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## PATCH DYNAMICS AND STABILITY OF SOME CALIFORNIA KELP COMMUNITIES<sup>1</sup>

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**Abstract.** This paper considers three concepts of stability as they relate to the dynamics of distinctive patch types of algal canopy guilds in southern and central California kelp communities: (1) persistence of a patch through more than one generation of the dominant species, which was evaluated by using life tables and observations of patch borders; (2) inertia or the resistance of different patches to invasion or disturbance, which was evaluated by artificially enhancing gametophytes by transplanting sporogenic material, by removing canopy, and by evaluating some important disturbance processes; and (3) resilience or recoverability of a patch following a perturbation sufficient to allow invasion of different species, which was studied by defining some of the mechanisms of successful invasion or succession. By working in distinct habitats in southern (Pt. Loma and Santa Catalina Island) and central (Pt. Piedras Blancas) California, we could evaluate different types of physical stresses as they related to these stability concepts.

Taller perennial canopy guilds were dominant competitors for light, but were more susceptible to physical wave stress. Dominance hierarchies in the competition for light appeared to be reversed in areas exposed to increasing wave stress. The main causes of mortality at Pt. Loma were entanglement with storm-dislodged *Macrocystis* plants and, in some areas, sea urchin grazing. Mortality in central California was due to winter storms. In most cases, distinct patches resisted invasion for > 10 yr. The mechanisms of resistance involved (1) competition for light and, possibly, nutrients, and (2) limits to spore dispersal. When succession occurred, it was often mediated by many factors, including seasonality of spore production, which coincided with winter storm-related mortalities; mechanisms of kelp dispersal, which were most effective via drifting plants and fragments of fertile material held against the substrate by invertebrates; and survivorship of gametophytes and small sporophytes, which was influenced by local scour and grazing. Appropriate spatial scales, stability, and succession studies in these kelp communities were determined by the size of the disturbed area, which varied from the free space resulting from detachment of single plants to the free space resulting from catastrophies such as overgrazing or unusual storms. Temporal scales were influenced by seasonality of disturbance and algal reproductive condition and aperiodic episodes of cool, nutrient-rich water advected into the patch.

There appeared to be conflicting morphological adaptations of the canopy guilds: exploitation of light was enhanced at higher canopy levels, whereas the lower canopy levels were better adapted to tolerate stress from wave surge. The adaptations of the algae appeared to form four distinct groups of tactics: (1) ruderals or plants, such as *Nereocystis* and *Desmarestia*, with opportunistic life histories; (2) kelps, such as *Macrocystis*, adapted to exploitative competition for light and nutrients; (3) kelps (*Eisenia*, *Dictyonium*) adapted to physical stress such as wave surge; and (4) those algae, such as corallines and *Agarum*, adapted to heavy grazing. Within any given area, the relative patch stability was determined by biological relationships; between areas, the patch stability patterns were attributable to physical differences.

**Key words:** *community; competition; dispersal; grazing; kelp; patch dynamics; predation; stability; stress.*

### INTRODUCTION

Stability and succession are two of the oldest shibboleths in the ecological literature. Both are general community concepts integrating many physiological adaptations, life histories, demographic patterns, interspecific relationships, and physical-biological interactions with the environment. Progress toward a gen-

eralized theory has been slow because both concepts depend upon many specific patterns of foraging and reproductive behavior, competition, predation, mutualism, dispersal, etc. Each is variably independent in time and space; most natural situations are characterized by disequilibria sustained by various levels and types of physical disturbance. Thus, for example, different communities may have similar levels of stability, but for different reasons. A mechanistic understanding of stability should remove such ambiguity.

Ecologists are increasingly becoming aware that many simplified but general theoretical models of stability are not applicable to natural systems. There is a welcome trend toward identifying separate components of stability (van Dobben and Lowe-McConnell 1975,

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Sutherland and Karlson 1977, Glasser 1979, Harrison 1979, Sutherland 1981, Connell and Sousa 1983) and using more appropriate theory (May 1973, Yodzis 1978, 1980, Crowley 1981, Paine and Levin 1981). In contrast, succession theory has continued its history of dissonance between those who see succession as an ordered community process (Clements 1916, Odum 1969) and those who see it as an individualistic phenomenon (Gleason 1917, Drury and Nisbet 1973, Connell and Slayter 1977). This historical collage of semantic confusion, dogma, and rediscovered concepts is summarized by McIntosh (1980). Despite the glaring inadequacies of highly idealized and structured concepts, theories, and rules, stability and succession do have underlying and intertwined components, and these can be integrated to formulate some level of general understanding (Yodzis 1978, Crowley 1981, Sutherland 1981).

In this paper, we evaluate the patch dynamics of California kelp communities in relation to stability and succession. The many nonexclusive hypotheses relating to the origin and dynamics of the ubiquitous existence of distinct patches in nature include the following: (1) patches are maintained by local physical characteristics tolerable to some species but not to others; (2) other species have not had the opportunity to colonize, and patches are ephemeral entities defined by relative dispersal patterns; (3) all species colonize together, but different life-history phenomena alone determine the composition of the patch; and (4) beneficial biological interactions such as mutualism enhance the successful colonization of certain species into patches, and deleterious interactions such as competition or predation prevent colonization. In nature, these alternate mechanisms are often complementary, but to some extent they can be tested by removal and transplantation experiments. For example, successful colonization by other species can falsify the first hypothesis; these colonizations combined with appropriate natural-history observations of dispersal, settlement, and survivorship, can falsify the second and third hypotheses.

We do not attempt a general consideration of stability concepts (cf. Sutherland 1981, Connell and Sousa 1983). Instead, we arbitrarily postulate that community stability has three components.

- 1) *Persistence* refers to the existence of a patch for more than one generation of the dominant population.
- 2) *Inertia (resistance)* refers to the resistance by a patch (ideally through more than one generation) to invasion or perturbation (Types I and II perturbations of Sutherland [1981]). That is, the patch is persistent despite being challenged.
- 3) *Resilience* refers to the return of a patch to its original composition following a perturbation suf-

ficient to allow colonization by different species (Type III perturbation of Sutherland [1981]).

Note that persistence is not a tautological result of longevity (Frank 1968), but can result from great inertia or resilience. Inertia implies a resistance to succession, whereas resilience can include an invasion followed by a recovery to the original patch composition.

Succession, the process of community change, was evaluated by studying the mechanisms by which new species successfully invade, colonize, and occupy patches. To the extent that our definition of stability involves resistance to invasion, succession and stability involve opposing processes. A fruitful approach to both is to study the interface between these conflicting processes.

Kelp communities offer certain advantages for this type of community research. There are distinct patch types composed of species of algae that can be categorized into vegetation layers distinguished by distinct morphological adaptations. These layers include (1) a floating canopy (*Macrocystis pyrifera*, *Nereocystis luetkeana*) supported at or near the surface by floats; (2) a stipitate, erect understory in which the fronds are supported well above the substratum by stipes (*Pterygophora californica*, *Eisenia arborea*, *Laminaria setchellii*); (3) a prostrate canopy in which the fronds lie on or immediately above the substratum (*Laminaria farlowii*, *Cystoseira osmundacea*, *Dictyoneurum californicum*); (4) a densely packed algal turf of articulated coralline algae (especially *Calliarthron* spp.) and many species of foliose and siphonous red algae; and (5) encrusting coralline algae such as *Lithophyllum* spp. and *Lithothamnion* spp. For each pair of layers, the taller guilds are temporary components of the lower lying guilds during their early life history. Although we address processes at the community level, we emphasize that the proper units of evolutionary study relate to the demography of component populations. For this reason, we focus on the survivorship of the kelp species under various experimental and natural conditions. Unfortunately, fecundity data are not obtainable for most kelps (see Chapman 1979, Gunnill 1980a, b).

A study of patch inertia should include independent measures of the stresses and disturbances that affect the community. Environmental perturbations that result in nonlethal physiological stress may have extremely important demographic consequences by reducing age-specific fecundity. This is especially true for algae that may survive but may not be reproductive because they are in habitats deficient in light or nutrients. Unfortunately, such sublethal physiological stresses are almost never independently quantified in community studies, including this one. In some cases, we had indirect evidence of such stress, and we mention this stress as an untested hypothesis. Similarly, stress from water motion, especially the extremely strong surges associated with storms, influences survivorship

as well as fecundity. Here again, we did not have independent direct measures (Sutherland 1981); we evaluated the effect of this stress on a relative scale by comparing habitats exposed to very different regimes of water motion (Fig. 1).

We emphasize that each algal species has unique levels of resistance to particular stresses. For example, algae store nutrients that are utilized when ambient nutrients are low but other physiological factors, such as light and temperature, are adequate (Chapman 1979, Gerard and Mann 1979). Similarly, algae are differentially susceptible to dislodgement by wave stress. Increased tolerance to wave stress may be associated with reduced competitive abilities in less stressful habitats. All algae have many such adaptations replete with various evolutionary compromises. We addressed interspecific or synecological questions about community organization, but whenever possible we posed our questions in autecological terms relative to the algae.

#### STUDY SITES AND METHODS

This paper is based on a 3-yr study in central California at Pt. Piedras Blancas, San Luis Obispo County; a 9-yr study at Bird Rock, Santa Catalina Island, Los Angeles County; and an intensive 10-yr study of the large *Macrocystis* forest off Pt. Loma, San Diego County (Fig. 1; see North 1971).

**Pt. Loma.**—The main study area was in the central part of the Pt. Loma kelp bed at a depth of 15 m (Fig. 1). The area includes several limestone reefs of 1–4 m vertical relief and several hectares of relatively flat sandstone substratum. The two main reefs, Virgin Reef and Jeff's Reef, run north-south, perpendicular to the onshore surge. In some areas, the reefs are fragmented into piles of limestone rubble, which we refer to as "boulder reefs." Pt. Loma is not protected by the Channel Islands, and so is exposed to much more severe sea conditions than Bird Rock or than most other mainland habitats in the southern California Bight. High late-summer temperatures and low nutrients frequently stress the *Macrocystis* off Pt. Loma (North 1971, Jackson 1977).

In 1971, a permanent 100-m line transect was established several metres shoreward of Virgin Reef. The north-south transect was laid through a dense patch of *Macrocystis* across a representative, relatively flat sandstone substratum. Except for a few small (5–15 cm) ledges and a small depression often filled with shifting sand, there was no topographical relief in the area. Quadrats of 0.25 to 15 m<sup>2</sup> were established along the line for purposes of mapping and evaluating survivorship of small kelps.

West and north of Virgin Reef were dense patches of stipitate and prostrate kelps (Fig. 2). Patch types were quite distinct (Table 1). In the early 1970s, most of the area seaward of the *Macrocystis* patches in this part of the Pt. Loma kelp forest was dominated by

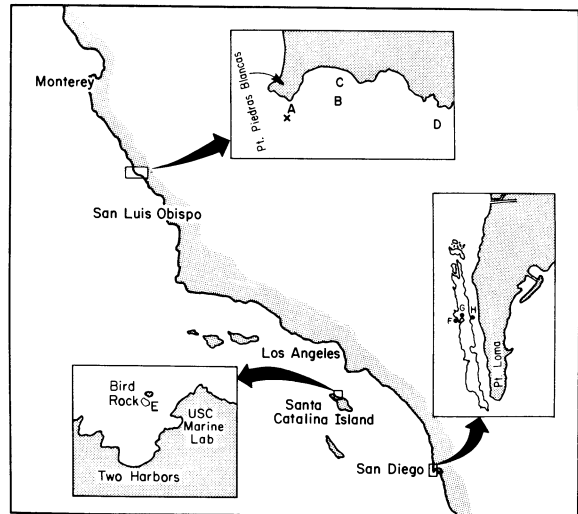


FIG. 1. Map of the coast of California between Monterey and San Diego showing Pt. Piedras Blancas, Bird Rock, and Pt. Loma study areas. At Pt. Piedras Blancas Sites A, B, and X are located within large *Macrocystis* canopies and Site D is in a dense grove of mixed *Pterygophora* and *Laminaria setchellii*. At Pt. Loma, Site F is at -18 m, Site G is the main Virgin Reef area in -15 m, and H is at -11 m. Site E is the Bird Rock kelp forest at Santa Catalina Island.

*Pterygophora* and small (4–30 m<sup>2</sup>) patches of prostrate kelps. There were smaller areas of dense turf structurally dominated by articulated coralline algae, mostly *Calliarthron* spp., bushy and foliose red algae, especially *Rhodymenia* spp., *Schizymenia pacifica*, and, in some areas, thick tufts of *Gelidium* spp. Areas around the reefs and the boulder reefs had been cleared of fleshy algae by sea urchins and were dominated by encrusting coralline algae. Such sea urchin/coralline areas are well known and have been termed "barren modes" by Lawrence (1975). (Subsequent to this study a growing sea urchin fishery has eliminated most of the urchins in these areas.)

Fifteen permanent 1-m<sup>2</sup> quadrats were haphazardly chosen and established within each of the stipitate and prostrate canopy guilds to follow survivorship. The corners of the quadrats were marked by large metal stakes, and the plants were individually tagged with plastic ties. Seven areas of 4–15 m<sup>2</sup> were cleared of their canopies in the late spring and summer of 1971, and recruitment and subsequent cohort survivorship were evaluated. The Virgin Reef area was the most intensively studied, but *Macrocystis* survivorship was also evaluated at areas 11 and 18 m deep on the inner and outer edges of the kelp forest. In these areas, 100-m transect lines similar to those at Virgin Reef were established in 1974.

Kelp have many life-history stages (Chapman 1979); there are problems in deciding at which point of the life cycle the study should begin. Most brown algae in



FIG. 2. Sketch of Virgin Reef area, Pt. Loma, showing patches composed of algae with characteristic canopy guilds, including the floating canopy of *Macrocyctis*, the stipitate canopy of *Pterygophora* and *Eisenia*, the prostrate canopy of *Laminaria farlowii* and *Cystoseira* and patches of turf and encrusting coralline algae. See text for details.

this study have the typical Laminariales life cycle involving an alternation of generations between the large asexual sporophyte and the microscopic sexual gametophytes. Briefly, biflagellate  $1n$  zoospores are released from sporophylls of the sporophyte; these settle on the substratum and grow into microscopic gametophytes, the males of which liberate biflagellate sperm or antherozoids. These sperms fertilize the eggs attached to the female gametophytes. The embryo grows into the large  $2n$  sporophyte. In this study no attempt was made to quantify the zoospores, which number in the millions (Anderson and North 1966, Chapman 1979, Kain 1979), or to measure the survivorship of the gametophytes. Neushul et al. (1976), Lüning and Neushul (1978), Charters et al. (1973), and Devanny and Volse (1978) attempted this, and the survivorship of gametophytes is apparently very low. Furthermore, *Macrocyctis* gametophytes live <50 d in the field (L. Deysher and T. Dean, *personal communication*).

We measured recruitment from the first appearance of small ( $\approx 5$  mm) blades visible to the naked eye. These tiny blades cannot be identified to species until they are 2–10 cm long, which takes 10–45 d. Their growth rates depend critically upon the availability of nutrients and the clarity and temperature of the water. We mapped these small blades during each visit. Blades that survived long enough for specific identification were traced through previous maps, and the date of recruitment of each individual was recorded. Obviously, the date of fertilization preceded our record of ger-

mination, but the time from zoospore liberation to visible recruitment is extremely variable (Neushul 1963, North 1971, Chapman 1979). Methods used to determine survivorship through various growth stages are discussed in Results.

Simple manipulations were done to test various hypotheses. Canopies were removed or thinned by cutting stipes with hedgecutters or simply by dislodging the holdfasts. To seed an area with kelp species, we placed sporogenic material in a small mesh bag that was nailed or tied to the substratum. Cages, made of 1.3-cm mesh monofilament net wrapped over wire or plastic frames, were monitored regularly for fouling. There was no evidence of any inhibition of light (inside and outside measurements of light intensity were identical) or of surge. We used unsophisticated instruments to measure the amount of light absorbed by each canopy. Because the units were variable and the precision was unknown, we report here only the observation that all light-meter readings inside and outside each canopy at Pt. Loma consistently indicated that 90–98% of the incident light was absorbed by each canopy of brown algae.

The most important cause of mortality of established *Macrocyctis* plants is entanglement with other drifting plants. These drifters dislodge attached *Macrocyctis* plants; as they drift, they pick up additional plants, and the result is a "snowball" effect. Rosenthal et al. (1974) observed a "snowball" containing up to 19 detached plants. We studied entanglement by drifters from Au-

TABLE 1. Abundance of kelps and turf at the Virgin Reef area, Pt. Loma, summer, 1972. Quadrats were placed haphazardly within each patch type except the *Macrocystis* forest, where consecutive quadrats along the transect line were censused.  $n$  = no. of quadrats.

Patch type and area	$n$	Kelp abundance (no. individuals/m <sup>2</sup> )					Algal turf cover (%)
		<i>Laminaria farlowii</i> $\bar{x} \pm SD$	<i>Cystoseira osmundacea</i> $\bar{x} \pm SD$	<i>Pterygophora californica</i> $\bar{x} \pm SD$	<i>Eisenia arborea</i> $\bar{x} \pm SD$	<i>Macrocystis pyrifera</i> $\bar{x} \pm SD$	
<i>Laminaria Cystoseira</i> patches in Virgin Reef area	17	6.7 $\pm$ 0.8	2.0 $\pm$ 1.8	0	0	0	78
<i>Laminaria Cystoseira</i> patches 100 m south of Virgin Reef area	27	7.1 $\pm$ 2.2	0.9 $\pm$ 1.1	0	0	0	61
<i>Pterygophora/Eisenia</i> patch by Virgin Reef	25	1.3 $\pm$ 3.8	2.8 $\pm$ 3.3	6.4 $\pm$ 0.8	0.9 $\pm$ 3.7	0	5
<i>Pterygophora</i> patch southeast of Virgin Reef	7	0	0.1 $\pm$ 0.4	7.6 $\pm$ 0.9	0	0	4
<i>Pterygophora</i> patch north of transect	10	0.4 $\pm$ 0.5	0.1 $\pm$ 0.3	7.5 $\pm$ 0.5	0	0	2
<i>Macrocystis</i> forest	400	0.03 $\pm$ 0.5	0	0	0	0.1 $\pm$ 0.3	0
Top of Virgin Reef, mixed turf	5	0	1.6 $\pm$ 0.7	0	1.4 $\pm$ 0.5	0	98
Boulders north of Virgin Reef; encrusting coralline algae	10	0	0.2 $\pm$ 0.4	0	0	0	0

gust 1973 through December 1976. Naturally and artificially dislodged plants in the three Pt. Loma areas (Fig. 1) were tagged and monitored at approximately monthly intervals until the drifter disintegrated or until we could no longer locate it. Random belt transects (usually 15–25 m long and 2 m wide) totalling  $\approx$ 1000 m<sup>2</sup> were censused every season in each of the Pt. Loma areas for several years for density, sizes of holdfasts, and number of stipes of *Macrocystis* drifters and the number of entangled but still-attached plants.

*Santa Catalina Island.*—This study site was a small kelp bed immediately west of Bird Rock near the isthmus on Santa Catalina Island (Fig. 1). The bed is protected from the east, west, and south, but is exposed to some winter storms from the north. It is thus relatively protected from strong wind action. Summer temperatures are relatively high; surrounding surface waters are possibly nutrient poor. We established three transects of 25  $\times$  2 m each at the 5, 10, and 15 m isobaths.

*Pt. Piedras Blancas.*—The kelp bed at Pt. Piedras Blancas (Fig. 1) was in an area dominated by reefs interspersed with small sandy areas along a sloping bottom 5–20 m in depth. *Dictyonium californicum*, articulated coralline turf, and a mixed understory of *Pterygophora californica* and *Laminaria setchellii* dominated the shallow areas of these reefs. Because the reefs were relatively small and discrete and thus relatively amenable to manipulations, we chose several study sites. Sites A and X were within a large *Macrocystis* canopy at a depth of  $\approx$ 5–18 m. Site B was within an extensive *Macrocystis* forest at a depth of 10–13 m. Site C was at the shoreward margin of a *Macrocystis* forest at a depth of 6m. Site D was about 1.5 km east of the point in a dense grove of mixed *Pterygophora* and *Laminaria setchellii* on a rocky bottom at a depth

of 9–10 m. Probably rarely were surrounding waters nutrient poor or temperatures stressfully high. Oceanic swells were generally northwesterly; southerly swells were associated with extreme winter storms. All sites were relatively shallow and were exposed to strong surge during the storms.

Unless otherwise specified, statistical significance was determined by single  $\chi^2$  or  $t$  tests. A result was judged "significant" if  $P < .05$ . (In most significant cases,  $P$  was  $< .01$ .)

#### RESULTS: PERSISTENCE OF PATTERNS WITHIN AND BETWEEN SITES

##### *Pt. Loma*

When the kelp forest off Pt. Loma was first surveyed, in 1857, it covered 15.4 km<sup>2</sup>. Its area was the same in the next survey, taken in 1911 (North 1971). These data, subsequent surveys, and the relative commercial harvest from this bed since 1916 are in North (1974). The bed maintained a relatively constant size during the late 1940s and the early 1950s, and then it declined relatively rapidly until 1962, when it occupied only 0.03 km<sup>2</sup> and yielded only 0.1 percent of the 1917 harvest (Fig. 3). Almost all of the kelp forests of southern California declined similarly (North 1971). Heavy grazing by sea urchins was the main proximal explanation for the decline (Leighton et al. 1966). According to several nonexclusive hypotheses, this shift to heavy grazing was due to (1) local extinction in the early 1800s of sea otters, an important predator of urchins and abalones; (2) overharvesting of kelp; (3) pollution from wastes; (4) overfishing by scuba divers of sea urchin predators (lobster and sheephead) and of possible sea urchin competitors (abalones); and (5) a change in near-shore currents that caused unusually warm water be-

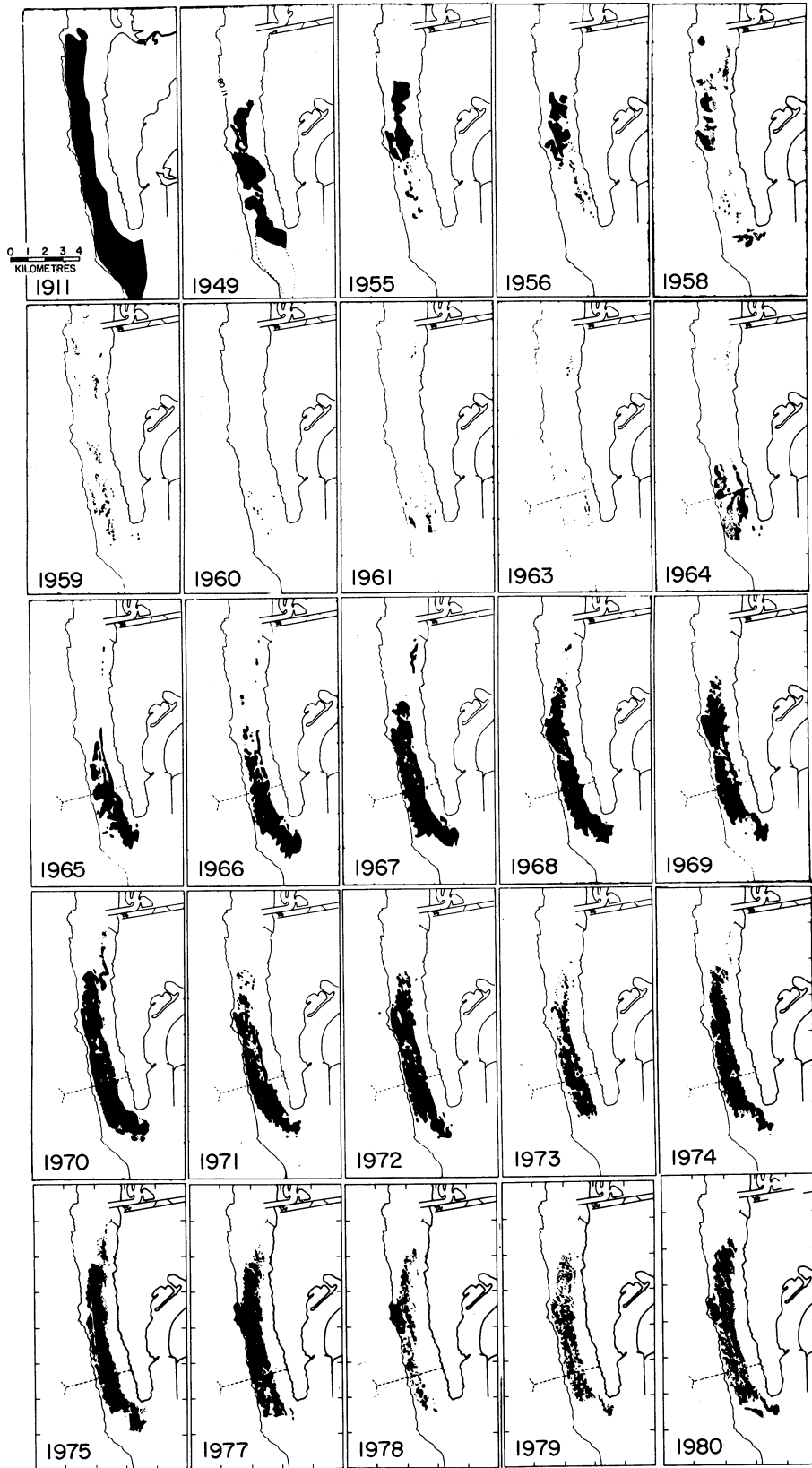


FIG. 3. Historical records of the surface canopy cover of the Pt. Loma kelp forest, courtesy of Wheeler J. North.

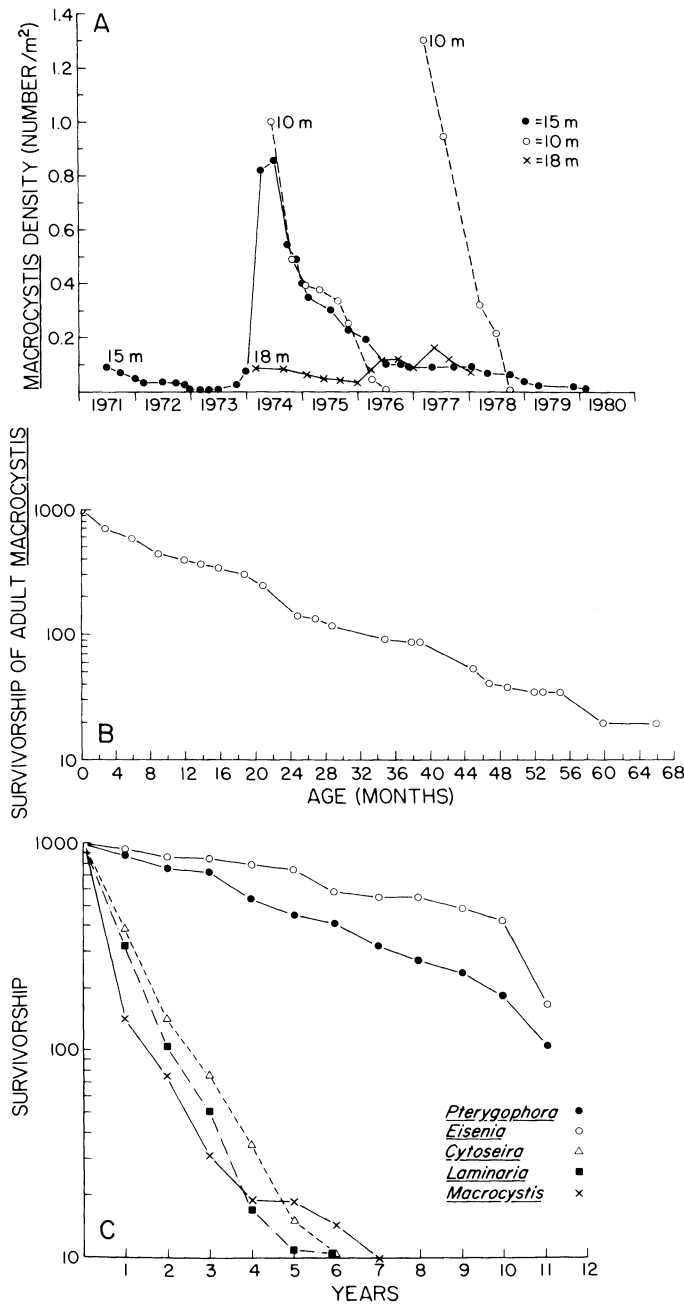


FIG. 4. Densities and survivorship of kelps at Pt. Loma. A. Densities of adult *Macrocyctis* over 10 yr at three isobaths. B. Survivorship of 321 *Macrocyctis* plants observed to reach the surface in early 1974. C. Survivorship of kelps observed to recruit at -15 m. Curves drawn from Tables 2-6.

tween 1957 and 1959 (Chelton et al. 1982). But the sea otters had been locally absent for some 130-150 yr, (Ogden 1941), and the kelp harvest had been constant during the early part of the century, so it is unlikely that either contributed much to the decline. The other hypotheses may at least partially explain the decline. In the mid-1960s, programs to reduce the sea urchin densities and procedures to improve sewage disposal were correlated with a recovery of the kelp

bed. Since 1967, the size of the bed has remained relatively constant. For the last 10 years there have been only localized urchin-abatement programs and a developing urchin fishery (Tegner 1980). Most of the recent fluxes seen in Fig. 3 were apparently caused by storms and, in some inshore and south Pt. Loma areas, overgrazing by sea urchins.

On a smaller scale, our study patches of *Macrocyctis*, *Pterygophora/Eisenia*, and *Laminaria/Cytoseira* (Ta-



TABLE 2. Life table for *Macrocystis pyrifera* at 15 m in Pt. Loma kelp forest. Four size classes were sampled as discussed in the text: of 1543 small blades, 300 survived 3 mo, to 5 cm; of these 300, 259 survived 6 mo, to 2 m; of 259, 35 survived 9 mo, to reach the surface. The adjacent permanent transect had 321 plants of the same cohort reach the surface and the life table was calculated from these plants; back-extrapolated numbers are based on these 321 plants and the percent survivorship of each of the censused size classes.  $l_x$  refers to the number of plants out of a cohort of 100 000 surviving to age  $x$ .  $e_x$  is the mean expectation of further life, at age  $x$ .  $q_x$  is the annual per capita mortality rate at age  $x$ .

Age (mo)	Number alive		$l_x$	$e_x$	$q_x$
	Observed	Back-extrapolated			
0	1543	14 152	100 000	0.24	.999
3	300	2752	19 446	0.49	.445
6	259	2375	16 782	0.30	.999
9	35	321	2268	1.16	.759
12	225		1590	1.35	.502
15	189		1336	1.34	.690
18	141		996	1.50	.362
21	126		890	1.41	.359
23	117		827	1.35	.346
25	109		770	1.27	.373
28	97		685	1.17	.730
30	78		551	1.26	.808
34	45		318	1.74	.239
36	43		304	1.64	.524
38	38		269	1.68	.377
44	30		212	1.57	.241
47	28		198	1.42	.589
48	26		184	1.44	.330
53	22		155	1.07	.643
56	17		120	1.10	.876
58	12		85	1.35	.407
60	11		78	1.29	0
61	11		78	1.21	0
63	11		78	1.04	.382
68	9		64	0.81	.501
75	6		42	0.50	.875
79	3		21	0.50	.848
86	1		7		

ble 1, Fig. 2) remained constant. The borders between the patches were first observed and marked in 1970 and 1971 and remained virtually unchanged through 1981. Moreover, R. McPeak (*personal communication*) has observed that at least one *Pterygophora* patch has persisted since 1946. There are, however, exceptions: *Macrocystis* has invaded a *Pterygophora* patch and a *Laminaria* patch, and a *Pterygophora* patch was invaded by *Eisenia*. During the study period, we never saw a lower canopy guild invade a patch with an overstory; that is, no *Laminaria* nor *Pterygophora* invaded *Macrocystis*, but the reverse occurred to a very limited extent.

*Survivorship of Macrocystis*—Measurements of survivorship of *Macrocystis* were begun in the summer and fall of 1971 at a depth of 15 m. Only two of the original 40 adult plants survived through spring 1974. The ages of these plants at the beginning of the study were not known. However, the size of the holdfast is

a rough indication of the age of the plant, and by this index almost all the plants were 2–4 yr old. Most of the plants were approximately 5 yr old when they died. This corresponds with the life expectancy of *Macrocystis* plants at Del Mar, California (Rosenthal et al. 1974).

The survivorship of all the plants that subsequently recruited to the surface canopy was followed through 1980. There was a pattern of a large recruitment of cohorts following storm disturbances, and a subsequent decline in density until the next strong recruitment. Fig. 4A shows the flux in the densities of the plants; Fig. 4B shows the survivorship of the 321 plants that reached the surface in 1974; and Fig. 4C shows the survivorship of *Macrocystis* and other kelps from the first appearance of small blades. The recruitment of the *Macrocystis* plants in the peak densities shown in Fig. 4B, C occurred during an upwelling in May and June 1973, following a major reduction in the surface

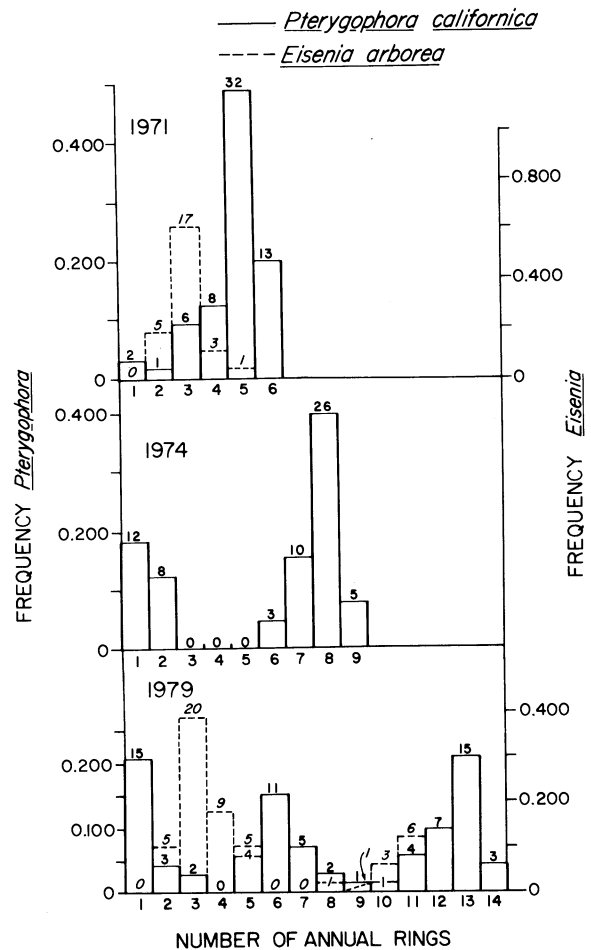


FIG. 5. Frequency histogram of growth rings for *Pterygophora californica* (—) and *Eisenia arborea* (---) in plants collected from the same place in 1971, 1974, and 1979, at the Virgin Reef, Pt. Loma. Numbers over bars are actual totals.

TABLE 3. Life table for *Pterygophora californica* at 15 m, Pt. Loma.  $l_x$  refers to the survivors at start of age interval  $x$ ,  $e_x$  refers to mean expectation of life for individuals alive at start of age interval  $x$ , and  $q_x$  refers to the mortality rate during age interval  $x$  to  $x + 1$ . The  $l_x$  data are calculated from the  $q_x$  column, which is calculated from the two columns of observed plants. There was no observed mortality for the 4–5 year old plants. Therefore the (0.193) is estimated from the mean annual mortality rate of the population of plants first observed as adults.

Age (yr)	No. plants observed		$l_x$	$e_x$	$q_x$
	From recruitment	As adults			
0	80		1000	5.25	0.163
1	67		838	5.17	0.104
2	60		750	4.72	0.003
3	58		725	3.87	0.276
4	42		525	4.15	(0.193)
5		83	424	4.02	0.048
6		79	404	3.19	0.203
7		63	322	2.88	0.127
8		55	281	2.22	0.145
9		47	240	1.51	0.213
10		37	189	0.78	0.432
11		21	107		

canopy by winter and spring storms. Surface water in late summer was unusually warm and was probably depleted of nutrients (Jackson 1977), and the new plants' growth temporarily ceased while they were still 2–3 m from the surface. By late 1973, conditions had improved; the plants reached the surface in early 1974.

Because new recruits occurred in patches of very high densities, different sampling schemes were employed to measure *Macrocystis* survivorship during three stages (from tiny-blade stage to plants that reached the surface). The survivorship of new recruits through the  $\approx 5$ -cm stage had to be monitored where there was reasonable certainty that all the tiny blades were *Macrocystis*. This was done by picking small fixed quadrats that included 30–150 blades. The blades were mapped and their survivorship was followed. This stage had a high mortality: only 300 of the 1543 observed recruits survived to reach 5 cm in length.

The next stage spanned the barely identifiable  $\approx 5$ -cm plants through plants 1–2 m tall. The fixed quadrats for monitoring survivorship at this stage were usually 1–16 m<sup>2</sup>. Possibly because these plants were monitored during relatively good environmental conditions in 1973 and 1974, when the plants grew fast, their survivorship was surprisingly high: 259 of the 300 observed 5-cm plants grew to be at least 1–2 m tall.

The third growth stage, plants from 2 m to the surface, was monitored in 5 × 2 m and 15 × 2 m transects, and in several 16-m<sup>2</sup> quadrats. During this stage, there was considerable self-thinning due to entanglement with cohort neighbors; only 35 of 259 plants survived to reach the surface. The young plants wrapped

around each other until they formed ropelike masses; then either the stipes broke or the holdfasts, still weakly developed, pulled free of the substratum. Either event usually killed the plant. On several occasions, however, the loose holdfast of an entangled plant became tangled in the holdfast of the attached plant and survived with the two holdfasts growing together. Within a few months the plants were superficially indistinguishable from solitary plants.

The life table (Table 2) was calculated from survivorship in each size stage. That is, 300 of 1543 recruits survived to 5 cm; 259 of 300 plants reached 1–2 m; only 35 of these 259 reached the surface. In most cases these were plants that had originally been counted. The 35 plants reaching the surface represented  $\approx 2\%$  of the 1543 recruits. Because we were concerned about possible monitoring disturbances due to entanglement with divers, these observations were made alongside but not on the permanent 100 × 4 m transect. On this transect, 321 plants from the same cohort reached the surface. To connect the two methods of estimating mortality, we assumed that these 321 adult plants represented 35/1543 of the original recruits. Hence, the calculation of Table 2 involved back-extrapolating the original recruitments as follows:  $321/(35/1543) = 14\,152$ . The subsequent survivorship data were for the 321 plants. Calculating life tables usually includes multiplying through by 1000, but, because the extrapolated number of recruits was so large, Table 2 was normalized to 100 000.

*Survivorship of Pterygophora and Eisenia.*—In the Virgin Reef area at Pt. Loma, *Pterygophora californica* occurred in large patches, some of which may have covered > 1 ha. Data on *Pterygophora* density and age frequency were collected west of Virgin Reef and north

TABLE 4. Life table for *eisenia arborea* at 15 m, Pt. Loma.  $l_x$  refers to the survivors at start of age interval  $x$ ,  $e_x$  refers to mean expectation of life for individuals alive at start of age interval  $x$ , and  $q_x$  refers to the mortality rate during age interval  $x$  to  $x + 1$ . The  $l_x$  data are calculated from the  $q_x$  column, which comes from the two columns of observed plants.

Age (yr)	No. plants observed		$l_x$	$e_x$	$q_x$
	From recruitment	As adults			
0	37		1000	7.32	0.081
1	34		919	6.92	0.088
2	31		838	6.54	0
3	31	53	838	5.54	0.065
4	29	50	784	4.88	0.060
5		47	737	4.16	0.191
6		38	596	4.03	0.079
7		35	549	3.33	0
8		35	549	2.33	0.114
9		31	486	1.57	0.129
10		27	423	0.72	0.556
11		12	188		

TABLE 5. Life table for *Laminaria farlowii* at 15 m, Pt. Loma.  $l_x$  refers to the number of plants surviving to age  $x$ ;  $q_x$  is the annual per capita mortality rate at age  $x$ ; and  $e_x$  is the mean expectation of further life in years, at attainment of age  $x$ .

Age (yr)	No. observed alive	$l_x$	$e_x$	$q_x$
0.2	531	1000	.97	.648
0.5	315	593	.95	.684
1.0	177	333	1.00	.661
1.5	103	194	1.04	.704
2.0	56	105	1.12	.609
2.5	35	66	1.28	.406
3.0	27	51	1.08	.395
3.5	21	40	.80	.816
4.0	9	17	1.05	.556
4.5	6	11	.98	.556
5.0	4	8	.75	.750
5.5	2	4	.75	.000
6.0	2	4	.25	1.000
6.5	0	0		

of the *Macrocystis* transect. There were no substantial differences between these local sites in 1971, but all the *Pterygophora* baseline survivorship quadrats were in the area west of Virgin Reef. Age frequencies were calculated from growth rings that, judging from the progression of the modal peaks at five rings in 1971, eight rings in 1974, and thirteen rings in 1979 (Fig. 5), represented annual increments.

The *Pterygophora* life table (Table 3) was not calculated in the same manner as the *Macrocystis* life table for several reasons. Once established, *Pterygophora* lived longer than the duration of this study, so it was not possible to follow the survivorship of a cohort. It was generally impossible to measure survivorship of tiny plants, because the plants could not be identified to species until they were at least 15–30 cm long, and most mortality had occurred by that time. For these reasons, the "recruits" were identifiable plants at least 15–30 cm in total length that may have been as old as 3 mo. Very early mortality was thus not included in the life table. Survivorship of the 80 plants observed to recruit in the quadrats was used to estimate survivorship for 0–5 yr. These recruits were first observed over several seasons, so they did not represent a true cohort. Survivorship of plants older than 5 yr was estimated from the observed mortality of 83 tagged adult plants present in 1971, which were predominantly (73%; Fig. 5) five- and six-year-olds. The inclusion of six-year-olds tended to increase estimates of mortality rates, but this was partially balanced by the inclusion of the younger age classes, which have a lower mortality rate. The survivorship column (and the curve in Fig. 4C) were calculated from the  $q_x$  column.

*Eisenia arborea*, which generally occurred in the study area in sites exposed to wave surge, grew as scattered individuals on the top of Virgin Reef as well as on the tops of large boulders and isolated reef outcrops. In 1971, the *Pterygophora* patch in front of Virgin Reef

had a density of 0.9 *Eisenia*/m<sup>2</sup> and 6.4 *Pterygophora*/m<sup>2</sup>. During this study, *Eisenia* seemed to replace *Pterygophora* (1.8 *Eisenia*/m<sup>2</sup> and 3.5 *Pterygophora*/m<sup>2</sup> in 1977) in this patch, but similar replacement was not seen in other *Pterygophora* patches. It is not clear why *Eisenia* invaded the Virgin Reef *Pterygophora* patch, although our intensive diving programs in that spot may have caused an opening in the canopy that allowed invasion by *Eisenia* that was seeded from the nearby plants on top of the reef. In our Virgin Reef study area, *Eisenia* was near the deep end of its vertical distribution range at Pt. Loma. When it grew along areas with high surge, such as the top of Virgin Reef, or along more shallow areas, the *Eisenia* plants were relatively short (30–50 cm) and bushlike (Charters et al. 1969). However, *Eisenia* growing in the *Pterygophora* canopy assumed a morphology almost identical to *Pterygophora*: the plants were exactly the same height (80–120 cm), and the characteristic *Eisenia* stipe bifurcation was not conspicuous. When the canopy was seen from above or below, it was hard to differentiate the species. In crowded canopies, identification required a careful examination of the top of each stipe for the bifurcation.

The *Eisenia* life table (Table 4) was computed like that of *Pterygophora*, except that the extant plants were assumed to be 3 yr old when first observed (Fig. 5). Thus, 81% of the observed 1971 population were 3 yr old or older. These results concern plants in the *Pterygophora* canopy, not those isolated plants on top of Virgin Reef. Survivorship was similar for *Eisenia* and *Pterygophora* (Fig. 4C).

*Survivorship of Laminaria and Cystoseira.*—The patches of prostrate kelps, dominated mostly by *Laminaria farlowii*, varied in size from 1 to 40 m<sup>2</sup>. As with the other patch types, *Laminaria* borders adjacent to *Pterygophora* and *Macrocystis* were essentially invariant from 1971 through 1979. Unlike the relatively long-lived *Pterygophora* and *Eisenia*, most of the *L.*

TABLE 6. Life table for *Cystoseira osmundacea* at 15 m, Pt. Loma.  $l_x$  refers to the number of plants surviving to age  $x$ ;  $q_x$  is the annual per capita mortality rate at age  $x$ ; and  $e_x$  is the mean expectation of further life in years, at attainment of age  $x$ .

Age (yr)	No. observed alive	$l_x$	$e_x$	$q_x$
≈0.2	198	1000	1.14	.535
0.5	135	682	1.05	.683
1.0	76	384	1.16	.694
1.5	42	212	1.40	.524
2.0	29	146	1.42	.424
2.5	22	111	1.29	.535
3.0	15	76	1.26	.360
3.5	12	61	1.00	.660
4.0	7	35	1.09	.490
4.5	5	25	.88	.640
5.0	3	15	.80	.556
5.5	2	10	.55	.750
6.0	1	5	.30	1.000
6.5	0	0		

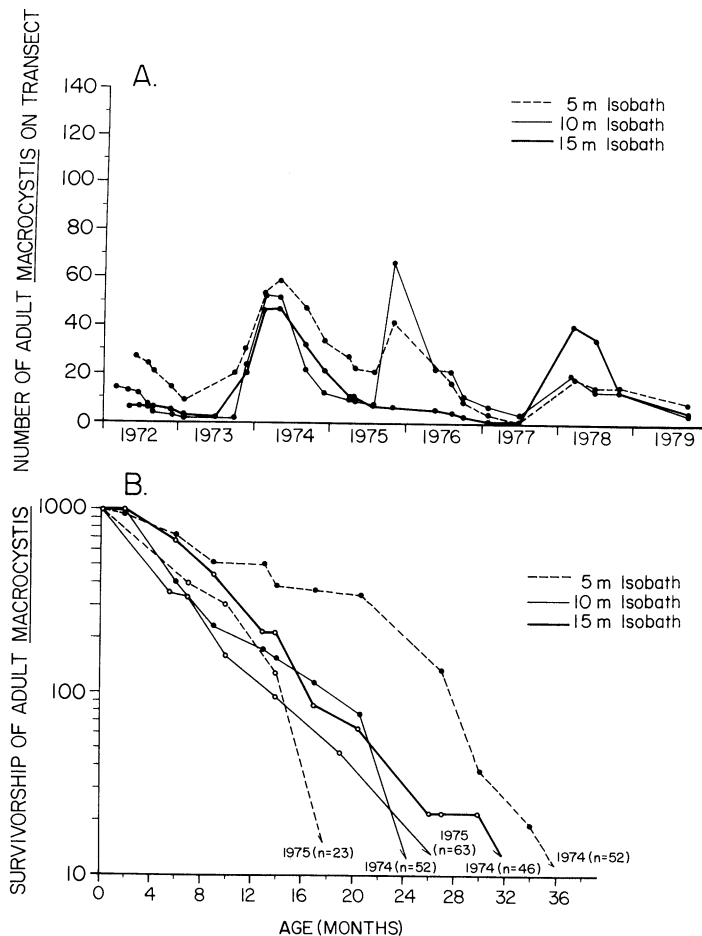


FIG. 6. Density (A) and survivorship (B) curves of adult *Macrocyctis* at three isobaths at Bird Rock, Santa Catalina Island over 8 yr.

*farlowii* had a relatively short life expectancy (Table 5), even though five plants from 1971 were still alive in 1977, when the last surveys were made. The life table (Table 5) was calculated from only the 531 plants observed to recruit and grow large enough to be identified. Because there was a high turnover with no apparent year-to-year variation in recruitment or mortality, these data were pooled over years.

*Cystoseira*, like *Eisenia*, appeared to be near the lower limit of its depth range, and all the plants appeared to be stunted. In contrast, there are luxuriant floating canopies in more shallow and protected areas such as Pacific Grove, California. At Pt. Loma, *Cystoseira* plants are uncommon and scattered. This alga seemed to occur most abundantly in *Laminaria* patches, although it also occurred at low densities throughout the *Pterygophora* and *Eisenia* patches (Table 1). Even very small *Cystoseira* are readily identifiable, so considerable recruitment was observed despite the fact that very few plants became reproductive. Many adult *Cystoseira* observed in 1971 survived through 1977, and the 189 *Cystoseira* observed alive in 1971 had a higher survivorship than the 198 observed to recruit. *Cysto-*

*seira* that survived > 1 yr had a higher life expectancy, but the survivorship and turnover rates of those observed to recruit were similar to those of *Laminaria* and *Macrocyctis* (Fig. 4C; Table 6).

In summary, patch constancy at Pt. Loma was exemplified by sharply defined and apparently stable boundaries. With the exception of patches of *Pterygophora* and *Eisenia*, each of the many marked patches persisted beyond the life expectancies of its component species. Since there was turnover within the patches but little invasion, we concluded that the patches were stable in persistence for several generations.

#### Santa Catalina Island

*Survivorship of Macrocyctis.*—The work at Santa Catalina Island focused on a survey of *Macrocyctis* rather than on patch dynamics. As at Pt. Loma, the *Macrocyctis* population size at three depth contours has clearly undergone major oscillations through time (Fig. 6). Nevertheless, the kelp bed at Bird Rock, Santa Catalina Island, has been present for many years. Hence this *Macrocyctis* forest also has had a persistence surpassing turnover times of its species (Fig. 6B). Re-

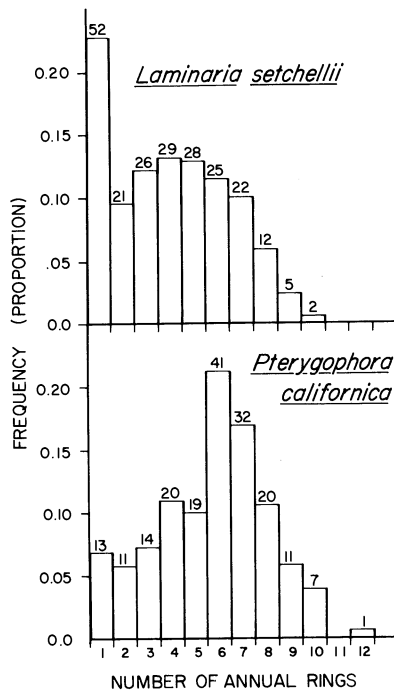


FIG. 7. Frequency histogram of growth rings of *Laminaria setchellii* and *Pterygophora californica* collected in the same area at Pt. Piedras Blancas, April 1977. Numbers over bars are actual totals.

cruitment on the three transects at Bird Rock paralleled but preceded the 1974 peak at Pt. Loma. This parallelism probably resulted from major disturbances at both sites by storms early in 1973; however, *Macrocystis* recruited and grew to the surface faster at Bird Rock, probably because the water there is much clearer. On the other hand, the shallower Bird Rock plants were more susceptible to storm damage and warm summer water with its presumably lower nutrients, and this may be why their survivorship was lower than that of adult plants at Pt. Loma (compare Figs. 4B and 6B). The constancies of patches of *Macrocystis* and of various understory species were not monitored, but the reciprocal clearing experiments discussed later suggested considerable inertia.

#### Pt. Piedras Blancas

Our study at Pt. Piedras Blancas, held 1976–1979, did not yield many data regarding the long-term constancy of patches in this relatively shallow, wave-exposed area. However, from field trips beginning in 1972, we know that the *Macrocystis* patch was present on the reef each summer, and that winter storms often thinned it considerably. The patches of *Nereocystis*, *Macrocystis*, *Pterygophora/Laminaria setchellii*, *Dictyoneurum californicum*, and articulated coralline algae seemed relatively invariant between 1976 and 1979.

In the southern California kelp forests, patches were seasonally constant over several years; in contrast, the

central California kelp forest was dominated by seasonal events. For example, *Nereocystis* is an annual plant. Also, the *Macrocystis* canopy was heavily thinned by winter storms and then would regrow from holdfast and remaining stipes, and from recruitment of new plants. After winter sporulation, the *Pterygophora*, *L. setchellii*, and *Dictyoneurum* fronds degenerated until there was little canopy. Since many of the ephemeral understory species began growth before the overstory canopies formed in the spring, the increased light on the bottom following winter degeneration of the canopies may have been responsible for the rich understory. The age-frequency distributions (based on stipe rings) of *Pterygophora* and *L. setchellii* (Fig. 7) suggested that these populations did not have the pulsed recruitment patterns of *Pterygophora* and *Eisenia* in southern California (Fig. 5). These distributions also suggested that the patches had been present for at least 10 yr, during which the stipitate populations had had a fairly regular recruitment.

Despite the physical differences among Pt. Loma, Santa Catalina Island, and Pt. Piedras Blancas, patch persistence seemed to be similar among these areas. The borders of the patches persisted throughout the study, and judging by life spans of component species, patches persisted much longer than the time taken by our study. Although we had no direct long-term observations in central California, different patch types in different habitats appeared to have similar constancy patterns despite markedly different demographic patterns of the populations.

#### RESULTS: INERTIA (RESISTANCE TO INVASION)

The fact that kelp patches persist longer than turnover times of their component populations suggests that the patches are resistant to changes resulting from invasion or competitive exclusion, or from other perturbations such as "normal" storms or grazing. Maintenance of such local equilibria could result if (1) other potential colonists are excluded by intolerable local physical conditions or by dispersal limitations; (2) new colonists grow slowly, so that colonization is not immediately apparent; or (3) various biological interactions maintain the integrity of the patch.

Because the borders of most patches seemed roughly invariant, we asked why the edges were stable even though the algae comprising one patch might have been expected to out-compete and displace those in another. (Consider the eventual displacement of *Postelsia* by mussels in the absence of disturbance [Dayton 1973, Paine and Levin 1981]). In each study site, reciprocal clearings were established to test hypotheses about the effects of various types of canopy competition.

Resistance to invasion is potentially encouraged by three general mechanisms: (a) the presence of an overstory inhibits the development of understories, (b) the presence of understory canopies adversely affects the recruitment of overstory species, and (c) limits to the

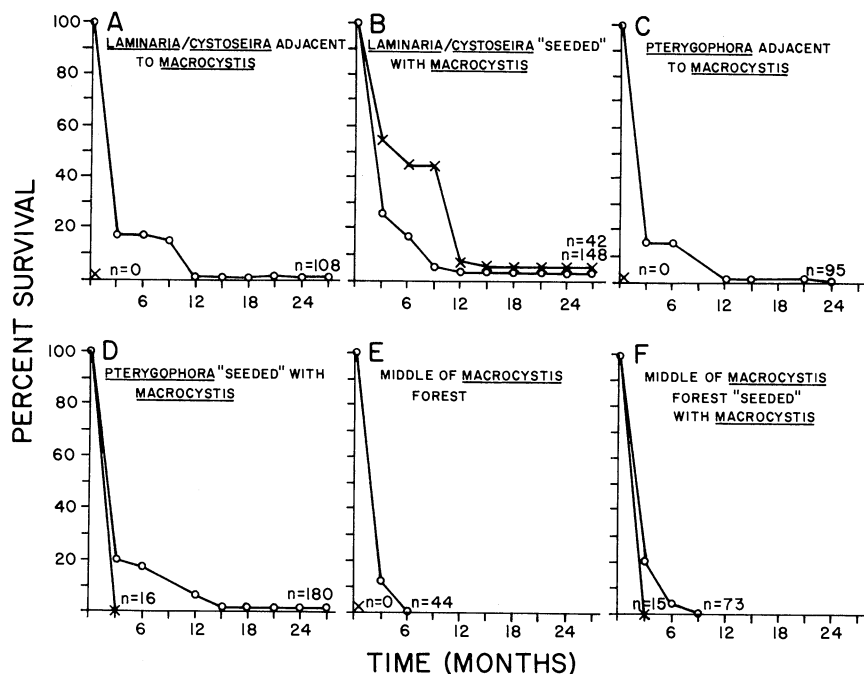


FIG. 8. Survivorship of *Macrocyctis* recruits in various patches at Pt. Loma. Experiments test effects of other canopies and dispersal capability on recruitment and survivorship.  $\circ$  refers to the treatment (resident species thinned or removed) and  $\times$  refers to adjacent unmanipulated control. n = initial number of recruits identified. Experimental seedings were done by nailing to the substrate mesh bags filled with fertile sporophylls.

effective distance of spore dispersal reduce the probability of a successful invasion. We examined these mechanisms at each study site. Most of these experiments were begun in 1974; exceptions are noted.

#### Pt. Loma

*Effects of canopies on Macrocyctis.*—Despite the presence of adult *Macrocyctis* next to a thick *Laminaria/Cystoseira* patch, *Macrocyctis* did not invade the patch during this study. However, when a 4-m<sup>2</sup> area was cleared of *Laminaria* and *Cystoseira* (Fig. 8A), 108 *Macrocyctis* sporophytes recruited into a 0.25-m<sup>2</sup> quadrat; 18 of these survived 3 mo. Some of the 108 tiny blades might not have been *Macrocyctis*, but all of the 18 survivors were *Macrocyctis*. The adjacent uncleared control had no recruitment of *Macrocyctis* (Fig. 8A). The one adult *Macrocyctis* that survived through this experiment grew to be a very large plant whose holdfast eventually covered much more than the 0.25-m<sup>2</sup> quadrat. Several *Macrocyctis* that recruited after the experiment also survived. By the second year after the experiment, *Macrocyctis* entirely filled the 4-m<sup>2</sup> cleared area; it persisted through 1982.

Two other experiments in patches of *Laminaria/Cystoseira* (not shown in Fig. 8) are relevant to *Macrocyctis* recruitment. In 1971, we cleared 1 m<sup>2</sup> of a *Laminaria* patch that was >30 m from the nearest adult *Macrocyctis*. Several *Macrocyctis* eventually germinated. A drifting adult *Macrocyctis* plant nearby was the suspected source of the *Macrocyctis* spores. A non-

cleared control only 1 m from the clearing had no *Macrocyctis* recruits. Two of the recruits to the cleared area survived to be long-lived adults. In 1980 we observed an isolated patch of seven large *Macrocyctis* covering an area much larger than the original clearing. Once the *Macrocyctis* patch was established in the *Laminaria* patch, it evidently slowly expanded.

In the second experiment, a clearing in a *Laminaria/Cystoseira* patch at least 10 m from the nearest *Macrocyctis* was made at the same time as the experiments shown in Fig. 8. In this case no *Macrocyctis* were identified in either the clearing or the adjacent control. This supports the hypothesis that *Macrocyctis* spore dispersal can be limited (Anderson and North 1966). In an additional test of this hypothesis, we filled small bags with fertile *Macrocyctis* sporophylls and nailed them in a 1-m<sup>2</sup> clearing in a *Laminaria/Cystoseira* patch. We similarly "seeded" an uncleared control nearby (Fig. 8B). The cleared area had 148 recruits; the control, 42. All recorded recruits were identified. The differences between the cleared and control areas were obvious. Interestingly, *Macrocyctis* had a higher rate of survival in the uncleared control than in the cleared area, especially in the early stages. In both cases, the new *Macrocyctis* patches persisted through 1979, and new plants have recruited from these plants. Thus, with heavy seeding, *Macrocyctis* can invade a patch of prostrate kelp.

Comparison of the uncleared control in which no *Macrocyctis* recruited naturally from adjacent adult

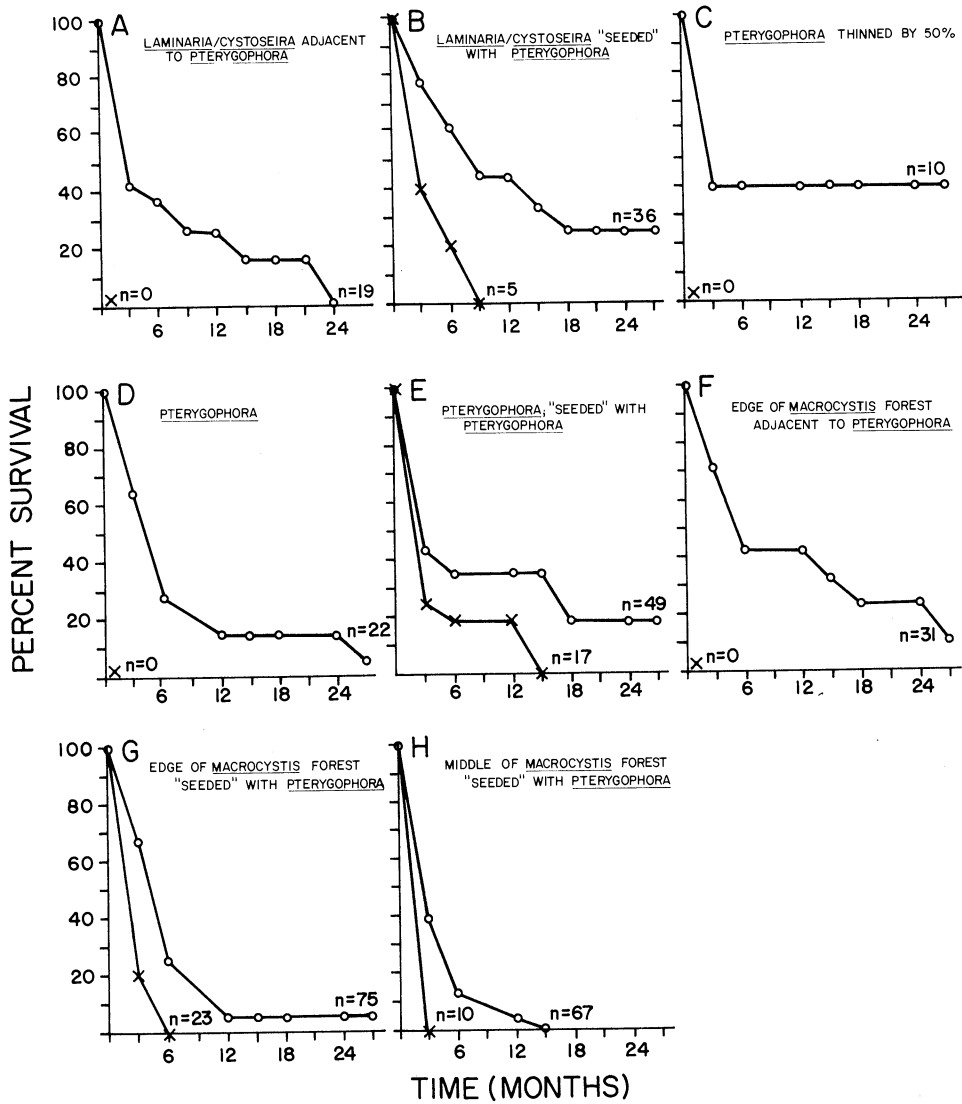


FIG. 9. Survivorship of *Pterygophora* recruits in various patches at Pt. Loma. Procedures and symbols as in Fig. 8.

plants (Fig. 8A) with the uncleared control in which 42 plants recruited from a presumably heavy inoculation of spores held against the substratum (Fig. 8B) indicates that light is not the sole factor preventing early growth of sporophylls. Thus, part of the inhibition by the *Laminaria/Cystoseira* canopy was probably caused by the canopy's physical interference with spore settlement and gametophyte survivorship. However, since the inoculated clearing had many more recruits than the inoculated uncleared control, *Laminaria/Cystoseira* canopy inhibition evidently resulted from both interference with spore settlement and competition for light.

Results were nearly identical in *Macrocystis-Pterygophora* experiments. When *Pterygophora* adjacent to *Macrocystis* were cleared, there was a heavy recruitment of *Macrocystis* in the clearing. There was no

recruitment in the uncut control (Fig. 8C). There was no *Macrocystis* recruitment in a *Pterygophora* clearing 15 m from the nearest *Macrocystis* plant (these negative data are not included in Fig. 8). Further, when a clearing was seeded with *Macrocystis* spores (Fig. 8D), there was recruitment of *Macrocystis* in both the clearing and the control, but recruitment in the clearing was higher than in the control. The *Macrocystis* that recruited from inoculated spores survived in the *Laminaria* patch, but none survived under the *Pterygophora* canopy. This suggests that *Pterygophora* patches are more difficult to invade than are *Laminaria/Cystoseira* patches.

The final *Macrocystis* experiment evaluated the effects of the *Macrocystis* canopy on its own recruitment (Fig. 8E and F). In this experiment a 20 × 20 m clearing was established in the middle of a *Macrocystis* for-

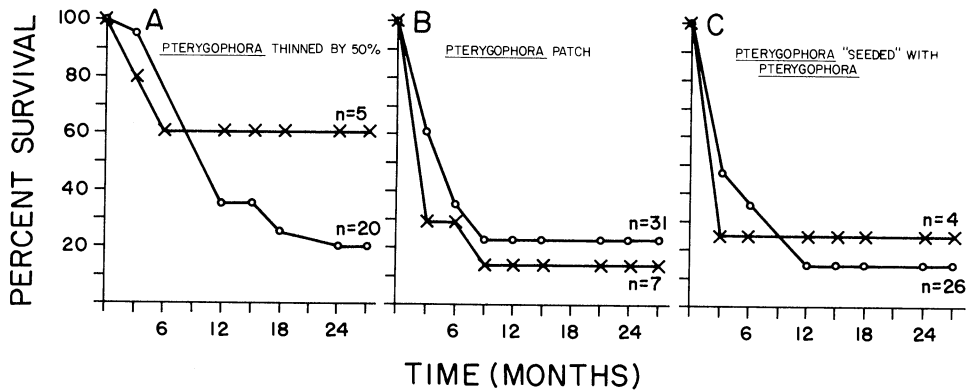


FIG. 10. Survivorship of *Eisenia arborea* recruits in patches of *Pterygophora*. Symbols and procedures as in Fig. 8.

est; also, five permanent 1-m<sup>2</sup> quadrats were monitored as controls. No recruitment occurred in the control quadrats, but 44 recruits were identified in the clearing. After spores were inoculated, 173 recruits were identified in the clearing, whereas only 15 were identified in the controls, and those 15 soon died. The differences in recruitment were dramatic, but during this experiment there were no survivors in either the clearing or the controls. In this forest, there was no canopy to interfere with the light. Grazing fishes and invertebrates were uncommon in the middle relative to the edge of the *Macrocystis*, so this type of grazing was unlikely to be responsible for the lack of recruitment. There was evidence of nutrient depletion, at least in the surface water (Jackson 1977). (Nutrients may be important resources limiting germination at San Onofre, near San Clemente, California [L. Deysler, *personal communication*]). During the period of this experiment there were adequate light and nutrients for growth in the other experiments outside the kelp forest. Thus it seems reasonable to hypothesize that nutrient depletion in the bottom waters of this *Macrocystis* patch was responsible for the lack of recruitment. We emphasize that *Macrocystis* often recruits within naturally produced clearings in kelp forests after adult plants have been pulled free. Even our experimental clearings were eventually filled with recruits that survived to become adults. The successful recruitment of *Macrocystis* inside a kelp forest may depend upon the cross-shore influx of water from periodic upwelling of clear, cool, and presumably nutrient-rich water. The transport presumably is via internal waves.

In summary, the other canopy species significantly inhibited *Macrocystis* germination and recruitment, but there was greater survivorship of those *Macrocystis* that did germinate below a *Laminaria/Cystoseira* canopy. In most cases, light was apparently the limiting resource. However, the lack of successful recruitment in a clearing inside a large *Macrocystis* patch suggests that nutrients may also limit recruitment. Dispersal of spores from attached *Macrocystis* seems limited with regard to the ability to invade other patches.

*Effects of canopies on Pterygophora and Eisenia.*—The ability of *Pterygophora* to invade other patches was evaluated with a similar set of experiments (Fig. 9) initiated in the fall of 1973. *Eisenia* is fertile in the late summer and the fall, and *Pterygophora* is fertile in the late fall and the winter (McPeak 1981, P. K. Dayton, *personal observations*). Dispersal of *Pterygophora*, like that of *Macrocystis*, seemed to be limited. It recruited in clearings in patches of *Laminaria/Cystoseira* and *Macrocystis* that were adjacent to adult *Pterygophora* (Fig. 9A and F). But it did not recruit in unseeded clearings in patches of *Laminaria* and *Macrocystis* that were not adjacent to *Pterygophora* (negative data not included in Fig. 9). This nonadjacent *Laminaria* clearing was only 2 m from the nearest *Pterygophora*. *Pterygophora* recruited from spores inoculated in clearings and controls in patches of *Laminaria/Cystoseira*, *Pterygophora*, and *Macrocystis* (Fig. 9B, E, G, and H). The clearings had more recruits and better survivorship, suggesting that spore availability and light are important determinants of the success of *Pterygophora* populations invading different patches. *Pterygophora* recruitment was evaluated in the clearings and controls (Fig. 9D) as well as in a 4-m<sup>2</sup> area in which the *Pterygophora* population had been thinned by 50% (Fig. 9C). There was some recruitment in the cleared area and none in the control. In contrast, there was a much heavier recruitment in a seeded clearing and its control (Fig. 9E). This again emphasizes the importance of both spore dispersal and light to the germination and survival of *Pterygophora*.

*Eisenia* did not form canopy patches; rather, it generally was a minor component of the *Pterygophora* canopy or grew in abundance only in the vicinity of reef tops. Factors affecting *Eisenia* recruitment appeared to be similar to those affecting *Pterygophora*, except that the *Eisenia* seemed more shade-tolerant (Fig. 10).

*Effects of canopies of Laminaria and Cystoseira.*—*Laminaria farlowii* had a faster turnover rate than the previously mentioned species (Table 5), and it survived better in these experiments than did other species (Fig.



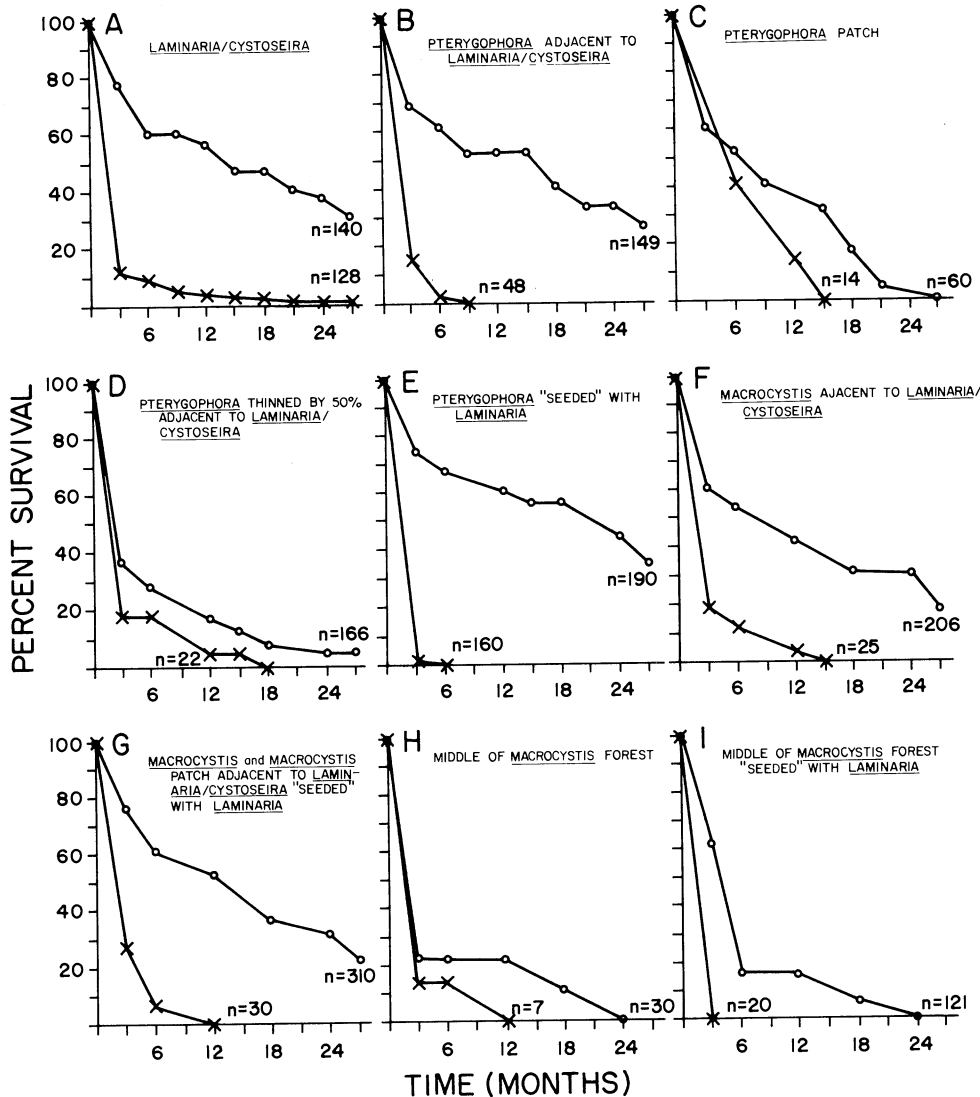


FIG. 11. Survivorship of *Laminaria farlowii* recruits in various patches. Procedures and symbols as in Fig. 8.

11). A clearing in a *Laminaria* patch had essentially the same *Laminaria* recruitment and survivorship through identifiable size with and without a canopy, but later survivorship was better in the absence of a canopy (Fig. 11A). In a clearance experiment in a *Pterygophora* patch adjacent to *Laminaria*, there was a marked effect of canopy on both recruitment and survival (Fig. 11B), but there were fewer recruits in a *Pterygophora* patch many metres from other *Laminaria* (Fig. 11C); this suggests some dispersal limitations. However, there was still much more recruitment than in the clearing (Fig. 11C). In the *Pterygophora*-thinned patch adjacent to a *Laminaria* patch, there was considerably more recruitment in the canopy-thinned area (Fig. 11D). In a *Pterygophora* patch seeded with *Laminaria farlowii*, recruitment was similar to that in the absence of a canopy, but survivorship was dramatically higher (Fig. 11E). Finally, in a *Ma-*

*crocyctis* patch, both the recruitment and survivorship of *Laminaria* were much higher in the absence of the *Macrocyctis* canopy in both seeded and unseeded situations (Fig. 11F-I).

Unlike the *Laminaria* canopy, the *Pterygophora* canopy strongly inhibited the recruitment of *Laminaria*. Some *Laminaria* did germinate under the *Pterygophora* canopy (Fig. 11B, C, D, and especially E), but survivorship was poor. In an experiment in a *Pterygophora* patch  $\approx 35\text{--}40$  m from a *Laminaria* patch, there was recruitment in both the clearing and the control (Fig. 11C). Although most of the original *Laminaria* plants died within 21 mo, their descendants persisted through 1979 in a small dense patch mixed with *Pterygophora*. Seeding had a conspicuous effect on recruitment in both a clearing and a control, but the plants under the *Pterygophora* canopy still failed to survive (Fig. 11E). The *Macrocyctis* canopy (controls

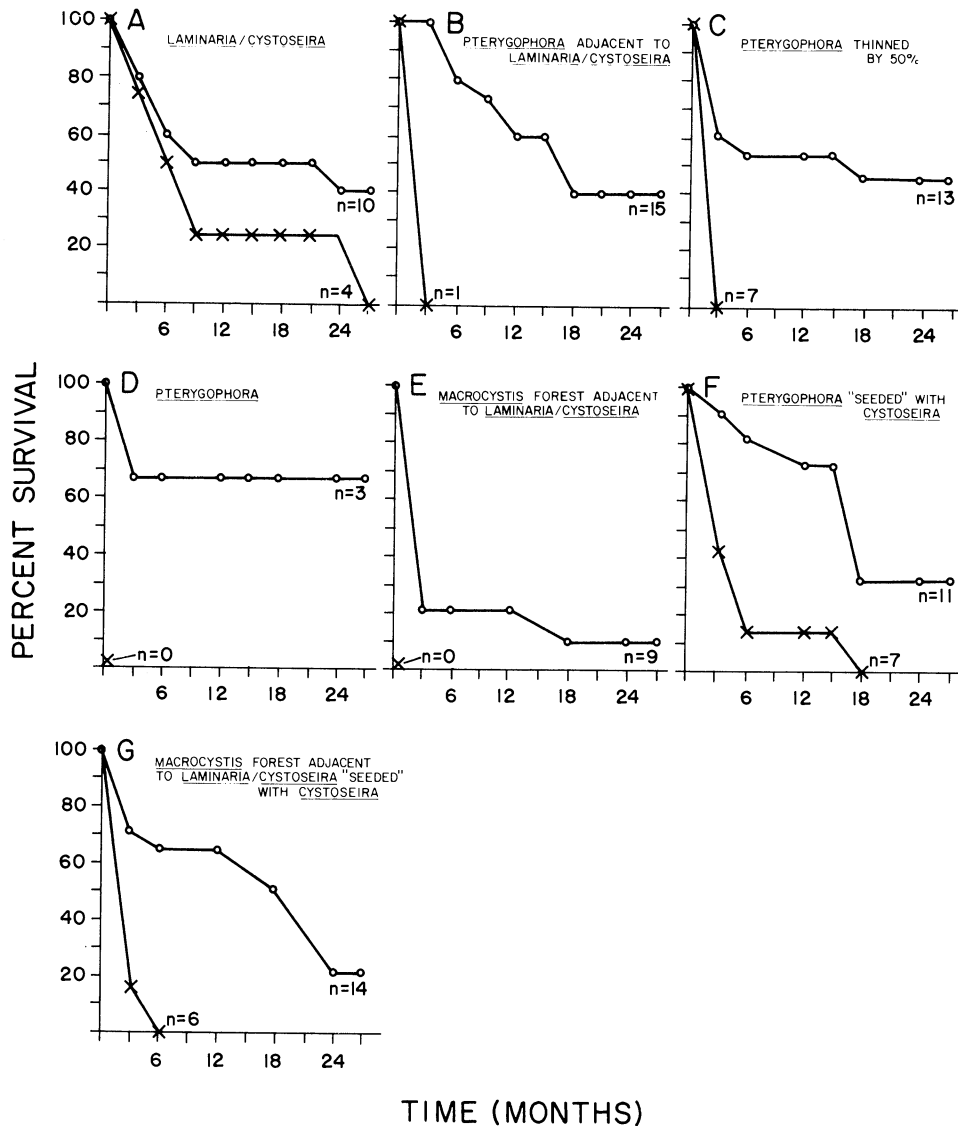


FIG. 12. Survivorship of *Cystoseira osmundacea* recruits into various patches. Procedures and symbols as in Fig. 8.

in Fig. 11F-I) also significantly reduced but did not eliminate *Laminaria* recruitment. We were unable to quantify reproductive condition in *Laminaria*, but it was clear that none of the plants surviving under the *Macrocystis* canopy was large or healthy enough to become fertile.

The response of *Cystoseira* to these canopy-clearing experiments was much the same as that of *Laminaria*, except that few *Cystoseira* recruited (Fig. 12). The same trends of higher recruitment and survival in clearings than under canopies were apparent, but the numbers were too low to allow any strong conclusions about canopy effects. Fig. 12 does not show the lack of recruits in the *Macrocystis* clearings and the unsuccessful attempts to seed the *Macrocystis* patch with *Cystoseira*. It is likely that none of the material we used to seed *Cystoseira* was fertile. It seems evident from the data

in Fig. 12 that canopy influences the long-term survival of *Cystoseira*.

It is clear from these experiments that *Laminaria* and *Cystoseira* dispersed more effectively than *Macrocystis* and *Pterygophora*. This was further demonstrated throughout this study by our field observations of relatively consistent recruitment of *Laminaria* and *Cystoseira*, which, however, usually did not survive to maturity. Though these species have a relatively high turnover rate (Tables 5 and 6), a few plants in *Laminaria/Cystoseira* patches survived throughout the study. Thus, they seem to be opportunistic species that, in the right conditions, are capable of relatively long survivorship. Indeed, the older plants had much tougher stipes, suggesting that a really complete demographic study would show different survivorship curves for young vs. old plants.

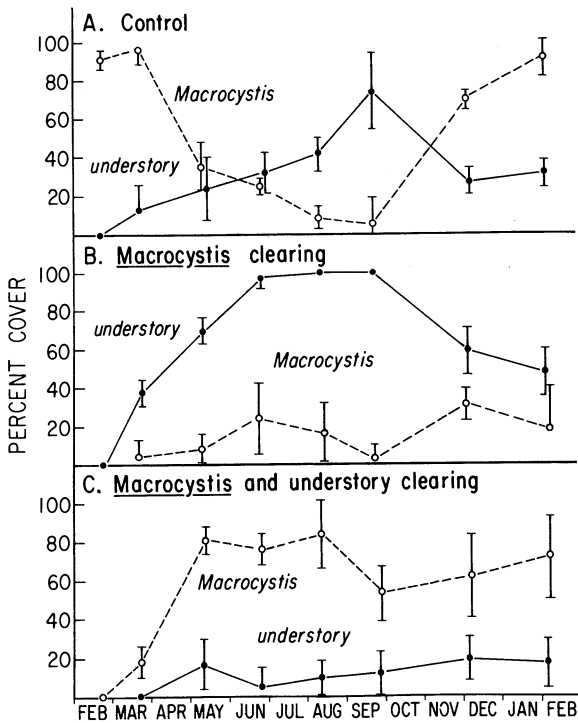


FIG. 13. Clearing experiments at Bird Rock, Santa Catalina Island, February 1971 through February 1972. Data are presented as means ( $\pm$  SD) of percent cover of *Macrocyctis* canopies and ephemeral understory canopies dominated by *Dictyota flabellata*, *Pachydictyon coriaceum*, and *Dictyopteris undulata*. Standard deviation calculated from arcsine-transformed data; depicted data have been back-transformed.

*Effects of turf on kelp recruitment.*—Two simple turf-cropping experiments were done at Pt. Loma in December 1974. First, a dense growth of *Gelidium robustum* interspersed with articulated coralline algae was cleared from two areas on top of Virgin Reef. Clearings and controls were adjacent to a large *Macrocyctis* plant. We subsequently identified 82 and 105 *Macrocyctis* recruits in the turf clearings and none in the controls. *Macrocyctis* survivorship in the clearings was not monitored, but 3 mo after recruits were counted, there were two robust *Macrocyctis* plants in each clearing. These four plants survived  $> 2$  yr before eventually being lost in winter storms.

Second, we cropped a turf of mostly *Calliarthron* spp. adjacent to a *Pterygophora* patch. Here, 49 *Pterygophora* and 17 *Laminaria* recruited to the 0.25-m<sup>2</sup> turf-cleared areas, and only 7 *Pterygophora* recruited to the control. The small recruits in the control disappeared within 1 wk, whereas one *Pterygophora* and seven *Laminaria* persisted well over 1 yr in the clearings; they and their apparent descendents were still alive through 1982.

The effects of various canopies on recruitment and survivorship of the algal turf species were not studied systematically, because the turf includes many taxa that we could not identify in the field. However, the dense

recruitment of small, fleshy red algae on the various experimental structures indicated that some species are effective dispersers. Similar observations of fast recruitment of unidentified coralline algae on artificial structures corroborated early findings of effective recruitment (Johanson and Austin 1970).

In summary, algal turf strongly inhibited recruitment of at least some kelps. Also, stipitates and *Macrocyctis* appeared to inhibit the formation of turf, which was very sparse under their canopies (Table 1).

#### Santa Catalina Island

*Effects of Macrocyctis canopy on Macrocyctis and understory.*—Our research at Bird Rock, Santa Catalina Island, focused on *Macrocyctis* survivorship. However, additional experiments on other canopy species showed the same general patterns observed at Pt. Loma. In one experiment, the *Macrocyctis* canopy was removed 15 February 1971 from an area 10  $\times$  10 m at a depth of 7–10 m and near the transects at Bird Rock. Six 1-m<sup>2</sup> permanent quadrats in the clearing were established; they and two large boulders in the clearing were mapped and photographed. Four 1-m<sup>2</sup> control quadrats were similarly monitored in an adjacent area. In two of the quadrats in the clearing, we removed the understory species on 24 March 1971. The luxuriant *Macrocyctis* occupied 85–100% of the canopy space of the control area in February. But it declined through the summer until it was almost gone. It recovered the next winter (Fig. 13A). Although we do not know the reason for the canopy dieback, it probably involved an increase in warm water and a reduction of nutrients.

In the *Macrocyctis* clearings, the understory, composed almost entirely of *Dictyota flabellata* and some *Pachydictyon coriaceum*, grew to relatively high abundances. The understory in the controls appeared to be released from light competition late in the summer when the natural canopy disappeared. On both boulders, there was immediate, very thick ( $> 100$  plants/m<sup>2</sup>) *Macrocyctis* recruitment; these individuals also died back during the summer. Unlike the *Macrocyctis* in the control, however, these *Macrocyctis* maintained high (50–80%) canopy cover, and the understory grew very little. This suggested that, in addition to the effect of *Macrocyctis* on understory growth, there was a reciprocal understory effect on *Macrocyctis* recruitment. There also were striking effects of both *Macrocyctis* and understory on *Macrocyctis* recruitment: 84 recruits/m<sup>2</sup> were counted in four *Macrocyctis*-cleared quadrats, but only two recruits were counted in the four control quadrats. In the two quadrats in which both the *Macrocyctis* and the understory canopies were removed, *Macrocyctis* recruitment was almost twice ( $> 150$  individuals/m<sup>2</sup>) that in *Macrocyctis* removal. A similar pattern occurred on the two boulders on which 206 plants were counted in a combined area of  $\approx 0.5$  m<sup>2</sup>. Heavy recruitment on the boulder tops was probably influenced by two factors. First, there was not much understory at the time of the overstory clearing; hence the *Ma*-

*crocystis* gametophytes were released from light competition in the same manner as those in the quadrats from which both canopies were removed. In addition, both the gametophytes and the young sporophytes were elevated off the bottom by at least 30 cm, which released them from the effects of scour, sedimentation, and other surface phenomena (Deviny and Volse 1978, and this paper).

*Effects of understory on Macrocyctis.*—In the early 1970s, the *Macrocyctis* population at Santa Catalina did not grow much below a depth of 15 m. The rocky substrata in the deeper areas had a thick growth of *Dictyota*, *Eisenia*, *Cystoseira*, *Laminaria*, *Agarum fimbriatum*, and *Sargassum muticum*. The hypothesis that at greater depths the understory inhibits the development of *Macrocyctis* was tested by using a series of clearings at two depth ranges: 15–18 m and 10–15 m. At a depth of between 15 and 17 m, a 5 × 5 m clearing of *Eisenia*, *Laminaria*, and *Agarum* was established 17 November 1972. Five permanent quadrats were monitored for *Macrocyctis* recruitment. By 2 February 1973, no recruits were seen. To test our hypothesis that the failure of recruitment resulted from restricted dispersal, we placed a small bag with fertile sporophylls in one of the quadrats. At the same time, two other understory clearings were established beside isolated mature *Macrocyctis* plants at depths of 15 and 18 m. By April 1973, there was a dense recruitment (>100 individuals/m<sup>2</sup>) of *Macrocyctis* in the canopy-cleared areas that had been inoculated or that were adjacent to fertile plants. No *Macrocyctis* recruited to any of the six quadrats in the uncleared controls, all of which had been “seeded.” *Macrocyctis* in the three cleared patches persisted at least through 1975, despite a fast recovery of the understory populations.

A 5 × 5 m area at a 13-m depth was cleared of *Macrocyctis* on 17 November 1972. Permanent quadrats were not established, but the sudden increase in cover of understory species noted previously (Fig. 13) also occurred here. Finally, in May 1975 clearings near the 10 and 15 m isobath transect lines were established and followed for ≈1 yr. Unquantified observations indicated that events followed a pattern very similar to that of the experiments presented in Fig. 13, except that the natural canopy dieback was less pronounced and the understory beneath the control did not escape as it had after the natural dieback of 1972. It is clear that both canopy competition for light and spore-dispersal limitation were important at Santa Catalina Island as well as at Pt. Loma.

In summary, overstory and understory relationships were similar at Pt. Loma and Bird Rock. Certainly, *Macrocyctis* suppressed the ephemeral understory (*Dictyota* and *Pachydictyon*). When both the ephemeral understory and the *Macrocyctis* canopies were removed, there was immediate strong *Macrocyctis* recruitment. Clearings of the long-lived understory kelp canopies (*Eisenia*, *Laminaria*, *Agarum*) returned to the preexisting complex unless the clearings were adjacent

to *Macrocyctis* or were seeded with *Macrocyctis*, in which case there was an extremely strong and persistent growth of *Macrocyctis*. This emphasized the importance of both understory competition and dispersal. (See Ambrose and Nelson [1982] for additional discussion.)

#### Pt. Piedras Blancas

*Interactions between Macrocyctis and Nereocystis.*—Our project in central California was too brief to obtain adequate survivorship data, but we did attempt to examine canopy relationships. Unlike southern California kelp communities, in which the floating canopy was composed almost entirely of *Macrocyctis pyrifera* (*Pelagophycus porra* was never sufficiently abundant to form a canopy), the kelp forest in central California had two species that formed surface canopies: *Macrocyctis pyrifera* and *Nereocystis luetkeana*. When attached to rocky substrata, both species could form extensive forest. Although mixed stands occasionally occurred, kelp beds were typically dominated by a single species. *Nereocystis* characteristically dominated shallower, more exposed localities, or localities with unstable cobble substrata. *Macrocyctis* dominated deeper, more protected localities, especially those with stable substrata. Unlike the perennial *Macrocyctis*, *Nereocystis* has an annual life cycle. From 1977 through 1979, in the vicinity of Pt. Piedras Blancas, dense surface canopies of *Macrocyctis* developed 1–2 mo earlier in spring than *Nereocystis* canopies did. In most cases, the fast recovery of *Macrocyctis* was associated with vegetative regrowth from extant holdfast systems rather than with recruitment of new sporophytes.

Because *Nereocystis* germination is known to be sensitive to light (Vadas 1972), we hypothesized that *Macrocyctis* is less sensitive and could competitively displace *Nereocystis*. We further suggested that *Nereocystis* could live in the *Macrocyctis* habitat were it not for the presence of *Macrocyctis*. To test the null hypothesis that *Nereocystis* cannot live in a *Macrocyctis* habitat, we cleared all *Macrocyctis* from two large (10 × 40 m) areas in a forest of *Macrocyctis* at Site A (October 1976) and Site X (December 1977) (Fig. 1). To ensure that spores of *Nereocystis* dispersed into the cleared areas, we nailed mesh bags containing dozens of *Nereocystis* sori to the bottom of the areas. Site A was at a depth of 5–18 m; Site X was 10–18 m deep. The control for both, situated between the two cleared areas at a depth of 11 m under an undisturbed canopy of *Macrocyctis*, was inoculated in a similar manner. The cleared area at Site A and the control area were first “seeded” in October 1977. Subsequent “seedings” were performed in the cleared areas at Sites A and X and in the control area in February and April 1978. We periodically removed recruiting *Macrocyctis* from the cleared area at Site A, but not from that at Site X.

By the spring of 1977, more *Nereocystis* plants had appeared in the cleared area at Site A than in the control area (31 vs. 0). The number of *Nereocystis* plants in

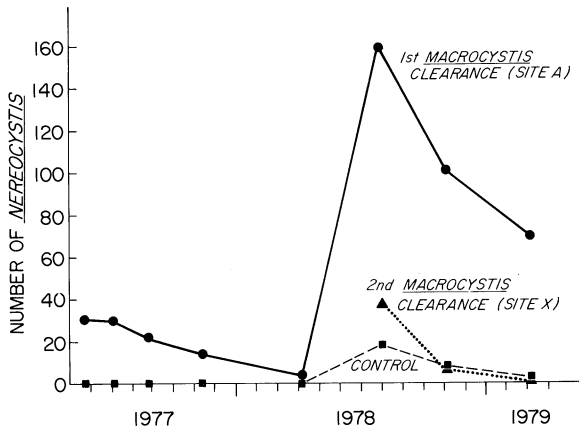


FIG. 14. Recruitment of *Nereocystis luetkeana* into areas cleared of *Macrocystis* adults at Pt. Piedras Blancas. Size of each clearance area was  $\approx 400 \text{ m}^2$ .

the cleared area declined steadily during 1977 (Fig. 14). The storms during the winter of 1977–1978 were particularly severe. Large swells opened gaps in the *Macrocystis* canopies at our study areas, and the formation of surface canopies of *Macrocystis* and *Nereocystis* was  $\approx 2$  mo later in 1978 than in 1977. By August 1978, 158 *Nereocystis* had grown in the cleared area at Site A, 73 had appeared in the cleared area at Site X, and 18 had grown in the control area, which had been thinned of *Macrocystis* by the storms. In the cleared area at Site X, where recruiting *Macrocystis* were not periodically removed, *Macrocystis* formed a surface canopy and significantly outnumbered *Nereocystis* by November 1978 (55 vs. 7). By March 1979, no *Nereocystis* remained in the cleared area at Site X but 52 *Macrocystis* that had overwintered dominated the canopy. Similarly, only two *Nereocystis* had overwintered in the control area, and new growth of *Macrocystis* quickly closed the gaps in the surface canopy.

These experiments indicated that *Nereocystis* could live in *Macrocystis* habitat, because *Nereocystis* lived and reproduced there after *Macrocystis* had been removed. But *Macrocystis* quickly recovered in the removal experiment at Site X. Thus, *Macrocystis* had a considerable resilience in its ability to recover from a local perturbation such as our removal experiment. Because the two experiments and the common control were at slightly different depths, potential depth specializations of the two species remain as alternate explanations.

**Effects of *Macrocystis* canopy on *Macrocystis* recruitment.**—*Macrocystis* recruitment was evaluated in the cleared areas at Site A, where the recruiting *Macrocystis* were continually removed, and at Site X, where they were not removed. At Site X, *Macrocystis* replaced *Nereocystis* as the surface canopy in only one season (1977–1978). *Macrocystis* was continually removed from Site A, but *Macrocystis* recruits were not removed from the two  $9\text{-m}^2$  subplots at depths of 10 and 18 m

that were established in April 1977. A third  $9\text{-m}^2$  plot was established at a depth of 11 m as a control area. The results of periodic counts of kelps in nine contiguous  $1\text{-m}^2$  quadrats within each of the three plots are presented in Fig. 15.

Recruitment of *Macrocystis* was significantly greater in the 10-m deep cleared plot than in the control plot from May 1977 until June 1978 (Fig. 15A). Winter storms opened a gap in the *Macrocystis* canopy directly above the control plot, and by August 1978 there were significantly more *Macrocystis* in the control plot than in the deep cleared plot. However, all plants in the control plot were shorter than 0.5 m, whereas most *Macrocystis* in the shallow clearance plot were tall enough to form a surface canopy. Through March 1979, abundance of *Macrocystis* was similar in cleared and control plots, but a surface canopy did not develop in the control plot. Initially, there were significantly more *Macrocystis* recruits in the deep (18 m) cleared plot than in the control plot (11 m). A sparse surface canopy

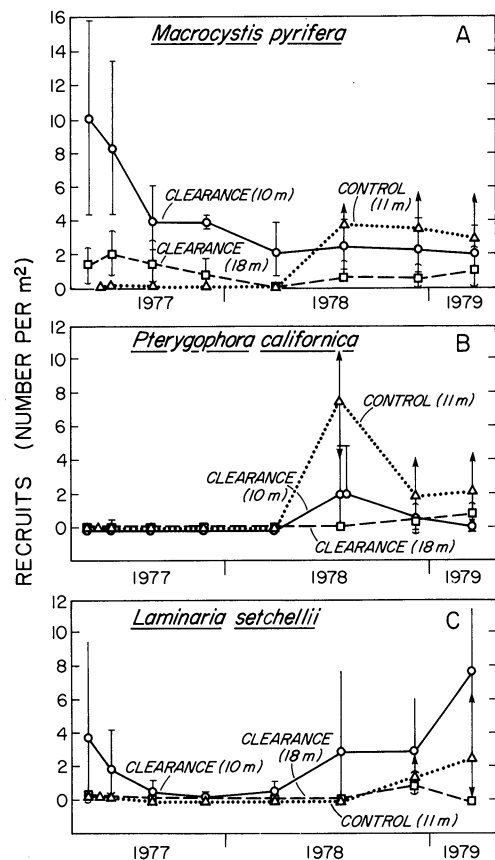


FIG. 15. Effects of *Macrocystis* canopy clearance on *Macrocystis*, *Pterygophora*, and *Laminaria setchellii* recruitment at Pt. Piedras Blancas. Depth of treatments is indicated in parentheses. Data are presented as mean densities of kelps, with 95% CI ( $n = 9$  quadrats); statistics calculated with square-root-transformed data. Depicted data have been back-transformed. Recently recruited *Macrocystis*  $< 0.5$  m tall not included.

developed from the deep cleared plot during the summer of 1977. By November 1977, numbers of *Macrocystis* were similar in deep cleared and control plots. This pattern persisted until the summer of 1978, when a "bloom" of *Macrocystis* developed in the control plot, probably in response to the severe storms of the preceding winter. During 1978 there were significantly more *Macrocystis* recruits in the control than in the deep cleared plot, but by March 1979 this difference was not significant. Recruitment of *Macrocystis* was significantly greater in the shallow (10 m) cleared plot than in the deep (18 m) cleared plot during 1977, but by the summer of 1978, numbers were no longer significantly different. A surface canopy had developed in the shallow plot, but had not developed in the deep plot during 1978. *Nereocystis* did not appear in any of the 9-m<sup>2</sup> plots, although several plants grew adjacent to the shallow cleared plot and the control plot.

Hence, the *Macrocystis* canopy had density-dependent effects on kelp recruitment, but the effects were strongly influenced by the seasonal reduction in canopy resulting from winter storms. In most instances, the storms did not dislodge the *Macrocystis* holdfasts, and the canopies recovered rapidly from these holdfasts.

**Resistance of *Macrocystis* to invasion of understory species.**—The *Macrocystis* removal experiments showed little effect on *Pterygophora* recruitment (Fig. 15B), but there was an initial pulse of *Laminaria setchellii* (a stipitate species similar to *Pterygophora*) recruits in the shallow cleared plot (Fig. 15C). However, by August 1977, *L. setchellii* densities were not significantly different among the three plots. This pattern persisted until the spring of 1978, when recruits of *L. setchellii* were again abundant in the 10-m depth cleared plot and in the control plot. By December 1978, differences in numbers were no longer significant. Following additional recruitment in the 10-m depth cleared plot and the control plot, density differences among the plots became significant in March 1979. There were no differences between the 18-m depth cleared plot and the 11-m depth control plot until late 1979.

The severe storms during the winter of 1977–1978 eliminated the canopy over the control plot and effectively produced another cleared area; nevertheless, some trends were apparent. In all of the *Macrocystis*-removal experiments, there was a marked bloom of *Desmarestia* spp. (see also Cowen et al. 1982). In shallow water, the floating *Macrocystis* canopy had a pronounced and negative effect on the recruitment and survival of *Macrocystis*. Deeper water *Macrocystis* did not develop a surface canopy during our experiments. Indeed, a consistent feature of the experiments was that the recruitment of all species was low (Figs. 14 and 15). The initial pulse of *Laminaria setchellii* in the shallow plot appeared to be eliminated by the developing *Macrocystis* canopy, but *L. setchellii* recruited and grew in the shallow plot after the storms. It seems likely that the *Pterygophora* and the *L. setchellii* were also influenced by vagaries of dispersal. *Nereocystis* seemed sensitive to

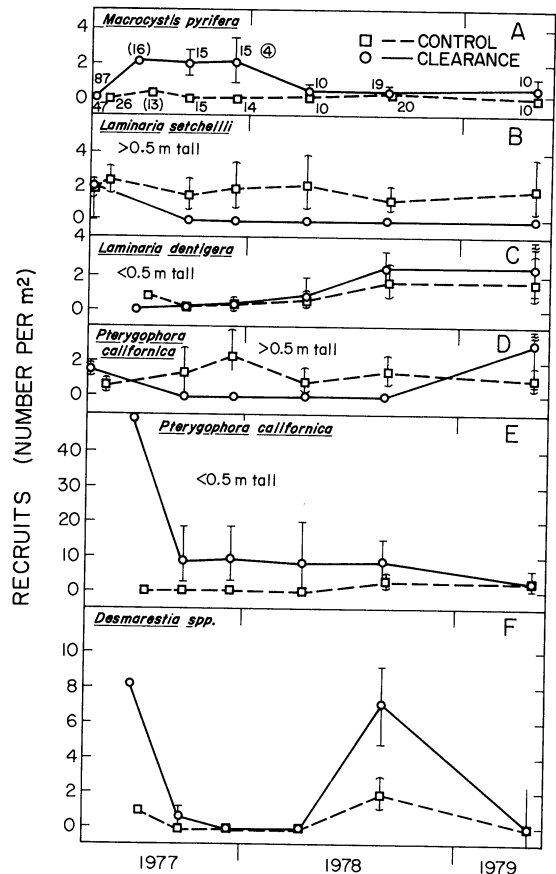


FIG. 16. Effects of removal of stipitate canopy (mostly *Pterygophora* with scattered *Laminaria setchellii*) at Site D, Pt. Piedras Blancas. Data are mean densities of kelp individuals in clearance and control plots with 95% confidence intervals; statistics calculated using the square root transformation. Sample sizes, given in part A, are the numbers of m<sup>2</sup> quadrats sampled on each date except those in parentheses, which were ¼ m<sup>2</sup> adjusted to m<sup>2</sup>.

the light reduction associated with canopies (Vadas 1968, 1972), because none recruited in these experiments.

In summary, understory species responded remarkably quickly to storm-caused disturbance in the *Macrocystis* canopy. However, in areas where *Macrocystis* persisted, it had a dominating effect on associated kelp species. In its presence, the understory species relied on a strategy of opportunism, which was more successful in the more frequently disturbed shallow water.

**Resistance of stipitate canopies to invasion.**—Dense mixed groves of the stipitate understory kelps *Laminaria setchellii* and *Pterygophora californica* typically occurred immediately adjacent to the shallow margins of *Macrocystis*. By removing all *L. dentigera* and *Pterygophora* from an area of ≈100 m<sup>2</sup> in April 1977, we tested the hypothesis that their canopy inhibits *Macrocystis* recruitment. Since there were no *Macrocystis* within 20 m of this area, we "seeded" the clearing and the control area. Significantly greater numbers of *Ma-*

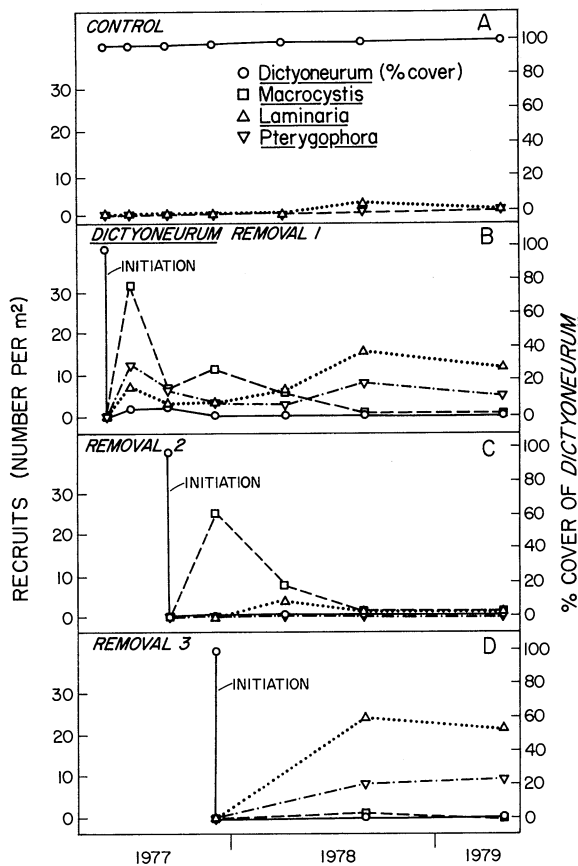


FIG. 17. Effects of removal of *Dictyoneurum californicum* canopies at Site D, Pt. Piedras Blancas. Data are densities of kelp recruits in the control and pre-*Dictyoneurum* removals done in May, September, and December 1977. By May 1979 the clearing in C was dominated by the holdfast of one large *Macrocyctis*.

*crocyctis* recruited in the cleared area than in the control (Fig. 16A). By September 1977, 71% of these plants had grown to the surface. Most *Macrocyctis* disappeared in the winter storms of 1977–1978; thereafter, there was no difference in *Macrocyctis* density between cleared and control areas.

Understory removal was followed by a dense settlement of *Pterygophora* (Fig. 16E). With adequate light and nutrients, spores can settle, go through the gametophyte stage, and produce identifiable sporophytes within a month of the canopy removal (L. Deysher, *personal communication*). But in our study the experiment was initiated in the summer, when *Pterygophora* is relatively infertile. This bloom may thus have resulted from the presence of existing *Pterygophora* gametophytes or from small sporophytes that responded to the increase in light with the removal of the canopy. No such recruitment was seen in the control area (Fig. 16D and E); we thus rejected the null hypothesis that the stipitate understory has no effect on *Pterygophora* recruitment. By August 1978, the difference between *Pterygophora* abundance in cleared and control areas

was not significant, indicating that *Pterygophora* growth was fast. In May 1979, abundances of young *Pterygophora* in the two plots were indistinguishable. Many *Pterygophora* that had settled in the cleared area had grown taller than 0.5 m, and the abundance of *Pterygophora* >0.5 m was also not significantly different between cleared and control areas.

Densities of young *Laminaria* did not differ significantly between clearance and control areas during this 2-yr experiment. Recruitment of *Laminaria setchellii* was sparse during 1977, but increased during 1978 (Fig. 16C). None of the *L. setchellii* in the cleared area had grown taller than 0.5 m by May 1979, so there were significant differences in the abundance of larger *L. setchellii* between the cleared and control areas throughout this study. Dense *Desmarestia* blooms occurred in cleared areas during the summers (Fig. 16F). At these times there were significantly more plants in the cleared area, and we again rejected the null hypothesis of no *Pterygophora* effect. Several *Nereocystis* plants recruited in the cleared areas, although we did not enumerate them; none were seen in the controls.

Stipitate canopy species thus had a strong inhibitory effect on the recruitment of *Macrocyctis*, *Pterygophora*, *Desmarestia*, and *Nereocystis* (see Reed and Foster, *in press*). However, young *Macrocyctis* that recruited in Site D were eliminated by a winter storm; they did not reappear the next season. Although *Macrocyctis* is dominant over *Pterygophora* and *Laminaria setchellii* (Fig. 15), the latter stipitate species resisted invasion by *Macrocyctis* and *Nereocystis* especially in more wave-stressed habitats.

*Resistance of prostrate canopies to invasion.*—In a strict sense, the ephemeral *Desmarestia ligulata* forms a prostrate canopy (Cowen et al. 1982). But beyond studying the effects that overstories exert on *Desmarestia*, we did not investigate *Desmarestia*'s role per se. However, we did study *Dictyoneurum californicum*, which appears to be a relatively long-lived rhizomatous kelp often forming a dense prostrate canopy similar to that of *Laminaria farlowii* at Pt. Loma. These patches appeared to be resistant to invasion by other algae. To test the null hypothesis of no *Dictyoneurum* effect, we removed *Dictyoneurum* by hand in patches  $\approx 1$  m<sup>2</sup> in area in May, September, and December 1977; we left a neighboring 1-m<sup>2</sup> patch as a control. We did not "seed" these areas.

The *Dictyoneurum* removal in May (Fig. 17B) was followed by a rapid, dense recruitment of *Macrocyctis*, *Pterygophora*, and *L. setchellii*. The *Macrocyctis* density declined; densities of the understory kelps declined somewhat, and then increased during 1978. By the final census (May 1979), this plot was dominated by *L. setchellii* and *Pterygophora*; there were no *Macrocyctis*. The removal in September (Fig. 17C) was followed by a dense recruitment of *Macrocyctis*; recruitment of understory kelps was sparse. By May 1979, this plot was dominated by one large *Macrocyctis* plant. This seasonal difference probably related to the fact that

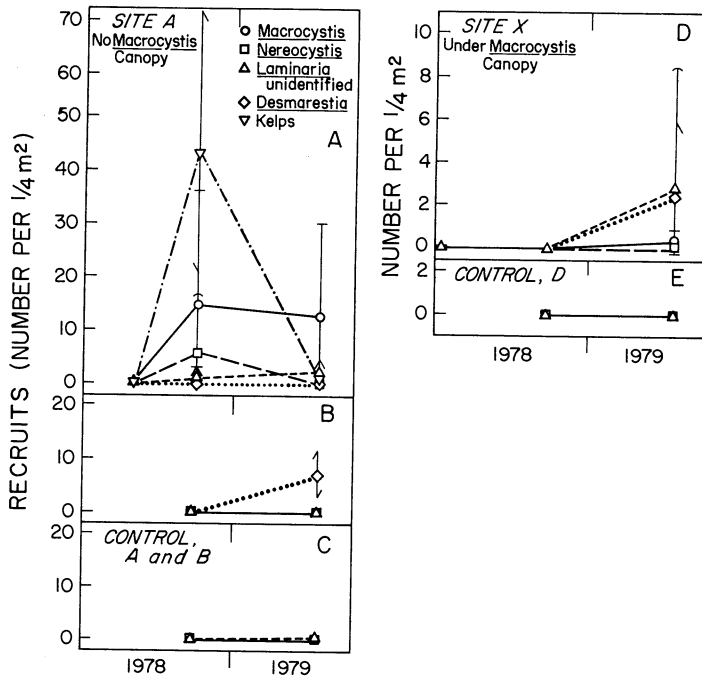


FIG. 18. Resistance of articulated coralline algal turf to invasion by brown algae at Sites A and X, Pt. Piedras Blancas. Data are mean densities of kelps recruiting into quadrats cleared of turf algae in August (A), November (B), and June (D) 1978. There was no recruitment into control quadrats (C [for A and B] and E [for D]). Vertical lines are 95% confidence intervals in A and D calculated from square root transformations ( $n = 8$  quadrats) and ranges in B ( $n = 4$  quadrats).

*Macrocyctis* remained fertile during the summer, while the other kelps released their spores in the winter. We did not census the December removal (Fig. 17D) until September 1978; at this time the plot was dominated by *L. setchellii* and *Pterygophora*; this pattern persisted through May 1979. The control area (Fig. 17A) experienced virtually no recruitment by any of these kelps. Thus, *Macrocyctis*, *L. setchellii*, and *Pterygophora* were capable of replacing *Dictyoneurum* only after *Dictyoneurum* was removed.

In summary, *Dictyoneurum* was very resistant to invasion. There were at least two potential mechanisms of *Dictyoneurum* resistance. First, this alga densely shaded the substratum. Second, the large, tough fronds may have scoured the other algae from the substratum via whiplash. However, scour from the adjacent fronds did not eliminate recruitment in the relatively small clearings. Although it was resistant, *Dictyoneurum* was not resilient over the duration of these experiments: there was no sign of its own recruitment into these cleared areas. However, with more time this alga will probably grow vegetatively into and recover the clearings.

*Resistance of articulated coralline red algal turf to invasion.* — Articulated coralline red algae formed a thick ( $\approx 10$  cm) dense turf over extensive areas of shallow ( $\leq 6$  m deep) reef tops. To test the hypothesis that the intact turf was resistant to invasion by kelps, in June 1978 we scraped articulated coralline red algae from two large patches at the edge of Site X, and in August

1978 we scraped two large patches in Site A. In each of these clearings four  $\frac{1}{4}$ -m<sup>2</sup> quadrats were established. In November 1978 four more  $\frac{1}{4}$ -m<sup>2</sup> clearings were established in Site A (Fig. 18B). Site A had no *Macrocyctis* and a very sparse *Nereocystis* canopy; Site X had a dense *Macrocyctis* canopy. These clearances and the adjacent undisturbed control plots were periodically censused by counting kelps.

The clearances of coralline algae at Site A resulted in a "bloom" of kelps (Fig. 18A). By May 1979 these plots were dominated by *Macrocyctis*. Kelps did not recruit after the June clearances at the edge of Site X (*Macrocyctis* canopy) until after November 1978. By May 1979, these plots were dominated by *Laminaria setchellii* and *Desmarestia* spp. (Fig. 18D). Thus, it appeared that when space was made available in the underlying articulated coralline red algal turf the presence of a *Macrocyctis* canopy had an important influence on recruitment by kelps. The timing of the initiation of the turf clearances also affected recruitment by kelps: November clearances (Fig. 18B) were dominated by *Desmarestia* in Site A and in the June clearing in Site X, both of which had no recruitment until after November 1978. There was no kelp recruitment in control plots. In addition, there was an explosive growth of red algae in the turf-cleared areas but not in the controls. The growth of red algae was not affected by the *Macrocyctis* canopy, since the response was identical in Sites A and X.

It is evident that articulated coralline turf was also



TABLE 7. Densities of attached *Macrocystis* and ratio of drifters (entangled clumps of unattached kelps) to attached plants at three isobaths at Pt. Loma. Each summary represents a survey area of 1000–1500 m<sup>2</sup>.

Year	Season	Inner (10 m)		Central (15 m)		Outer (18–20 m)	
		Density (attached plants/m <sup>2</sup> )	Drifters/attached	Density (attached plants/m <sup>2</sup> )	Drifters/attached	Density (attached plants/m <sup>2</sup> )	Drifters/attached
1974	Summer	1.00	0.00	0.85	0.03	0.06	0.02
	Fall	0.43	0.003	0.536	0.02	0.05	0.10
	Winter	0.31	0.002	0.21	0.04	0.07	0.08
1975	Spring	0.37	0.013	0.26	0.07	0.04	0.09
	Summer	0.29	0.009	0.19	0.02	0.08	0.03
	Fall	0.24	0.047	0.22	0.01	0.04	0.01
1976	Winter			0.11	0.009	0.08	0.08
	Spring	0.10	0	0.10	0.18	0.11	0.05
	Summer	0.04	0	0.10	0.04	0.12	0.02
	Fall	0	0	0.48	0.01	0.09	0.03
1977	Winter					0.16	0.02
	Spring			0.12	0.008	0.12	0.02
	Summer	1.45	0.0009	0.28	0.01	0.09	0
	Fall	0.953	0.001	0.74	0.04		

very resistant to invasion because there was a heavy kelp recruitment to clearings in the coralline turf but almost never to the turf itself. The abundance and composition of these recruiting kelps were strongly affected by season and the presence of an overstory canopy. These experiments were too brief to indicate the eventual outcome of perturbations or the mechanisms of coralline resistance. Mechanisms may have included shading, chemical defenses of the corallines, and herbivory by small animals in the turf. Also unresolved in this experiment was the issue of turf resilience, but work elsewhere (Pt. Loma in this paper; Johanson and Austin 1970) suggests that there is a strong *Calliarthron* recruitment in cleared areas, indicating the potential of strong resilience.

#### RESULTS: INERTIA (RESISTANCE TO DISTURBANCE)

A study of resistance stability should include quantification of both the effects of disturbance on survivorship and the resistance of the populations to these disturbances. At Pt. Loma the most important sources of mortality for adult plants and of disruption of patch structure are storms that dislodge *Macrocystis* plants. On occasion, grazing by sea urchins is also a very important disturbance. These disturbances and their consequences were studied at Pt. Loma. We have no relevant data from Santa Catalina Island, but we present some short-term observations and experiments from Pt. Piedras Blancas that again emphasize the importance of storms.

#### Pt. Loma

*Storms and drift algae.*—Almost all the mortality of adult *Macrocystis* in the areas 15 and 18 m deep resulted from entanglements with drifting *Macrocystis*. This corroborated our earlier Del Mar study (Rosenthal et al. 1974); it has become clear that entanglement

is both an important general disturbance phenomenon and an important means of dispersing spores. Our data for seasonal mortality patterns in the outer, central, and inner areas of the kelp forest (Table 7) indicated that the densities of attached plants decreased from shallow to deep areas; the shallow area also had proportionally fewer drifters. The densities of attached plants at depths of 10 and 15 m declined with time, reflecting the survivorship of the dense 1973 recruitment (Fig. 4B). The 1977 recruitment at 10 m (Fig. 4A) is also seen in Table 7. Mortality resulted more from the mutual entanglement of attached plants rather than from entanglement with drifters or from herbivore. The reason for the lower proportion of drifters in the shallow area is that the holdfast bundles of these young plants were small enough that the plants floated to the surface after pulling free, thus eliminating the probability of damaging stipe entanglement. This was demonstrated by our efforts to create drifters by prying holdfasts off the substratum; in the shallow zone the young plants floated immediately to the surface, but in deeper water the larger holdfasts of the plants bounced along the bottom and eventually became entangled with attached plants.

Most new drifters appeared after storms in the winter and spring detached the plants. These detached plants became entangled in others, which then often became dislodged, contributing to the "snowball effect" as the drifter picked up more plants. The average number of detached plants in each drifter was 4.7 (range: 1–19). In the studied areas at 15- and 18-m depths, the mean number of attached plants entangled by a drifter was 1.8 (range: 0–7). Otherwise, there was no pattern in year, season, or depth.

To test whether older, possibly senescent, and relatively postreproductive plants were more likely to become drifters or to suffer mortality from entanglements, we derived a rough estimate of a plant's age

from the volume of the holdfast bundle. We measured >100 drifters in each area; except for a slight tendency for the drifters to be older, there was no significant difference.

How long does a drifter persist? What is the turnover rate of the plants within a drifter? The life expectancy of a drifter is clearly very important to the population of potential victims. Furthermore, drifting plants themselves lose stipes with each encounter, and holdfasts drop out of the drifters. It is not unusual to see unattached, stipeless holdfasts bouncing around the bottom. Because of vandalism on surface tags, we had to use subsurface tags to mark drifters. The plants then had to be located from shore coordinates and lengthy underwater searches. This was inefficient, and most plants were lost before they disintegrated. Minimum longevity estimates of drifters range up to 18 mo (Table 8). Because the plants had already been adrift for an unknown length of time when they were tagged, and because plants were usually lost before they disintegrated, we have no measure of maximum longevity. We attempted a direct measure of longevity by prying plants loose from the substrata, but all but two were lost. In these, the tagged holdfasts broke free of the drifters 10 and 11 mo after they had been pried loose. In each case the drifters had had four recent victims, and each seemed likely to continue drifting and entangling for many months. None of the holdfasts of preexisting drifters survived more than 7 mo, suggesting a relatively fast turnover of plants within a drifter. While we saw the disintegration of only one drifter, many were in the process of disintegrating in the late summer, when surge is reduced, entanglements are few, and the surface canopy of the drifter weakens in the warm, probably nutrient-depleted waters. Under these conditions the stipes become brittle and senescent, and eventually the holdfast mass breaks free and sinks.

How many plants does a drifter encounter and entwine? Of these, how many die because of the encounter? Of the 447 plants encountered by 35 drifters, 57% became detached (Table 8). Most encounters fouled over 75% of the stipes of the attached plants; usually, all of the entangled stipes were broken. When the entanglements occurred within 5 m of the bottom, they were usually lethal. The attached plants that survived were usually entangled in the upper 5–10 m of the canopy, leaving many young stipes below the entanglement. The plants most likely to be pulled free usually were younger than 2 yr and still had poorly developed holdfast systems, or were older than 4 yr and had holdfast bundles that had decomposed in the central region and were attached only by the outer haptera. The plants 2–4 yr old had robust holdfasts and usually died only if all or most of their stipes were broken. So entanglements effectively cull young and old plants. Our mortality estimate (Table 8) is conservative because, although every encounter cost the attached plants several and sometimes most of their stipes, encounters were considered mortalities only if all of the stipes of a plant

TABLE 8. Longevity of drifters and total numbers of plants encountered and killed by each during observation period. Each estimate is very conservative, as the drifters were lost before they disintegrated.

Area	Drifter	Time observed (mo)	Total number plants encountered	Number of plants killed by encounter
10-m site	M	2	3	3
	18	1	1	0
	II	3	5	2
15-m site	BB	16	25	15
	GG	10	8	4
	HH	6	6	3
	MM	3	13	3
	LL	2	6	1
	ZZ	13	9	6
	QQ	6	10	2
	V	12	13	12
	W	8	7	6
	G	8	8	7
	H	10	22	12
	R	10	19	11
	U	6	14	7
	KK	8	15	12
	K	14	21	11
	T	9	36	21
	33	4	5	2
	DD	3	10	8
I	4	11	10	
J	4	11	10	
L	3	15	3	
P	4	9	1	
S	6	16	8	
W	3	11	2	
EE	3	5	4	
18-m site	D	18	24	18
	G	5	15	8
	S	2	2	0
	B	4	8	4
	C	10	25	15
	CC	11	25	16
	AA	7	12	10

were broken. Because holdfasts bereft of their stipes commonly survive at Pt. Piedras Blancas, we followed 50 Pt. Loma holdfasts that had lost their stipes from entanglements or experimental cutting, and found that even holdfasts with luxuriant sporophyll bundles and young stipes all died. We later observed plants that had been entangled with drifters but had not lost all of their stipes (hence had been considered survivors) and found that they were also dead. Thus, the 43% survivorship estimate (Table 8) is very optimistic, since many of the entangled plants died later.

In summary, drifting *Macrocystis* encountered a mean of 2.14 (SD 1.0) plants/mo and killed a mean of 1.24 plants/mo. The deeper area had the higher percent mortality per encounter (65% at 18 m; 56% at 15 m), perhaps reflecting the fact that the deeper plants were older and more vulnerable. Both areas had a mean of 1.3 plants killed per drifter per month. It is risky to extrapolate this to an annual mortality rate, but a rough estimate of 0.15 mortalities per drifter per year applied to the relative densities in the 15 and 18 m areas (Table

7) suggests that drifters kill  $\approx 50\%$  of the adult population each year. Despite the crudeness of the estimate, drifters are clearly a major source of *Macrocystis* mortality in the outer Pt. Loma kelp forest.

*Sea urchin grazing.*—Echinoids are well known to have the potential of overgrazing and destroying algal communities (see Lawrence [1975] for a general review; North [1971] and Leighton [1966] for a review of southern California kelp beds). Thus, we expected sea urchins to have a major role in disturbance in this community. We found, however, that, with the exceptions of our 10–12 m area and occasional “plague” (see North 1971) areas, sea urchin grazing was not a major disturbance despite the fact that sea urchins have the potential of killing *Macrocystis* plants by grazing on holdfasts or eating through the primary stipes. Two species of sea urchins, *Strongylocentrotus purpuratus* and *S. franciscanus*, have been the most destructive grazers at Pt. Loma (North 1971, Tegner 1980). *S. purpuratus* is relatively sedentary and, under normal conditions, remains cryptic and eats drift algae. *S. franciscanus* is much larger and more active, and forages nocturnally from refuges such as ledges. On occasion, the sea floor is covered with high densities of both species, and in these (“plague”) situations the urchins are much more active and destructive.

As demonstrated in the Caribbean for fishes (Randall 1965) and *Diadema* (Ogden et al. 1973), and at Santa Catalina Island for *Centrostephanus* (Nelson and Vance 1979), herbivores can maintain bare zones around their refuges. This is common in the Pt. Loma kelp community, where areas in front of ledges and devoid of fleshy kelps offer urchins refuges from predation (Tegner and Dayton 1977, 1981). Boulder fields have high urchin densities and tend to be barren of fleshy algae. *Balanophyllia elegans*, a solitary cup coral, seems especially common in these bare zones (Gerrodette 1981).

In December 1972, we tested the hypothesis that these bare zones are mediated by the grazing of *S. franciscanus* by removing the urchins from two 1-m<sup>2</sup> areas of a small ledge and from a 4-m<sup>2</sup> area in a boulder field. In each case, the area was quickly colonized by 100% covers of *Dictyota flabellata* and *Desmarestia ligulata*. By the spring of 1973, the quadrats in front of the ledges were dominated by *Calliarthron* and *Laminaria farlowii* (25 and 37 recruits/m<sup>2</sup>, respectively) and by scattered *Cystoseira*. Boulders were covered with *Calliarthron* and *Gelidium*, and three *Eisenia* plants were present. Control areas maintained their urchin populations. By 1975, the urchin populations had recovered, and most areas had only coralline pavement. *Balanophyllia* seemed partially dependent on the urchin grazing in the flat, bare zone in front of the ledges, because their populations declined in both ledge areas where urchins were removed (from 117 to 14 corals/m<sup>2</sup> and from 207 to 5 corals/m<sup>2</sup>), whereas the control quadrats remained relatively constant (from 143 to 129 corals/m<sup>2</sup> and from 79 to 85 corals/m<sup>2</sup>). Tegner and Dayton (1981) argued that urchins are usu-

ally confined to these refuge areas by predation by asteroids (*Pycnopodia helianthoides*, *Dermasterias imbricata*), spiny lobsters (*Panulirus interruptus*), and especially the California sheephead (*Semicossyphus pulcher*).

The heavy *Macrocystis* recruitment in 1973 produced a dense growth in the 10-m site, which was thinned by mutual entanglement to 1.0 adult plants/m<sup>2</sup> by 1974 (Fig. 4A). During the summer of 1974, urchin grazing on the small holdfasts of the young plants became very conspicuous, and by December 1975 the *Macrocystis* population had been eliminated in this area. At least 75% of the mortality resulted from urchin grazing (M. Tegner, personal communication). No measures were taken to control urchins. In late 1976 and early 1977, another massive *Macrocystis* recruitment resulted in another dense forest (1.3 adults/m<sup>2</sup>) that was virtually eliminated by urchin grazing in late 1978. This pattern was observed only in the shoreward edge of the *Macrocystis* forest. It is similar to the pattern observed in Nova Scotia (Mann 1977).

In isolated areas throughout the kelp bed, a similar phenomenon occurs: a large urchin population develops, urchin mobility increases, and “fronts” of urchins move outward, consuming all the kelp plants they encounter. In the past, a commercial kelp harvesting company controlled the urchins with quicklime (North 1971).

#### *Santa Catalina Island*

The Bird Rock site at Santa Catalina Island was periodically subjected to winter storms. However, we did not quantify their impact. Indeed, the relatively small size of the kelp forest argued against drifters having an effect similar to that seen at Pt. Loma, since drifters would leave the forest before doing much damage. Summer canopy diebacks, which appeared to result from warm water and low nutrients, were the main effect of physical stress that we observed at Bird Rock. The sea urchin *Strongylocentrotus franciscanus* was replaced on the protected northeastern side of the island by the more tropical *Centrostephanus coronatus*. Neither *Centrostephanus* nor *S. purpuratus* seemed to exert an important effect on *Macrocystis* at Bird Rock (Nelson and Vance 1979).

#### *Pt. Piedras Blancas*

Frequent strong surge and devastating winter storms were probably the most important sources of kelp mortality along the central California coastline. In areas of cobble or unstable substrata, there may have been an almost complete mortality of kelp plants during the winters. Such an area immediately north of Piedras Blancas was dominated by the annual *Nereocystis*; after one severe winter storm, windrows of *Nereocystis* washed ashore  $\approx 200$  m and crossed the heavily traveled Highway 1 (Big Sur Highway). Two drifters of *Nereocystis* that were washed onto the beach contained at least 59 and 128 plants; the *Nereocystis* holdfasts

were mostly attached to cobbles that had been uplifted and carried ashore. These storms seemed to break the stipes on mature *Macrocystis* attached to the stable reef substrata; in contrast, storms at Pt. Loma dislodged holdfasts. These different effects are important since the plants at Pt. Piedras Blancas quickly regrew new stipes in the spring. Physical stress dominated this habitat. Grazing stress was minimal because sea urchins existed only in refuges from sea otters (*Enhydra lutris*) (Lowry and Pearse 1973).

In summary, several types of disturbance and stress were important to California kelp communities. Storm-generated surge and waves were directly responsible for much mortality and stipe loss at Pt. Piedras Blancas, where storms are an important annual event. While we have very few data on storm-generated plant loss at the protected Santa Catalina Island site, we have seen there an occasional heavy mortality following winter storms. At Pt. Loma, storms did dislodge plants, but the dislodged plants often persisted, entangling and dislodging many other plants. This entanglement mortality was very important, as it had the potential of killing a large fraction of the adult *Macrocystis*. Sea urchin grazing in this area could be an important mortality source to macroalgae, but the effects of sea urchins in central California were mitigated by various predators, especially sea otters. Hence, sea urchins maintained coralline barrens as they grazed out from refuges. At Pt. Loma, they occasionally numerically swamped their predators and eventually destroyed most macroalgae in a limited area. There are sites at Pt. Piedras Blancas where wave stress seemed to select for lower canopies, the floating < stipitate < prostrate < turf canopies constituting a hierarchy of resistance to surge.

#### RESULTS: A SUMMARY OF PATCH INERTIA STABILITY

We observed that distinct patches persisted beyond the life expectancy of their component individuals, and we tested several mechanistic hypotheses regarding this resistance to invasion. The hypothesis that in most habitats patch types are maintained by local physical characteristics tolerable to locally existing species but not to others was negated by the successful recruitment of various species following removal of the preexisting plants.

A related hypothesis that a patch persists because there has been insufficient time for dispersal to adjacent patches was at least in part negated by the persistence of the edges of the patches, where dispersal was not limiting. However, the crux of this hypothesis involves the dispersability of the potential invaders, and we found that in most cases recruitment was much enhanced by seedlings which suggests that effective dispersal may still have been an important limiting factor. Finally, fast turnover times and reproductive potentials that were high relative to patch persistence tended

to negate the hypothesis that life-history characteristics alone determine the patch composition.

Several types of disturbances were important to kelp populations. In southern California, storms caused a gradient of disturbed areas of *Macrocystis*, ranging from the "scars" of single holdfasts that were usually recolonized by spores left from the detached plant to cleared areas as large as several hectares that resulted from massive entanglements after unusually severe storms. Similar entanglement mortalities of the annual *Nereocystis* occurred in central California. But while Pt. Piedras Blancas *Macrocystis* often lost most of their stipes, their holdfasts seemed more strongly attached; we never observed drifting clumps of *Macrocystis* at Pt. Piedras Blancas. The stipitate plants were occasionally dislodged by storms, but at both Pt. Loma and Pt. Piedras Blancas they seemed resistant to surge. The "storm related" mortalities usually resulted from plants' losing their fronds or being knocked over far enough that a sea urchin could catch their fronds. The prostrate and turf canopies seemed to thrive in rough water and were never observed to be affected by storms.

Temperature and nutrient stresses are known to be important to *Macrocystis* canopies in southern California (North 1971, Jackson 1977). We frequently observed canopy diebacks in summer and early fall. But usually the *Macrocystis* plants themselves did not die, because fends below the thermocline were not affected. We saw no evidence that temperature or nutrient stresses affected the other canopy types. In the Los Angeles area there have been large-scale recoveries of kelp beds following improved sewage treatment (Wilson et al. 1980). The devastating effects of sea urchin grazing seen in other habitats occurred also in the shallow area at Pt. Loma and in patches elsewhere at Pt. Loma. In most cases the sea urchin populations are controlled by several predators (Tegner and Dayton 1981).

Thus, through canopy competition and the swamping of the recruitment of potential invaders by extremely heavy and localized spore releases of the resident plants, most kelp patches successfully resisted invasion. Disturbances were ubiquitous and had potentially important consequences, but their impacts were variable in time and space. For these reasons, it is important to understand successional processes that result in patch resilience.

#### RESULTS: PATCH RESILIENCE

##### *Description and mechanisms of succession*

Successional processes in this system were determined by studying seasonality of disturbance and plant reproduction, dispersal, survivorship of recruits, and competition. These parameters are discussed for Pt. Loma and Pt. Piedras Blancas.

*Role of season in the availability of space and spores.*—Seasonality of algal recruitment has pro-

nounced effects on the structure of most algal communities (Northcraft 1948, Lee 1965, Vadas 1968, Dayton 1971, 1975a, Kain 1979). In southern California kelp communities, there were two separate aspects to seasonality: provision of suitable space, and seasonality of spore releases and gametophytic development.

As discussed earlier, most of the mortality of the Pt. Loma kelps occurred from winter storms that resulted in two types of spatial clearings in *Macrocystis* patches. In one type, large canopy areas were cleared of many *Macrocystis* plants by storms; subsequent recruitment largely depended on factors present before the clearings, especially on the proximity of adults and the dispersability of spores. In the second type, large solitary holdfasts broke loose, leaving conspicuous scars and resulting in a spatial mosaic. In the second type, algal recruitment depended on spore availability, which has a seasonal component; but in most cases the plant that broke loose inundated the clearing with spores.

There are two ways to monitor seasonality of spore release. Probably the most satisfactory approach is to monitor the reproductive condition of individual plants. This was easily done quantitatively for *Pterygophora*, *Eisenia*, *Macrocystis*, *Laminaria*, and *Cystoseira*, which have conspicuous sori, sporophylls, or reproductive bodies. Except for *Macrocystis*, these plants have a distinct seasonal release in the late fall and early winter (McPeak 1981). Neushul (1963) observed that spores of *Macrocystis* are continuously released. Our observations confirmed the continuous fertility, but at Pt. Loma and Bird Rock, the apparent decrease in late-summer fertility was associated with the warmer and probably nutrient-depleted summer waters. At Pt. Piedras Blancas, winter storms eliminated much of the foliage, including the sporophylls. The second approach to evaluating the seasonality of spore release is to monitor the germination of sporophytes. This approach was relatively unsatisfactory, because there was a time lag of several weeks between the release of the spore and the eventual germination and growth of a sporophyte large enough to identify. An increase in light intensity may have triggered the release of gametes and the appearance of sporophytes, which did not, therefore, result directly from the seasonality of spore release from the sporophyte generation. Thus, by opening the canopy, storms may have contributed importantly to the observed seasonal recruitment.

In summary, whether from the fall-winter spore release or from the physical triggering of the gametophytes in the spring, recruitment increased in the late winter and the spring (e.g., Fig. 6A).

*Mechanisms of algal dispersal.*—The effective radius of spore dispersal for a number of large brown algae is surprisingly limited. For example, Anderson and North (1966) found that the recruitment of *Macrocystis* sporophytes from an isolated plant is limited to an area within a radius of 5 m; *Alaria esculenta* is limited to  $\approx 10$  m (Sundene 1962); and *Postelsia palmaeformis*

is limited to  $< 3$  m (Dayton 1979), an observation corroborated by Paine (1979), who suggested 1.5 m as a more realistic limit. The hypothesized reason for such limited distance of sporophyte recruitment in spite of high spore production involves the fact that male and female gametophytes must be close to each other to ensure fertilization. This limited spore dispersal seems to be a general phenomenon for kelp and suggests that spore dispersal from a stationary plant is a much less effective means of colonizing than is dispersal by drifting fertile sori and sporophylls (Dayton 1973).

Drifting fertile algae included entire plants as well as pieces of fertile material. The entangled bundles of *Macrocystis* drifters were particularly important because they caused many of the clear spaces in patches of *Pterygophora* and *Eisenia* as well as in *Macrocystis* forests. After clearing the areas, the drifters inoculated them with large doses of spores. It is difficult to deduce the mechanisms that resulted in the observed patchy recruitment pattern without seeing the actual process.

We attempted to quantify the amount of drifting fertile reproductive material by using paired drift traps emplaced parallel to the shoreline. We found no consistent trend in traps facing north or south. But among the drift, we almost always found fertile pieces of *Macrocystis*, *Laminaria*, *Eisenia*, and *Pterygophora*. In addition, a great deal of red algal material was collected, much of which was probably also fertile. We had similar success when the drift traps were placed on the sand habitat 3 km north of the Scripps pier in La Jolla; in this case, the nearest kelp beds were  $> 2$  km in each direction, yet a great deal of fertile material was captured in the traps. This effective long-range dispersal was also observed on artificial habitats (Fager 1971) off the Scripps pier and on an artificial granite reef on the sand flat north of Scripps. On the artificial granite reef, *Macrocystis* recruitment resulted from both drifting plants and drifting sporophyll fragments.

Because a large number of spores need to settle in a limited area to ensure fertilization, the drift material needs to be held in place for a certain period of time. Many herbivorous animals augment this drift dispersal by capturing and holding material, which inoculates the immediate area before it is consumed. Recruitment was observed after fertile drift fragments were captured (*Diopatra* captured *Macrocystis*, *Pterygophora*, and *Laminaria farlowii*; *Haliotis rufescens* captured *Macrocystis* and *Pterygophora*; and *Strongylocentrotus* spp. captured *Macrocystis*, *Pterygophora*, and *L. farlowii*.) In particular, the urchins were probably very important because they were ubiquitous in ledges and boulders and were very adept at snaring drifting algae. This urchin effect was tested indirectly in the urchin-removal experiments discussed under Sea Urchin Grazing. Urchins in the controls snagged kelps such that the surge moved the fronds against the overhanging ledges, which had significantly higher kelp recruitment than the ledges above urchin-removal areas (27 *Macrocystis*, 42 *L. farlowii*, and 17 *Pterygophora*, compared to

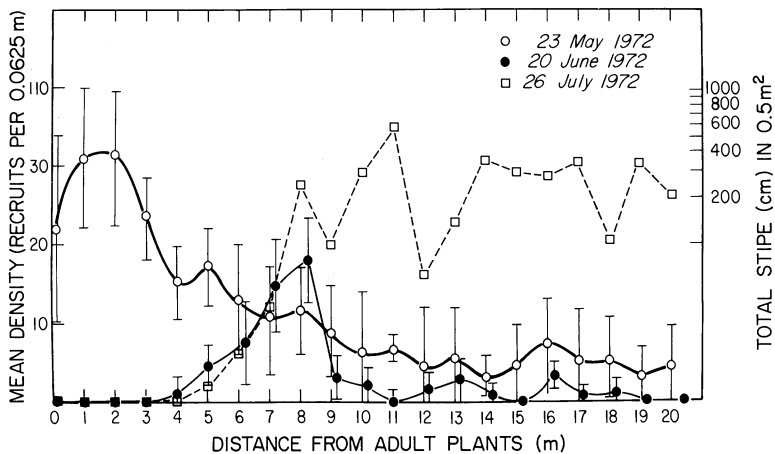


FIG. 19. Germination, survival, and growth of *Macrocyctis* as a function of distance from adult plants along two permanent transects running shoreward into areas cleared of sea urchins with quicklime at Pt. Loma on 25 April 1972. Germination and survival (○, ●) given as densities for 23 May and 20 June 1972. Growth or biomass of recruits (□) estimated by total length of stipes measured on 26 July in  $\frac{1}{4}$  m<sup>2</sup> quadrats spaced along the two transects. Error bars on density means are  $\pm 1$  SD,  $n = 6$ , with square root transformation of the data prior to statistical procedures. Depicted data have been back-transformed.

3 *Eisenia* in the urchin-removal areas). In each case, fertile pieces of the recruiting species had been observed being held by the urchins in the control areas.

*Dispersal, survivorship, and growth in a large clearing.*—Sea urchins sometimes begin to forage actively, especially when they are deprived of drift. This often results in the formation of urchin fronts that denude an area of all macroalgae, leaving a pavement of coralline algae (Leighton et al. 1966, North 1971). Typically, urchins remain in the cleared area in numbers sufficient to ensure that no significant growth of kelp become reestablished. One management practice is to spread quicklime over these urchin fronts and the remaining barrens. The quicklime kills most of the echinoderms, especially the sea urchins, and there is always a fast recovery of macroalgae. One such operation was done 25 April 1972 in a patch of several hectares at Pt. Loma. This gave us the opportunity to observe dispersal, survivorship, and growth of algae into a large clearing.

Recruitment and survivorship patterns (Fig. 19) in this clearing were reminiscent of Janzen's (1970) predicted seed shadow, but mortality and lack of growth adjacent to adult plants probably resulted from competition with the floating canopy for light. There was some recruitment throughout the clearing. The high density of recruits adjacent to fertile adults (Fig. 19) implied a heavy inoculation of spores. As a parallel to seed dormancy in terrestrial situations, gametophytes may exist, somewhat immune from grazing, for several weeks. Thus, dispersal does not have to be a single event, because the gametophytes can accumulate over time. We observed heavy recruitment along the tops of ledges in the quicklimed area, suggesting that the sea urchins had snagged fertile drift material that had inoculated the ledges. Furthermore, there was a marked recruitment swath along the patch of a drifting *Ma-*

*crocyctis* plant that had moved through the site a week before the clearing.

An important lesson from this and many other quicklime operations is that there is dispersal into large clearings. Even though recruitment is lower as the distance from the adults increases, survivorship and growth is usually adequate for a complete *Macrocyctis* colonization into a habitat made available by an episodic event such as an extreme storm, or a sea urchin dieoff due to management procedures or disease (Pearse et al. 1977, Pearse and Hines 1979). Thus, the above considerations and colonization of isolated reefs suggest that kelps disperse long distances, often from drifting fragments of fertile material. Yet we have shown experimentally that they effectively do not invade other established kelp patches (Figs. 8–12). Dispersal into large or isolated areas is very different from dispersal into small clearings where local plants release sufficient spores to swamp the limited drift dispersal.

*Success of dispersal: survivorship of young recruits.*—What are the important factors influencing the survivorship of recruits? Here we discuss the patterns of mortality from sources associated with the substratum, especially from scour, herbivores, and fishes. Fishes may simply eat smaller algae or may kill them incidentally while foraging on animals associated with the algae.

Our various experiments and baseline observations showed a pattern of epiphytic recruitment of young brown algae on *Pterygophora* stipes in which successful recruitment was rare near the base of the stipe, suggesting a higher mortality at the base. To quantify this pattern, near Virgin Reef we cut the fronds from 50 *Pterygophora* plants so that whiplash would not be a factor. The area was heavily inoculated in November 1973 with bundles of fertile reproductive material from *Laminaria*, *farlowii*, *Pterygophora*, and *Macrocyctis*.

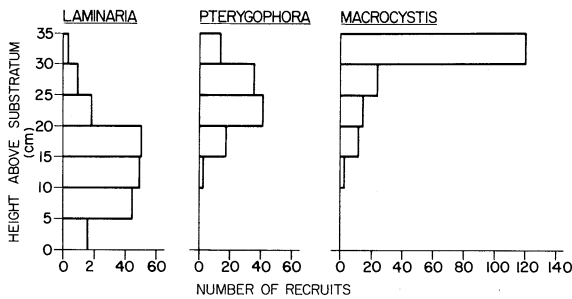


FIG. 20. Recruitment and subsequent layering of *Laminaria farlowii*, *Pterygophora californica*, and *Macrocyctis pyrifera* on bladeless *Pterygophora* stipes at different heights above the substratum near Virgin Reef, Pt. Loma.

In January 1974, we observed that *L. farlowii*, *Pterygophora*, and *Macrocyctis* had recruited in rather distinct layers on the stipes of these 50 plants (Fig. 20). Similar results were observed but not quantified on adjacent *Pterygophora* with intact fronds. Similar recruitment had also occurred on thin, round pieces of wood we had arranged in a "pegboard" design, and on a similar array of floating pieces of polypropylene lines that we used to see if the pattern was peculiar to *Pterygophora* or occurred generally. Whether this pattern of distinct layers resulted from competitive interactions among the recruits or from differential susceptibility to a substratum-associated mortality is not known. Furthermore, the experiment did not differentiate grazing effects from the effects of sand and sediment scour (Devinney and Volse 1978). We attempted a rough measure of scour by placing candles and paraffin blocks on the sea bottom. We found a pronounced vertical effect: almost all of the scour and abrasion

occurred along the bottom 15–20 cm of the candles and blocks.

To separate scour and grazer effects, we suspended, at 1, 10, and 25 cm above the substratum, stipes that had been epiphytized by kelps, so as to eliminate benthic grazers but not scour or water-column grazers (Fig. 21). *Laminaria* and *Eisenia* resisted mortality much better at 1 and 10 cm above the substratum than did *Pterygophora* and *Macrocyctis*, which suffered almost complete mortality within 10 cm of the substratum. Hence, *Laminaria* and *Eisenia* appeared to be more tolerant to scour or planktonic grazers.

We also attempted to evaluate grazing by small herbivores or microherbivores, fishes, and echinoderms. In one set of experiments, we used 14 scoured Plexiglas plates that had been inoculated with *Macrocyctis* and cultured through germination by W. J. North. Concrete blocks supported the plates  $\approx$  10 and 20 cm above the substratum to reduce scour effects. Five of the plates were protected by a monofilament net that allowed entry by microherbivores but excluded larger fishes and echinoderms. This net did not interfere with light or water movement and was not fouled during the month-long experiment.

Two days after the plates were set out, two plates without cages were cleaned by the asteroid *Patiria miniatra*. After 1 wk, 10 of the 14 plates had been cleaned of much of the small algae. Of these, two and possibly three were cleaned by *Patiria*; but no *Patiria* were in the vicinity of the other seven, which may have been grazed by fishes, especially halfmoons (*Medialuna californiensis*) and opaleyes (*Girella nigricans*). Also by the end of the 1st wk four of the five plates that had been protected with the net still had most of the algae, suggesting that cropping by larger animals was an im-

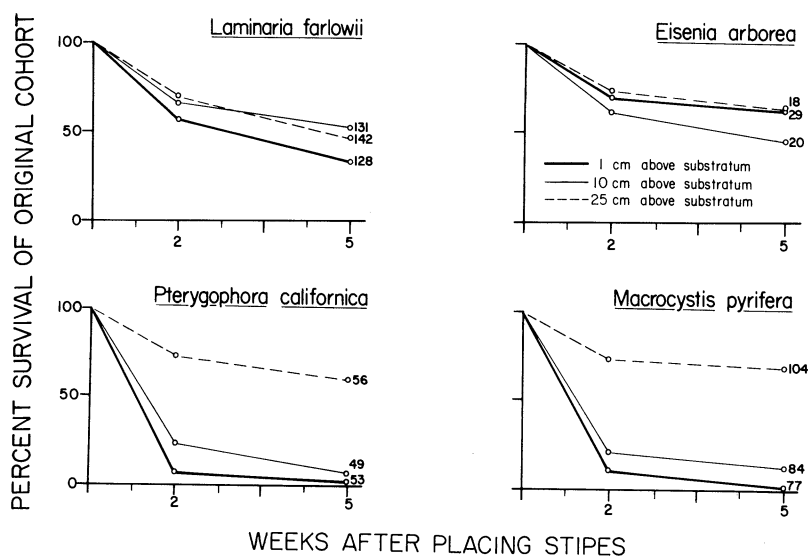


FIG. 21. Differential substratum-associated mortality of kelp recruits of the indicated species on pieces of stipe suspended at three heights above substratum near Virgin Reef, Pt. Loma. Numbers at right of lines give original number of small sporophyte blades on each stipe at the beginning of the experiment.

portant source of mortality. Two weeks after the plates had been established, however, the plates under the nets were being grazed by "microherbivores," mostly amphipods and polychaetes. Indeed, at this point, the vestigial algae ( $\approx 10\%$  cover) on the uncaged controls of two plates looked healthier than the algae on the protected plates. A week later, the plates under the nets had been completely cleaned, apparently by the microherbivores. The plates that had been cropped in the 1st wk still had a few *Macrocystis* plants that were in good condition. *Senoritas* (*Oxyjulis californica*) and sheephead (*Semicossyphus pulcher*) nosed around the uncaged plates, but they did not appear to be grazing on them. One sheephead ripped at the net of one of the protected plates, possibly trying to get at a polychaete tube that was conspicuous on the plate. This trend continued through the 4th wk after the plates were established, but shortly thereafter the blocks were disturbed by a storm, thus terminating the observations.

A similar set of experiments was done concurrently with the *Pterygophora*-stipe experiments (Fig. 21), in which stipes with young kelps (almost entirely *Macrocystis*) growing on them were placed under different cages, "roofs," and controls, and over various substrata. The stipes and a few wood and polypropylene stipe substitutes with small *Macrocystis* plants were suspended 15–20 cm above various substrates, including sand, thick *Calliarthron* turf, plastic grass doormats, and natural substratum with very thin turf. Monofilament net was placed over frames made from plastic laundry baskets and dishpans. These cages probably interfered with light penetration and water movement to a slight extent, but this seemed trivial because the experiment was short.

All 14 plants placed over a sand-filled depression with no cages died within 1 wk. A total of 57 plants in three treatments (cages, roofs, and controls) were placed over a very thick coralline turf, and they too were killed within 1 wk. Astro turf doormats and natural substrata had similar results (Fig. 22). The small plants on stipes placed within a cage or under a roof initially had much higher survivorship than the control did; but after the early mortality in the control, there was no additional mortality, and the remaining plants grew rapidly and looked healthy. In contrast, the plants that were protected initially showed higher survivorship but then had increasing evidence of herbivore in the form of small bites; they all eventually died. Early mortality in controls was significantly higher ( $P < .01$ ) than in cages; mortality probably resulted from grazing by fishes, because echinoderms could not reach the stipes. The plants (all *Macrocystis*) in the controls that survived were very healthy.

The plate and stipe experiments shared a common theme: unprotected small plants experienced immediate, nearly complete mortality that was significantly higher than the protected plants. We know that in several cases this resulted from cropping by *Patiria* and

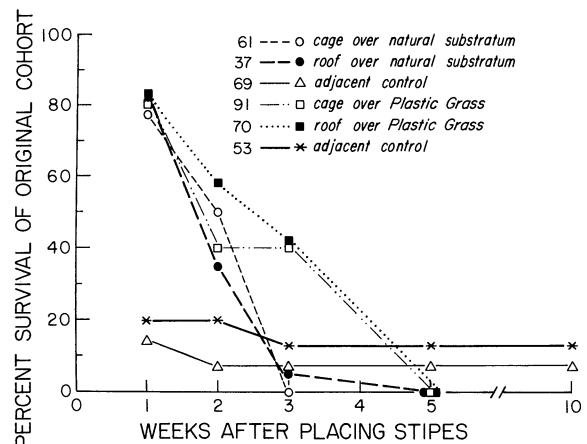


FIG. 22. Survivorship of young kelps placed under cages or roofs over natural substrata without turf and over artificial herbivore-free turf (plastic grass doormats) and adjacent controls at Pt. Loma. The number of plants in each actual cohort is given in the line key. Not shown are the results of 14 plants placed over a shallow ( $\approx 3$  cm) sand-filled depression and 57 plants placed in the three treatments (cages, roofs, controls) over a thick coralline turf; all died within 1 wk. All plants surviving to grow large enough to be identified were *Macrocystis pyrifera*.

fishes. After 3 wk, however, all the plants protected from larger animals were dead, and the few unprotected survivors thrived. One hypothesis is that the large fishes and echinoderms respond quickly to gametophytes on plates or to small blades on *Pterygophora* stipes, but that the young plants often survive when protected. However, fish such as *Oxyjulis californica* (Hobson 1971, Hobson and Chess 1976, and Bernstein and Jung 1979) cropped the microherbivores, which became abundant when protected by cages from their predators. The microherbivores eventually eliminated the small algae. An observation that corroborates the hypothesis is that the stipes placed over the coralline turf were quickly stripped of their small kelps even when protected in a cage; the coralline turf is a rich habitat for small crustacea and polychaetes (Hobson and Chess 1976, A. Ebeling, *personal communication*). This effect was similar to the artifacts associated with cages on soft bottoms where small predators accumulate (Virnstein 1977, Dayton and Oliver 1980).

This hypothesis received further support from observations made during turf-cropping experiments. As coralline turf and the fleshy red algal turf (mostly *Gelidium*) on the top of Virgin Reef were removed, we observed a fish feeding frenzy. Dozens of small sheephead, *Semicossyphus pulcher*, and senioritas, *Oxyjulis californica*, ate isopods, amphipods, polychaetes, and encrusting animals such as bryozoans, sponges, and compound tunicates exposed during turf removal. Dozens of kelps recruited in both the coralline-turf and the algal-turf clearings, but none recruited into adjacent controls. The coralline turf was adjacent to *Pterygophora* adults, and the recruits were mostly *Pter-*



*ygophora*; the *Gelidium* turf was near a *Macrocystis*, and most of the recruits were *Macrocystis*.

These experiments suggest that there was a delayed positive effect from picker fish, which restricted microherbivores to refuges in thick turf. However, the turf-cutting experiments have several alternative explanations, including a simple physical interference with kelp settlement; light competition with kelp recruits, such as seen in the intertidal zone (Dayton 1971, 1973, 1975a, b, Lewis 1976); and a possible chemical allelopathic defense against epiphytes or sloughing of epidermis, or both. The latter explanation has never been demonstrated in the sea (but see Kittridge et al. 1974), but we believe that it does occur, particularly in coralline algae and such encrusting algae as *Ralfsia* (Fletcher 1975), *Hildenbrandia*, *Petrospongium*, *Lithophyllum*, and *Clathromorphum*. In addition, cages may attract mobile microherbivores. If these mechanisms are at work, they certainly function in a complementary rather than an exclusive manner, but we have not been able to separate them, despite several attempts with artificial *Calliarthron* and attempts to rid rocks of microherbivores by using chemical relaxants and various types of insecticides.

*Mechanisms of succession at Pt. Loma and Pt. Piedras Blancas.*—Most mortality of *Macrocystis* resulted from entanglements with drift *Macrocystis*. Another source of mortality for stipitate and prostrate kelps was being detached or thrust against sea urchins by strong surge. Both mortality sources had strong seasonal patterns, because surge increases during winter storms. The reproductive patterns of the kelps during the late fall and the winter seemed keyed to this disturbance. The same is true in the intertidal zone (Dayton 1975a). Other, nonseasonal sources of mortality also included grazing by sea urchins, which occurred in a patchy manner in this community. In evolutionary time, sea urchin outbreaks were probably rare due to the presence of the sea otter (*Enhydra lutris*). At the present time, sea urchin populations are usually controlled by a complex of other predators and canopy effects on larval recruitment (Tegner and Dayton 1981).

In most succession and equilibrium studies, effective dispersal is an important but often overlooked phenomenon. Our results corroborate earlier studies suggesting that spore dispersal of kelps is rather limited. But dispersal via drifting plants or fertile plant fragments was effective but often unpredictable in time and space. Once a plant propagule was dispersed and germination occurred, there were several very important factors that diminished the probability of survival. These included competition for light or nutrients, scour, and grazing by a number of herbivores. Such factors were affected by the precise location of the propagule settlement and the effectiveness of predation on the herbivores. A thin canopy of *Laminaria*, *Cystoseira*, or *Pterygophora* enhanced survivorship of recruits to a certain extent, suggesting that an early refuge from fishes can enhance successful recruitment. In most cases,

all of the above parameters hindered successful invasion and succession of a patch, and tended to enhance the resistance stability of the particular patch.

We have presented many examples of resistance stability at Pt. Piedras Blancas. But we have few observations of the process of patch succession beyond the apparent shading effects when overstories succeed understories. We did investigate one process by which *Macrocystis* appeared to invade *Pterygophora* patches. After storms, *Pterygophora* that have *Nereocystis* and *Macrocystis* growing on their stipes are commonly seen on the shore. Perhaps the epiphyte drag increases the probability that the *Pterygophora* will be pulled free, as observed by Dayton (1973) and Sousa (1979). We hypothesize that this mechanism is one means by which *Pterygophora* are killed and their patches invaded.

To test this hypothesis, in April 1977 we tagged 119 stipitate plants in Sites A and C and removed the epiphytes from half of them. Unfortunately, 1977–1978 was an unusually rough year, and the plants had a low survival rate. There was no epiphyte effect on *Laminaria dentigera*. When *Pterygophora* in the two sites are lumped, 53% of the plants without epiphytes survived, but only 18% of the control plants survived. This difference was significant ( $\chi^2$ , Fisher's Exact Test,  $P \leq .05$ ).

The *Pterygophora* stipes were commonly occupied by limpets (*Collisella instabilis*) and snails (*Calliostoma* and *Tegula* spp.), and there was a significant inverse correlation between numbers of epiphytes and limpets. These grazers appeared to feed on epiphytes, and usually there was no apparent effect on stipe tissue. This suggests the hypothesis that, by inhibiting the epiphyte effect, limpets increase the resistance stability of the *Pterygophora* patch. We tested this hypothesis by tagging 120 *Pterygophora* in Sites A and C. In each site we removed epiphytes from 20 plants, removed limpets from 20 plants, and left 20 plants as controls. In contrast with the severe winter of 1977–1978, the winter of 1978–1979 was relatively mild, and the plants had a uniformly high survivorship. Probably for this reason, the within-site comparisons were suggestive but not significant ( $\chi^2$ , Fisher's Exact Test,  $P \leq .09$ ). But again, when the data from the two sites were lumped, there was a highly significant increase in mortality of the plants without limpets over the plants with only epiphytes removed ( $\chi^2$ , Fisher's Exact Test,  $P \leq .01$ ). Clearly, there were other complicating factors, including relative exposure to surge, *Pterygophora* density, year-to-year differences, and quality of substratum. Nonetheless, it was also clear that the interplay between the grazers on the stipes, the epiphytes, and storm surge was an important component of the resistance of *Pterygophora* patches to invasion.

These are but a few of the many processes that resulted in the observed patterns of succession. We know that this complex community has a great many more such mechanisms that are yet to be documented. Clearly, the processes resulting in the patterns of disturbance

and subsequent colonization of the disturbed patches are very complex.

#### DISCUSSION

The most recent reviews of stability (Sutherland 1981, Connell and Sousa 1983) emphasize the need for the recognition of proper scales in time and space. If either scale is sufficiently limited, the community is never stable; if either scale is sufficiently large, the community is always stable. The time scale should be longer than the generation time of the structurally important foundation species (Dayton 1972), and the spatial scale should, ideally, be adequate to provide enough propagules and proper environmental conditions for recruitment and survival through reproduction of the foundation species. Both reviews cited above also emphasize that it is important to define the perturbation and the rareness of equilibrium states so important in theoretical treatments.

Ecologists work within several scales, and sometimes their conclusions cannot be generalized (Dayton and Tegner 1984). In this paper we have focused on a community level of organization. Natural communities are aggregates of patches and guilds within which there are strong biological interactions (McNaughton 1978, Paine 1980, Yodzis 1980). The nature of these biological interactions can vary considerably, and within a patch or guild the interactions often determine the local stability. The larger scale or community stability, however, is determined by the aggregate of the separate patch dynamics, by the types of interactions between the patches, and especially by the physical regimes that strongly influence so many of these relationships. In many natural systems, such patches have different patterns of local stability influenced by such factors as physical stress and disturbance, competition or predation, or dispersal and behavior. Obviously these factors often work synergistically. We have considered the following three types of stability in this paper. (1) Persistence stability refers to the existence of a patch longer than one generation of the dominant population. Although the patch has no apparent perturbation, it is likely to have been subject to the nonapparent Type I perturbations of Sutherland (1981). (2) Resistance stability refers to the persistence of a patch despite its subjection to perturbation (Types I and II of Sutherland). (3) Resilience stability refers to the recovery of a patch following a perturbation sufficient to allow colonization by different species. We have described various aspects of stability in kelp forests representing varying degrees and types of environmental stress.

Persistence of a kelp patch can tautologically be a function of plant longevity (Frank 1968). Therefore, a definition must also have a time scale sufficient to include more than one generation. Our survivorship data at Pt. Loma and Santa Catalina show that our patches have persistence stability despite the fact that a few individual plants survived throughout the 10-yr study period. A more operational definition of persistence

stability should accommodate those more common situations in which the established population within the patch turns over but is not invaded by neighboring species. This subsumes our definition of resistance stability, but allows a much more general treatment of stability since it is possible to include situations in which an instantaneous determination of the age structure of a population (such as that derived from tree rings) shows continued recruitment without apparent invasion. We imply that most of the patches we have studied have both persistence and resistance stability at all three sites. Still unresolved is the issue of maximum time scale for which these concepts are relevant, since all patches are eventually perturbed or invaded.

The resistance to invasion often implies competitive exclusion, although a host of other mechanisms can act synergistically. Our observations and clearing experiments show that, all else being equal, there is a straightforward dominance hierarchy of competition for light that is determined simply by canopy height. In addition, however, a definition of patch stability must also integrate the effects of stress or perturbations. While not quantified, a reverse hierarchy seems to prevail when wave stress increases. For example, the floating canopy of *Macrocystis pyrifera* may give it a competitive superiority, but may also make it more vulnerable to wave stress. This can be seen in the highly wave-stressed Site D at Pt. Piedras Blancas, where *Macrocystis* was unable to persist despite clearings and successful experimental transplants of *Macrocystis*. All transplants were ripped out by the severe winter storms that had no apparent effect on the stipitate and prostrate canopies. Other examples are the offshore submarine Cortez and Tanner Banks on the outer continental shelf of southern California. These habitats receive very strong waves. They have no *Macrocystis*; however, the stipitate *Eisenia arborea* is common (Lewbell et al. 1981). Another example of greater susceptibility to stress in the fuller canopies includes the southern California area in which the canopy of *Macrocystis* floats above the thermocline, where it is exposed to temperature and nutrient stress (Jackson 1977). And finally, *Macrocystis* is a preferred food of important herbivores, especially sea urchins (Leighton 1966, Leighton et al. 1971). *Nereocystis* appears to have an extreme adaptation to such disturbances in that it is an annual plant that appears to be competitively inferior to other kelps (Vadas 1968, 1972) and is a preferred food for herbivores (Vadas 1968, 1977). In all of these examples, the stipitate species (*Pterygophora californica*, *Eisenia arborea*, and *Laminaria setchellii*) seem more tolerant of physical stress and are not as effectively grazed upon as is *Macrocystis*. Finally, the prostrate species (*Laminaria farlowii*, *Cystoseira osmundacea*, and *Dictyoneurum californicum*) seem extremely tolerant of physical stress; *Dictyoneurum* is especially tolerant of wave stress, possibly because it has a vigorous rhizomatous holdfast enabling effective asexual horizontal growth. The prostrate forms also

seem more resistant to grazing (Leighton 1966, P. K. Dayton, *personal observation*).

Because resilience stability is defined as the recovery of a population following a replacement, it reveals the dynamics of stability and is evaluated by following succession after a perturbation. Given a perturbation, the pattern of succession is influenced by dispersal capabilities and variable recruitment, depending on season, substratum type, and heterogeneity as well as on many biological factors. The rate of succession or relative resilience also integrates dispersal and competition as well as physiological tolerances. We found at Pt. Loma that *Macrocystis*, *Pterygophora*, and *Eisenia* disperse less effectively than *Laminaria* or *Cystoseira*; the latter, however, appear to be inferior competitors for light with the higher canopies. Resilience depends upon the area of the effective disturbance. Small disturbances kill only a few individuals, and the patch is almost certain to be recolonized by members of the existing species, both from preceding sporulations and by being swamped by spores from the nearby plants. Larger disturbances bring the relative dispersal abilities of the different species into play, and the disturbed patches are more likely to be invaded. Because there are strong seasonal effects on the life histories of these kelps, and because individuals, especially the gametophytes (Lüning and Neushul 1978), are sensitive to highly variable environmental factors, it is not realistic to attempt to define threshold areas at which invasion becomes more likely.

Once *Macrocystis* germinates and grows above competing canopies, it is an effective invader; such invasions rarely occur naturally in areas with low levels of disturbance. For example, the *Macrocystis* artificially seeded into small clearings in heavy understory at all areas survived several years. At Pt. Loma and Bird Rock, there were second-generation plants, so *Macrocystis* can survive and reproduce in such areas. Furthermore, at both Pt. Loma and Bird Rock, *Macrocystis* expanded  $\approx 1$  m into the adjacent *Pterygophora* during the next 5–8 yr.

Our limited data suggest that in areas with very low levels of disturbance, *Macrocystis* rarely invades dense understories. But if disturbance is sufficient to detach a few plants or break off pieces of sporophyll, *Macrocystis* can invade other guilds by various mechanisms, especially by the drifting of clumps of fertile *Macrocystis* plants that simultaneously cause a destructive swath of mortality and saturate the disturbed area with spores. In addition, when there are high levels of disturbance from storms (Pt. Loma and Pt. Piedras Blancas) or probable temperature and nutrient stresses (Bird Rock), *Macrocystis* can be invaded, at least temporarily, by many understory species. Thus, as with the resistance of *Postelsia palmaeformis* (Dayton 1973, Paine 1979), *Macrocystis* resistance depends upon a low level of disturbance. *Macrocystis* can be eliminated by high frequencies of disturbance or by catastrophes.

These observations support Grimes's (1979) idea that plants tend to adapt to become ruderals, competitors, or stress-tolerators. We saw that "K" selected species can be adapted for competition (the deeper understory at Bird Rock) or to tolerate stress (the stipitate species of *Dictyonium* at Pt. Piedras Blancas). Additional support can be seen in the San Juan Islands, Washington, where understory species outcompete the canopy-forming annual *Nereocystis* (Vadas 1968), and at Amchitka Island, Alaska, where stipitate kelps seem much more tolerant of severe storms than the canopy-forming perennial *Alaria fistulosa*, which behaves as a ruderal (Dayton 1975b). The rhizomatous *Laminaria longipes* at Amchitka Island seems to be an especially effective stress-tolerator (Dayton 1975b), as is *Dictyonium* at Piedras Blancas.

We suggest that there should be an additional component of Grimes's stress-tolerators for those species that resist stress from grazing; that is, grazer tolerators. At Pt. Loma and Piedras Blancas, the turf resists invasion, probably either by allelochemicals or by the grazing of the abundant small crustacea and polychaetes that it harbors. Although the possibility of allelochemical defenses complicates the interpretation of the resistance stability of the turf, the coralline algal pavements associated with urchin barrens are common components of many algal habitats (reviewed by Lawrence [1975]) and were seen in the urchin-dominated boulder patches and reefs at Pt. Loma. Other kelp-community examples of grazer tolerators include urchin barrens in tidepools (Paine and Vadas 1969; Dayton 1975a) and areas free of sea otters in Alaska (Estes and Palmisano 1974), Nova Scotia (Mann 1977), and Chile (P. K. Dayton, *personal observation*). Other grazer tolerators include *Agarum* spp. (Vadas 1968), *Desmarestia* spp., and *Codium* species (P. K. Dayton, *personal observation*). That these grazer-tolerator communities are maintained by intensive grazing is often demonstrated by removing the grazers and observing immediate algal recruitment and succession (Lubchenco 1978; Menge and Lubchenco 1981). Many parallel examples occur in terrestrial situations (Harper 1977).

It is important to note that almost all of the observed patches in kelp forests, certainly those of southern California, fall between the extreme situations described above. Indeed, *Macrocystis pyrifera*, the most conspicuous and functionally important species, is one of the first species to be eliminated in physically (wave or sand scour) stressed and grazer-stressed habitats. Clearly, the kelp guilds are differentially adapted to these extremes, and almost every patch in a kelp forest is influenced by different levels of these environmental gradients, which subtly influence the algal composition. Patch resistance and resilience are expected to vary in the different microhabitats of any community. The message from our study is that *within* a given study area biological variables define patch stability, but *be-*

tween study areas the main differences are physical, especially storms, surge, scour, temperature, and sometimes nutrient depletion.

Within a community at a given area, the processes we have defined, such as competition, dispersal, various disturbance agents, and seasonality, all relate to local or patch persistence, resistance, and, to a limited extent, resilience. But resilience in the sense of recoverability and of a more global stability is strongly dependent upon oceanographic factors such as temperature, nutrients, and water visibility, all of which are strongly influenced by longshore currents, by cross-shore transfer via internal waves, by local weather conditions, and even by large-scale climatological events that have a strong effect on the biota in the California Current (Chelton et al. 1982). Other important biological factors include switching thresholds of fish such as the halfmoon, opaleyes, and senioritas (Bernstein and Jung 1979). In some cases, these environmental variables relate to linear ecological responses, but probably in most cases the variables are not linear (habitat structure and internal tides), and they elicit threshold responses (compensation point in photosynthesis and behavioral thresholds, especially with regard to foraging). The overall situation may appear chaotic and stochastic, but each response is deterministic, if complicated. Given additional information regarding the roles of light, temperature, and nutrients, a reasonable understanding of stability should be available within the framework we have presented.

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