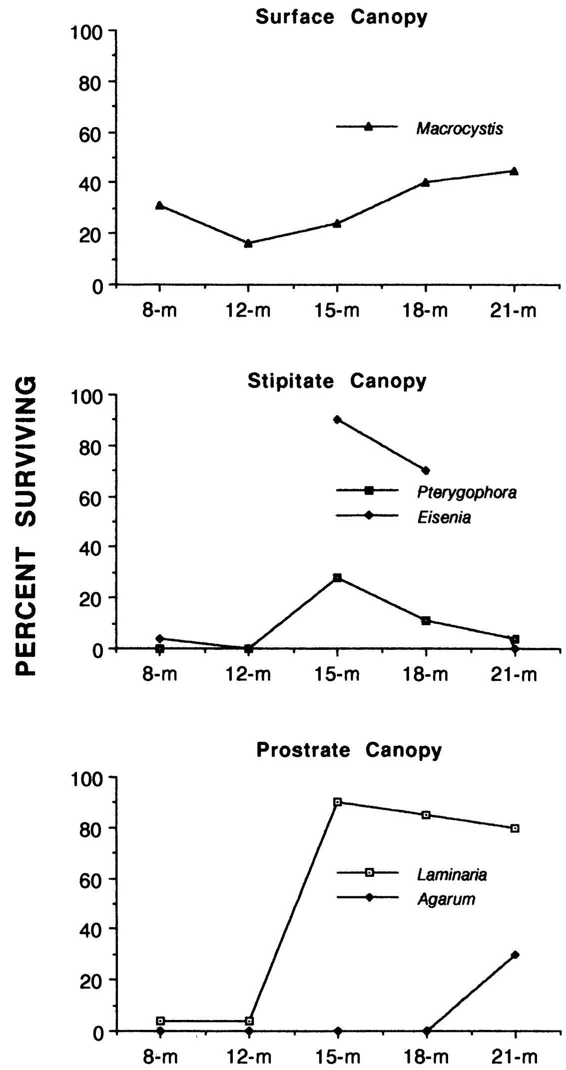

FIG. 13. Survival of tagged 8–10 mo old kelps in five clearings across the depth gradient in the center of the Point Loma kelp forest after the January 1988 storm. The *Pterygophora* data were compromised by tag loss.

TABLE 4. Survival of *Macrocystis pyrifera* (no. survivors/total no. plants) at five sites in the Point Loma kelp forest after the January 1988 storm as a function of the degree of damage.

Site	Damage category* I	II	III	IV	V	Total survival by site (%)
18-m Central	0/22	3/9	3/3	4/5	9/9	39.6
15-m	0/38	4/19	1/8	7/10	5/7	20.7
12-m	0/44	1/12	0/1	0/2	1/1	3.3
18-m North	0/24	0/35	0/3	0/0	0/8	0
18-m South	0/49	0/9	0/7	0/3	0/8	0
Survival by category (%)	0	9.5	22.7	55.0	53.6	

* The categories of damage starting with the most severe are: I. holdfast gone or severely damaged; II. all stipes broken off; III. all but one to three stipes broken off; IV. stipes broken off >2 m above the holdfast; and V. minimal to no apparent damage. Values in the table are the number of plants surviving to September 1988 over the number of plants in each damage category at each site. A total of 11.8% of the plants at all sites combined survived until September 1988.

the center of the forest. It is interesting to note that almost 10% of the plants that had lost all their stipes grew new stipes and survived through the year. This implies that the holdfast or primary stipes can become meristematically active and indicates that the loss of all the stipes does not necessarily mean that the plant is dead. Loss of stipes has been, in fact, our criterion of death, and we emphasize that regrowth did not happen for any of the mortalities reported in Dayton et al. (1984) and in the earlier years of the present study. It is likely that the unusually cold waters associated with La Niña accounted for this difference. No *Macrocystis* at either the North or the South 18-m sites survived to October, in strong contrast with the central forest 18-m site at the same depth.

C) *Holdfast stress and age-specific survivorship.*—Age-specific *Macrocystis* survivorship was different between the 1970s and the 1980s. In the benign 1970s we found that 2- and 3-yr-old *Macrocystis* survived storm and entanglement mortality better than other ages at Point Loma (Dayton et al. 1984), but the plants that survived the 1988 storm showed a very different pattern. Waves apparently stressed the primary stipes of giant kelp plants just above the apex of the holdfast, presumably by extreme bending or torquing at this point. After the storm, old hapteral tissue began to blacken and die and new haptera grew out of the primary stipes several centimetres above the old haptera. This initially led to bundles of new and unattached haptera, but eventually the new haptera grew down to a point where they could attach to the substrate. As the old haptera died and rotted, plant survival appeared to be a race between attachment of the new hapteral growth balancing the increased drag of new frond growth and the next set of big waves. The smaller the holdfast, the smaller the distance the new haptera had to grow to re-attach. Thus the young plants that recruited the previous spring developed healthy holdfasts more quickly than older plants, especially those with very large holdfasts. By May 1988, the 1-yr-old plants generally had re-attached, but hapteral growth on older plants was only a fraction of the way to the substratum. Some larger plants never produced new hapteral growth, the holdfasts eventually rotted, and most plants older than 15 mo that had survived the January storm were dead by June. At this time the robust canopies produced by the 1-yr-old plants in experimental clearings at 15, 18, and 21 m were very distinct from surrounding mixed-age canopies, suggesting increased vigor as well as survivorship of young plants. Because of this unusual form of stress on *Macrocystis,* there was a marked difference between the age-specific life expectancy resulting from this storm and other disturbances.

D) *Effects of drift algae on sea urchin grazing.*—The availability of drift kelp has important effects on sea urchin foraging, and the 1988 storm affected both the kelp and the drift. Immediately after the storm we collected drift from 400 m^2 at each site. We collected 0.04 g/m^2 at 12 m, 1.11 g/m^2 at 15 m, 4.4 g/m^2 at 18-m Central, 0.6 g/m^2 at 18-m North, and 1.0 g/m^2 at 18-m South. These are extremely low values and demonstrate that virtually all the kelp biomass detached by the storm was also swept out of the kelp forest. Qualitative observations indicated that drift algal abundance remained low for several months because of the low standing stock. In comparison, while average drift abundance determined from monthly collections at these sites from spring 1983 through the end of 1986 varied seasonally and spatially between areas, the average value for winter was 8 g/m^2. In 131 collections during this period, only seven values fell below 1.0 g/m^2 and six of these were associated with destructive sea urchin grazing at 18-m South (Tegner and Dayton 1991).

Sea urchin behavioral switches were observed at 18-m North and 18-m South after the 1988 storm. At 18-m North, 41 of 65, and at 18-m South, 27 of 76 *Macrocystis* survived the storm, but all succumbed to a combination of sea urchin grazing and storm-related stress in the months after the storm and were gone by September 1988. A massive *Desmarestia* bloom carpeted 18-m North that summer and effectively ended the grazing event there, as the urchins avoid *Desma-*

restia (Dayton 1985*b*). *Macrocystis* sporophytes germinated as the *Desmarestia* died off about a year later, and this area recovered. There was no *Desmarestia* recruitment at 18-m South, the sea urchins moved through the site as a front, and eventually eliminated even the coralline algal turf. As mentioned, sea urchin recruitment increased at this site from 1988 through 1990 (P. K. Dayton et al., *unpublished data*), and this site remained an urchin barren until early 1991 when one of the two urchin species died of an unknown disease, and kelp recruited in September.

E) *Gastropod grazing.*—Sea urchins are usually the main kelp herbivores, but in special cases gastropods can also have important effects. The trochid gastropod, *Norrisia norrisia,* is occasionally a serious grazer on *Macrocystis* (Leighton 1971, Stebbins 1986). While the 1988 storm may have caused some *Norrisia* mortality, there appeared to be a very large increase in the ratio of *Norrisia* to *Macrocystis* biomass at our 12-m clearing where the 8–10 mo old plants that had survived the storm were down to an average of 1.1 stipes per plant (range 0–3). To test the null hypothesis that *Norrisia* had no effect on the survivorship of the kelps, all *Macrocystis* within the clearing ($N = 38$) were tagged and all snails were removed weekly from two of the four quadrats of the clearing. The experiment was terminated when a massive bloom of *Desmarestia* changed the availability of snail food and its access to *Macrocystis.* At this time the pooled survival rate of the plants in the two snail removal quadrats was used to calculate the expected survival rate in the control quadrats for χ^2 analysis. The results indicate that significantly more *Macrocystis* survived in the snail removal quadrats ($.05 > P > .025$). The remaining plants had added considerable biomass, new hapteral tissue had attached to the substratum, and their long-term survival seemed likely.

Discussion

The principal questions were: "Do large-scale episodic events override biological or equilibrium mechanisms as major structuring processes?" "Are different areas within the kelp forest characterized by different processes across longshore (water condition) and cross-shore (light and temperature) gradients?" "Do patches or biological structure persist through time and these events?" As is usually the case, the answers to simplistic questions must be strongly qualified by appropriate natural history. Episodic events definitely overcame equilibrium mechanisms in the short term, but in our situation the biological mechanisms recovered quickly but with rate differences among the various areas within the kelp forest. Here we first review the scales of disturbances that emphasize their episodic nature. Next we evaluate the temporal and spatial differences in demographic parameters and carrying capacities. Finally, we find that despite the ecological mayhem, patches in some areas did persist in the face of remarkably strong *Macrocystis* recovery, suggesting that site pre-emption injects a certain level of stability to patch dynamics.

Scales of disturbances

To evaluate the importance of large-scale episodic events, it is very important for proper perspective to consider the historical disturbance and succession records of this community. The carbon stable isotope composition of the anoxic varved sediments of the Santa Barbara Basin, in which phytoplankton and kelp contributions can be differentiated on the basis of the $^{13}C/^{12}C$ ratio, has been highly variable in sediments dating back 150 yr. Temporal correlations of ^{13}C-enriched carbon, probably of kelp origin, in the sediments with known El Niño or severe storm events suggest that large-scale disturbance of kelp populations is a regular occurrence (Schimmelmann and Tegner 1991).

The area of the Point Loma *Macrocystis* canopy was vastly reduced between 1911 and 1949 (Dayton et al. 1984: Fig. 3). The area continued to decrease through the 1950s until the massive El Niño of 1957–1959 almost eliminated the giant kelp. It is important to note that the kelp was declining before the El Niño and that this was also true at Palos Verdes in the Los Angeles area (Wilson et al. 1977). At Point Loma some of the early loss may have resulted from rocky habitat being covered by sand following the dredging of Mission Bay. It is clear that both the Point Loma and Palos Verdes kelp forests were also stressed by waste disposal practices of the time, which have since been improved. While the 1957–1959 El Niño event had 4 wave episodes >3 m, the 1982–1984 event had 10 (Seymour et al. 1984). Thus fewer stressed adult plants were left after the latter event to reduce subsequent recruitment. The 1957–1959 event was also associated with massive numbers of sea urchins grazing on kelps already stressed by the warm water. This too may partially explain the very slow recovery from the 1957–1959 El Niño (Tegner and Dayton 1987, 1991).

Research from 1958–1975 directed by W. J. North resulted in annual reports that document only one significant wave event in 1960, and no others until 1980. The apparent explosion of sea urchin populations observed in the late 1950s persisted, and management through the 1960s and most of the next decade focused on controlling sea urchins as the kelp recovered. Thus while there were few important physical disruptions, the kelp forest continued to be disturbed by red and purple sea urchins, *Strongylocentrotus franciscanus* and *S. purpuratus,* respectively. Tegner and Dayton (1987) consider in detail the causes of the differences in urchin grazing between the two ENSOs. The 1970s was an even milder decade than the 1960s. While there were still localized areas with severe sea urchin grazing, especially south Point Loma, the area of the kelp forest expanded and declined in relation to storms and water conditions. The most common results of physical stress were dieback of canopies correlated with warm, presumably nutrient-poor water conditions during the late summer and loss of biomass due to storms.

The 1980s were very different from the preceding two decades because the kelp forest was exposed to massive physical disturbances. The extraordinary number of intense storms during the winter of 1982–1983, unprecedented in this century (Seymour et al. 1984), had a devastating effect on California kelp forests. The kelp mortality during the ENSO was followed in 1985 by high mortality due to amphipod grazing, apparently a secondary effect of the ENSO (Tegner and Dayton 1987). Just as kelp populations were stabilizing in 1986–1987, the January 1988 storm provided the largest recorded disturbance; it had several unforeseen consequences. As expected, there were clear correlations between increasing depth and survivorship. Unexpectedly, however, the storm damaged *Macrocystis* plants by torquing and breaking the primary stipes, often leaving an intact holdfast system. In many cases we observed regrowth from the primary stipes suggesting that they still had active meristematic tissue. In addition, hapteral regrowth favored young 1-yr-old plants rather than the 2–3 yr old plants that usually have highest survivorship. Not only did the storm kill many of the plants, it swept them and drift algae from the kelp forest; the effect of this was to increase the adventitious grazing of sea urchins. And because the storm reduced the biomass of kelp plants, the grazing of a normally unimportant herbivorous gastropod was concentrated so that it significantly reduced kelp survivorship. Thus the 1980s provided not only a large number of disturbances, but also major contrasts in their physical and biological characteristics and implications for community structure.

Events at much smaller spatial scales can affect larger scale issues. Some disturbances result in dense *Desmarestia* recruitment, which can inhibit kelp recruitment for months to over a year. These inhibitions range in area from a few square metres to hectares. A very typical type of *Macrocystis* mortality results from becoming tangled with a drifting conspecific (Dayton et al. 1984). The drifting mass of kelp can scour an area of several square metres and pull the holdfasts of additional plants loose from the bottom, leaving scars. These disturbances usually result in localized recruitment of *Macrocystis,* causing a more mixed age class structure. Because different ages have different resistance to disturbance, this can produce a more resilient *Macrocystis* population.

In summary, it is clear that this community is exposed to massive episodic events as well as small-scale disturbance and recruitment events. On the other hand, there is ample evidence of prompt recovery from massive disturbances with distinct spatial patterns. More important, there is evidence of equilibrium or intraspecific regulation of *Macrocystis* plant or stipe densities as well as several types of interspecific effects on recruitment and growth.

Density and demographic patterns in time and space

There are spatial patterns within the kelp forest in abundance and survivorship of each kelp species that relate to gradients in depth, light, temperature, and water motion. Storm mortality is strongly depth dependent and the inner edge of the *Macrocystis* forest at Point Loma appears to be set by the height of breaking waves (Seymour et al. 1989). Recruitment density also decreases with depth. Mortality of *Macrocystis* that survived the ENSO storms was dramatically lower at the end of the forest sites relative to 18-m Central during the 1983 El Niño summer; these sites face into longshore currents where they may be exposed to water not depleted of nutrients by the rest of the forest (Tegner and Dayton 1987). Conversely, *Macrocystis* mortality after both the ENSO and the 1988 storms was very much higher at the two ends of the forest relative to 18-m Central.

The long-term density data for *Macrocystis* (Fig. 4) show large oscillations in shallow water, whereas the densities in deeper water are much more consistent. At the 12-m Central site the *Macrocystis* population was characterized by large fluctuations over the last 20 yr, twice being eliminated in the 1970s by sea urchin grazing and twice in the 1980s by storms. The densities rebounded from the disturbances of the 1970s, but not in the 1980s when *Desmarestia* induced delays. In each case, they slowly declined to consistent values of 0.3 to 0.4 plants/m^2. At the 15-m Central site *Macrocystis* had one strong recruitment in 1974. There was heavy ENSO mortality followed by a strong recovery until the 1988 storm. The asymptote differed between decades as it appeared to be 0.08 to 0.10 plants/m^2 in the 1970s and a little over 0.20 to 0.50 plants/m^2 in the 1980s, 2–5 times that of the 1970s.

The 18-m sites differed from the shallower sites and from each other. The 18-m Central site was buffered from the disturbances; it had fewer storm mortalities, lower recruitment, no *Desmarestia* interference, and strong recoveries. The 18-m North site had a stronger post-ENSO recovery but suffered greater storm mortalities after both disturbances. The 18-m South site has consistently been anomalous. It appears stressed by water flushed from San Diego Bay, and by a combination of higher urchin recruitment rates at all 18-m sites relative to forest interior sites (Tegner and Dayton 1991) juxtaposed with lower plant recruitment and growth at 18-m South. At 18-m Central the *Macrocystis* density asymptote varied from 0.05 to 0.15 plants/m^2 in the 1970s as compared with 0.13 plants/m^2 in the 1980s. These 18-m Central data are remarkably consistent with the 18-m asymptotes at the north and south parts of the kelp forest, which varied from

0.13 to 2.0 plants/m^2 (Figs. 4 and 5). Thus the three 18-m sites had approximately the same carrying capacity, which was similar to that of 18-m Central in the 1970s. The cohort densities from the line transects (Fig. 5) show similar patterns, with the 18-m Central site being much more constant. The only difference between the decades was at the 15-m site. This may relate to variations in age composition; after the major disturbances such as experienced in the 1980s, the ages of plants within a patch tended to be homogeneous. More likely it results from the fact that the kelp harvesting company did not harvest our study area in the 1970s but did in the 1980s; removal of the canopy allows more light to penetrate, which increases stipe production.

The *Macrocystis* survivorship data (Fig. 12) show several unexpected and interesting trends. First, considering that they recruited during very different periods, there is a remarkable coherence among the cohorts. Second, the shallower 12- and 15-m sites had more linear survivorship curves, suggesting that the mortality rates were relatively constant and independent of time, whereas the deeper 18-m sites had nonlinear curves, suggesting that survivorship is higher and constant, then decreasing abruptly with old age. An explanatory hypothesis is that because the deeper sites have less wave-related mortality than the more shallow sites, the plants tend to be older, with weaker holdfasts than those in shallow water. Third, in the absence of excessive grazing, the maximum longevity is remarkably uniform at ≈50 mo.

Because the stipes are most sensitive to the amount of light, they may be a more sensitive measure of carrying capacity than plant density. We observed an increased number of stipes per plant with increasing depth, but there seemed to be an asymptote of ≈4–6 stipes/m^2 in the 1980s (Fig. 6). Comparable data in the 1970s were very similar, 5.8 stipes/m^2 in 1976.

Pterygophora has marked depth-related densities, with the highest being in 8–15 m (Table 1); these density patterns parallel the patch size patterns (Table 2). With regard to the transect sites, their densities were similar among sites (Fig. 7), as all but the 12-m populations were remarkably constant through 1984 to 1987. Only the more shallow 12- and 15-m sites were densely colonized after the 1988 storm. Interestingly, except for the manipulated 12-m site, *Pterygophora* never developed dense canopies in the face of intense *Macrocystis* competition. This is despite continued *Pterygophora* recruitment during the ENSO disturbances to the *Macrocystis* canopy. *Eisenia,* never very common, was remarkably resistant during the ENSO disturbances and, in deeper water, the 1988 storm. Unlike *Pterygophora, Eisenia* has very low recruitment and then in limited areas; it usually grows more slowly. *Eisenia* does have high densities in patches in shallow water and sometimes in deeper water.

The *Laminaria* population has its highest densities in the inner and outer portions of the kelp forest (Table 1) and its biggest patches at 15 m and shallower (Table 2). In contrast, the percent cover data from the transect sites had the maximum densities at the deeper sites where it seems to have much greater survivorship than inferred by Dayton et al. (1984) at 15 m. *Laminaria* showed a much stronger response to the ENSO than did *Pterygophora,* but was consistent from 1986–1988. In some areas *Laminaria* has maintained patch boundaries over two decades despite the disturbances.

The normal observation of *Desmarestia* is that they are restricted to isolated patches cleared by storms or where sea urchins had been removed. After colonizing disturbances, *Desmarestia* grow quickly until late fall, when they usually begin to disappear. *Desmarestia* seem to depend upon particularly severe disturbances that produce clean substratum; then, once established, they often cause a local or patchy delay in the kelp recovery, which can be remarkably persistent. One of the interesting effects of the ENSO and especially the 1988 storm was the very dense growth of *Desmarestia.* In several areas *Desmarestia* significantly inhibited the recovery and growth of the three species of kelp (Figs. 10 and 11). The *Desmarestia* inhibition persisted up to 2 yr after the storm at 15 m. *Desmarestia* had a much more general and pervasive impact at 12 m; their effects at 15-m and 18-m North were patchy. A *Desmarestia* bloom in the north was correlated with the local cessation of sea urchin grazing, as echinoids often appear to avoid *Desmarestia* (Dayton 1985*b*). In the northern area this led to kelp recovery. In the southern area, however, the urchins persisted until spring 1991, when one species suffered an almost complete mortality. By October 1991 there was massive recruitment of kelps at 18-m South.

We have observed both morphs of *Desmarestia ligulata* (Chapman 1972); the most common is *D. ligulata* var. *ligulata* with *D. ligulata* var. *firma* appearing in deeper water. We observed an interesting polymorphism between the "stringy" *ligulata* and the "frondose" or blade-like *firma* morph (Chapman 1972). There were particularly dense patches at the 21-m and 15-m sites; as might be expected from the terrestrial literature on leaf morphologies (Horn 1971), the deeper, darker 21-m site has only the broad *firma* morph with long (>1 m) fronds, whereas the dense *Desmarestia* canopy at the lighter 15-m site was composed mostly of the *ligulata* morph. Another species, *D. tabacoides,* is thicker and rather rare.

Competition, disturbance, and patch persistence

Despite *Macrocystis* dominance under conditions of scramble competition, we found that in the central part of the forest most of the established understory kelp patches marked in 1971–1972 at 15 m actually persisted through 1991. If patch structure within the community persists through these major disturbance events, it is strong evidence that small-scale biological processes are more important to these populations than episodic disturbances. Work at 15 m during the 1970s (Dayton et al. 1984) suggested that within-patch disturbances of individual plants or small aggregates of plants were followed by recovery of the preexisting species. Experimental clearings at the edge of patches demonstrated that the boundaries were not inviolate, as neighboring patches could invade, whereas clearings in the middle of the patches did not result in invasions unless spores were introduced. This suggested that the patches are maintained by competition for light and availability of reproductive propagules. Thus these patches appeared persistent and resistant to invasion. Observations of small-scale disturbances and the clearing experiments suggested that most of the patches were also resilient in that they recovered from a disturbance that removed existing individuals (Dayton et al. 1984).

The transect data differed from those of the patch boundaries first marked in 1971–1972 (Dayton et al. 1984), as many *Pterygophora* and *Laminaria* patches have resisted invasion through the summer of 1991. The situations after the ENSO and the 1988 storm were different. For the first time since they were marked, many of the understory patches were heavily damaged by the 1988 storm, so that there was no effective understory canopy. More important, the bottom was sandblasted and the coralline turf was stripped, often to bare rock, and in some places as much as a centimetre of the bare rock was removed. This eliminated or much reduced any "seed bank" storage of gametophytes that might normally speed patch recovery. Thus the importance of short-distance dispersal was much reduced, and that of long-range dispersal (Reed et al. 1988) became prominent. Scattered new patches of understory kelps could still be discerned for many months after the storm, but many such patches disappeared beneath the *Macrocystis* canopy. The unusually good growth conditions of 1988–1989 resulted in scramble competition convincingly won by *Macrocystis* (Figs. 5 and 9). In contrast, some marked patches at 15 m persisted, often immediately beside *Macrocystis.* Indeed, Tables 1 and 2 demonstrate surprisingly large understory populations and patches. Thus the storm erased much of but not all understory patches. Those that have been observed to persist may have done so largely as a result of adult survivorship, because of the apparent sandblasting effect on the density of gametophytes.

Effects of a major El Niño on patches.—A massive disturbance in southern California kelp forest communities such as that of the ENSO had never been observed, and the stability of these patch types was unknown. The ENSO battered but did not remove the understory except in very shallow areas. However, the *Macrocystis* was almost eliminated in some areas and heavily damaged in others (Dayton and Tegner 1984), and almost all the *Macrocystis* patches were opened for invasion. There was immediate heavy recruitment of *Pterygophora*; it not only invaded the *Macrocystis* but all the other patches as well. There was a long period after the storms when the water was exceptionally clear (Dean and Jacobsen 1986), with apparently adequate nutrients along the bottom, and all species enjoyed unusually good recruitment. This continued for the entire 2-yr period of the ENSO, but despite this recruitment, the *Macrocystis* usually died or stopped growing at the 2–4 stipe stage when they grew into the nutrient-poor water. Nevertheless, they continued to germinate and recruit at least to the 2-stipe stage. Meanwhile some dense populations of *Desmarestia, Laminaria,* and *Pterygophora* persisted at the shallow stations; only the 18-m areas had lower recruitment levels. But the *Macrocystis* had been thoroughly invaded by *Pterygophora.* When the water conditions returned to normal, some *Macrocystis* were above the understory, grew rapidly, and shaded the understory. In shallower sites enough light gets through the understory canopies to allow the persistence of other kelps, although with reduced growth and fecundity (Table 3). Nevertheless, the competitive dominance of *Macrocystis* was quickly exerted. In depths of 15 m and deeper, however, the understory plants that survived the ENSO storms seemed to take advantage of the nutrient-enhanced bottom water, and their canopies recovered much faster than *Macrocystis,* which continued to grow into the warm, nutrient-poor water. In this sense, the existing understory canopies persisted, but few if any took over new areas.

Interactions between Macrocystis *and* Pterygophora.—The major mechanism by which *Macrocystis* dominates *Pterygophora* appears to be competition for light (Pearse and Hines 1979, Dayton et al. 1984, Reed and Foster 1984). Dense *Macrocystis* canopies reduce subsurface light intensities enough to reduce understory gametogenesis and growth. Both kelps generally have massive sporophyte germination following a disturbance of the surface canopy, but usually the *Macrocystis* rapidly overgrows the *Pterygophora* (Pearse and Hines 1979, McPeak 1981, Dayton and Tegner 1984, Dayton et al. 1984, Reed and Foster 1984). The shaded *Pterygophora* may hang on without growth or reproduction and eventually die unless canopy gaps occur. Alternatively, if there are sufficient disturbances to the surface canopy, the *Pterygophora* may persist and develop sufficient canopy to inhibit further *Macrocystis* recruitment (Dayton et al. 1984, Reed and Foster 1984). The low probability of three consecutive years of major disturbances to *Macrocystis,* the time required for the successful *Pterygophora* patch establishment at 12 m, demonstrates how hard it is for *Pterygophora* to invade *Macrocystis* patches and become established at the relatively shallow sites. The differences between the strength of the *Pterygophora* resistance to *Macrocystis* invasion at 12 and 15 m depth suggests that there is a light threshold (Deysher and Dean 1986) for *Macrocystis* between 12 and 15 m depth at Point Loma.

Stability: persistence and recovery

With regard to the questions of generation turnover and stability (see Sutherland 1990), it is worth noting that there were several generations of *Macrocystis* involved in the local persistence of its population during the last 20 yr. Most of the understory patches were also marked by considerable turnover from storm damage. Thus at Point Loma it appears that patches persist longer than the maximum life of the individual.

The storm of January 1988 was an altogether new type of disturbance within our time frame (Dayton et al. 1989, Seymour et al. 1989). In the two shallowest sites (8 and 12 m), surge and sand scour eliminated an extraordinarily high proportion of the plants. Dense recruitment of *Pterygophora* and *Macrocystis* followed, with the subsequent scramble competition favoring *Macrocystis.* Much the same is true for the 15-m site, but here the damage was patchy. The completely cleared sites were colonized by *Desmarestia,* which exerted a marked delaying effect on kelp succession. In these cases the *Macrocystis* were strongly impacted by the *Desmarestia* for several months. The established understory patches were also battered, but by late summer 1988 the patch borders were still discernible. Cold, nutrient-rich water characterized a 1988–1989 La Niña which was associated with widespread recruitment and strong growth of *Macrocystis,* and a marked subsequent thinning of the damaged *Pterygophora* and *Eisenia.*

It would appear that patch stability was very different at each site. In the shallow sites *Macrocystis* recruited strongly, maintained a heavy canopy, and swamped massive recruitment of *Pterygophora. Macrocystis* was very dominant at 12 m and no natural understory patches persisted. At 15 m *Macrocystis* and understory both recovered strongly from the ENSO disturbances, but the *Macrocystis* dominance was not generally as pronounced as it was on the lines, and all the patches marked in 1971–1972 persisted through the 1988 storm. Damage in the three 18-m sites was patchy, and while there were no formally delineated patches, some which were well known to us persisted. Deeper water *Macrocystis* had good recruitment and strong canopy development, which was associated with the loss of *Laminaria* and *Pterygophora* along the lines.

Certainly one obvious conclusion from this study is that *Macrocystis* behaved as a highly effective opportunist as it continued strong recruitment throughout the 1982–1984 ENSO and generally after the 1988 storm, under both good and bad conditions for growth. But most dramatically, wherever it does occur in the Point Loma area, with the exception of short-term *Desmarestia* delays, it was usually able to exert very strong competitive dominance under conditions of scramble competition. Nevertheless, understory species are abundant (Table 1) and patches do exist (Table 2). The real question that remains unanswered is how patches of understory kelps became sufficiently established to resist invasion by *Macrocystis.*

CONCLUSIONS

Do large-scale episodic events and nonequilibria conditions override biological or equilibria mechanisms as dominant structuring roles in the kelp forest? As Williamson (1987) asks, are communities ever stable? If there are important episodic disturbance events capable of overriding biological structuring processes, they should have become apparent during the last decade, which included the most massive ENSO event ever recorded and a storm of such magnitude may not have occurred for 200 yr. Certainly the disturbances have resulted in many lag effects (such as the *Desmarestia* outbreaks, changes in sea urchin grazing patterns, and apparently the amphipod grazing episode), which have resulted in considerable site-to-site variance. In most areas, *Macrocystis* had such a powerful competitive dominance over the other kelp species that it recovered very quickly from each disturbance episode. However, in all areas it appears that some patch structure persisted. The most common observation is that of strong *Macrocystis* recruitment, which continued through the ENSO and occurred after the 1988 storm. This was followed by self-thinning of *Macrocystis,* which, within 2–3 yr, leveled off at asymptotes not very different from those of the relatively disturbance-free 1970s. The recruitment windows (Deysher and Dean 1986) probably did occur, but we saw little evidence that in themselves they were important, as we always found dense germination soon after any disturbance. The patterns at Point Loma were very similar to those of Naples Reef (Ebeling et al. 1985). The stability of many of the patches suggests that site preemption has lasting consequences in this kelp forest as it does in terrestrial communities (Louda and Renaud 1991). In this case the mechanisms revolve around the interplay between competition with rapid understory reproduction, long-distance spore dispersal, and perhaps storage effects of long-lived gametophytes (Dayton 1985*a*).

In summary, the Point Loma kelp forest exhibits periods of density dependence marked by occasional density-independent disturbance. Some patches have considerable resilience or long-term stability (sensu Williamson 1987, Sutherland 1990), whereas others are ephemeral in the presence of strong *Macrocystis* dominance. As Murdock and Walde (1989) and Nisbet and Bence (1989) point out, kelp populations exhibit density-vague dynamics at local levels, with patch or ensemble dynamics offering larger scale stability. Regarding the questions posed in the Introduction, large-scale episodic events such as El Niños, La Niñas, and rare storms can exert large-scale impacts, but small scale responses such as density vague recruitment and survival often allow prompt recovery. Different areas within the kelp forest are characterized by different species-specific responses, but at Point Loma, the local spatial differences are overshadowed by the general strong competitive dominance of *Macrocystis pyrifera*.

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