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Ecological Monographs, Vol. 55, No. 4. (Dec., 1985), pp. 447-468.

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THE STRUCTURE AND REGULATION OF SOME SOUTH AMERICAN KELP COMMUNITIES¹

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Abstract. The main objective of this study was to evaluate how physical stress and herbivores influence the distribution, abundance, size frequency, and mortality of the giant kelp, *Macrocystis pyrifera*, in the southeast Pacific. These factors were studied for the kelp and the echinoid herbivore *Loxechinus albus* over a wide latitudinal range (56°–42° S) of South America on RV *Hero* cruises in 1972 and 1973. There were large kelp forests with many large plants in the southern Isla de los Estados and Tierra del Fuego sites. Sources of kelp mortality in these sites include entanglement with drift plants and heavy encrustation of bivalves. This resulted in a considerable amount of drifting kelp, and the sea urchins appeared to have abundant food and did not attack living kelp plants. Nevertheless, the urchin densities usually were relatively low and the *Loxechinus* size frequencies skewed to larger size classes, suggesting that their populations may be limited by larval availability in the Westwind Drift. There were also some large kelp forests in the northern Golfo Corcovado and Isla Chiloé areas, but here the kelp forests seemed relatively ephemeral and *Loxechinus* appeared to be harvested by humans. The intermediate latitudes (54°–46° S) in areas semiexposed to oceanic waves were characterized by situations in which *Loxechinus* overexploit the kelps and maintain urchin–coralline algae “barren grounds.” In these areas kelps occur only where urchin access is restricted by wave exposure, ephemeral clumps of *Desmarestia ligulata*, and rarely, by a predator, the asteroid *Meyenaster gelatinosus*. In many areas the shallow distribution of *Macrocystis* was restricted by competition with the large fucoid *Durvillaea antarctica*. These relationships were evaluated by removal and addition experiments. Much more important than latitudinal relationships to both kelp and urchin distribution and abundance patterns were exposure gradients, from shores subject to strong oceanic swells to protected fjords. Transect data suggest that *Loxechinus* disappear from protected waters before *Macrocystis*. Thus in some semiprotected habitats there are very dense patches of kelps without grazers; kelp removal experiments in these habitats suggest strong density-dependent kelp interactions. In still more protected sites, the *Macrocystis* growth form changes, the plants appear to have low fertility, and there is very low recruitment.

Summarizing, the *Loxechinus* population seems restricted by larval recruitment in the face of the Westwind Drift in the far south, perhaps by sedimentation or fresh water in protected fjords, and by human fishing in the north. The very low *Loxechinus* densities in the far south are correlated with large kelp forests in which the main kelp mortality results from drifting *Macrocystis* plants. The kelp populations appear limited by physical factors in the fjords and by *Loxechinus* grazing in most other areas.

Key words: *Argentina; biogeography; Chile; community; Desmarestia; Durvillaea; kelp; Loxechinus; Macrocystis; sea urchin–barren.*

INTRODUCTION

Macrocystis pyrifera has an unusually broad geographic distribution including most cold temperate southern ocean islands and continents north of the Antarctic Convergence (Mann 1973) and in the north-eastern Pacific from central Baja California to San Francisco, California. It is most studied in southern California, where it has been well documented that sea urchins (*Strongylocentrotus* spp.) are capable of overexploiting *Macrocystis* populations (Leighton et al. 1966, North 1971). However, in California the sea urchin populations usually are prevented from reaching sufficiently high densities to overgraze the *Macrocystis* by predators such as sea otters (McLean 1962), lobsters, and some fishes (Tegner and Dayton 1981,

Cowen 1983). Generalizations emerging from southern California suggest that the dynamics of the kelp and sea urchin populations and the intensities of their interactions are influenced strongly by wave stress and large-scale oceanographic processes (Dayton et al. 1984, Dayton and Tegner 1984a, b, Ebeling et al. 1985). Large kelp forests have been described in South America (Darwin 1860, Skottsberg 1941, Neushul 1971), and while it is reasonable to speculate that there are functional parallels between North and South Pacific *Macrocystis* forests, analogous kelp–sea urchin–predator relationships have not been described.

Recent studies from both the southern (53° S) and northern (40° S) regions of the *Macrocystis pyrifera* range in Chile have indicated that the kelp–sea urchin parallels do not exist (Castilla and Moreno 1982, Moreno and Sutherland 1982, Santelices and Ojeda 1984a, b). In the North Pacific *Strongylocentrotus* spp. are capable of removing almost all the fleshy algae, re-

¹ Manuscript received 18 June 1984; revised 25 February 1985; accepted 6 March 1985.

sulting in a sea urchin–coralline algal pavement or barren ground (Lawrence 1975). But in the above South American studies, the apparent ecological counterpart, *Loxechinus albus*, was observed to eat only drift algae and not to over-exploit *Macrocystis*.

The kelp–sea urchin relationships are important in almost all temperate and boreal shores (Lawrence 1975, Hagen 1983), yet patterns are not constant and there is increasing discordance in their interpretation (Choat and Schiel 1982). This paper describes the relationship between populations of *Macrocystis pyrifera* and sea urchins, especially *Loxechinus albus*, as influenced by latitude and degree of wave exposure. Densities of *Macrocystis* and sea urchins from a wide range of habitats (Fig. 1) suggest that in some habitats *Loxechinus* does over-exploit fleshy macroalgae and in other areas it does not. Such a large-scale biogeographic overview of this relationship is valuable for several reasons. First, it better demonstrates which patterns dominate in particular environmental situations. More important, by defining generalizations and apparent exceptions, it enables ecologists better to focus on the identification of specific environmental factors and biological processes which maintain particular ecological patterns. I consider several hypotheses that may be important to the dynamic relationship between *Macrocystis* and urchins, including physical and biotic refugia from *Loxechinus*, *Macrocystis* mortality from encrusting species, which in turn contributes drift food to *Loxechinus*, canopy competition, availability of *Loxechinus* larvae, and the potential importance of urchin exploitation by humans.

MATERIALS AND METHODS

This paper is based on data collected on two RV *Hero* cruises. The first began at Punta Arenas, Chile, 26 October 1972, and worked north from Bahía Campana (53°56' S, 70°29' W) to Punta Lelbun on Isla Chiloé (43°46.9' S, 73°30.3' W) on 23 November. The second cruise started at Ushuaia, Argentina, on 3 May 1973. The first leg of the second cruise worked around Isla de los Estados and the southernmost coast of Tierra del Fuego; the second leg attempted to visit sites from the first cruise. Most of the stations were visited only once and most are unique in some respects. However, experiments were established at several stations on the first cruise and most of these stations were revisited on the second cruise.

Most data were collected by scuba diving. Intertidal levels were measured from estimated mean low water; subtidal depths were not corrected for tidal level. The uneven topography and sometimes difficult water conditions forced a certain amount of flexibility in our procedure. Belt transects with lengths of 5 to 50 m and widths of 1 to 4 m were used. These transects were laid along isobaths in order to quantify depth effects where possible. Most data were collected in situ, but in a few cases they were obtained from photographs.

Adult *Macrocystis* are defined arbitrarily as plants with fronds reaching the surface or with four or more stipes. Mean holdfast diameters rather than stipe numbers are presented as an indication of plant size and age because we have found stipe numbers to be variable in California. The proportion of detached plants was often recorded because their subsequent entanglement is known to be a major source of mortality (Rosenthal et al. 1974, Dayton et al. 1984). Percent data were arcsine transformed for statistical calculations. Permanent study locations were marked with nails, yellow rope, and, when appropriate, with floats. *Macrocystis* plants were tagged with numbered plastic tags attached to the holdfast with rubber bands. When *Macrocystis* plants were removed to evaluate their effects on other algal species, the entire holdfast was removed. The fronds of intertidal *Durvillaea antarctica* and *Lessonia nigrescens* were removed above the holdfast. The *Loxechinus* size frequency data were usually obtained from field collections of a restricted area in which an effort was made to obtain all the urchins from a given area (usually 1–3 m²), but not all boulders were turned and a few tiny urchins may have been missed. The measurements were made with centimetre rules. *Loxechinus* usually were eliminated by smashing them with a hammer. In all cases the controls were adjacent to or relatively close to the removal areas. Because of logistic and time constraints this was unavoidable, but it does result in an artifact because the urchins from the control area may move into the cleared area, thereby decreasing the control area population. The consequence may be a reduced urchin effect in the control, resulting in a conservative effect on the comparative evaluation of the urchin role.

RESULTS

While this paper emphasizes the kelp–sea urchin relationship as it is affected by gradients in wave exposure and latitude, the organization is difficult because there is no objective definition of wave exposure, and the data were collected on cruises in the austral spring and fall. With the exception of the most southern region, the kelp–urchin relationship seemed more strongly influenced by the degree of wave exposure than meridional trends. Despite efforts to sample across the wave exposure gradients and to do field experiments, the data are so influenced by the general south–north cruise tracks that results must be presented in geographic regions. In many cases the seasonal differences may influence the algal patterns; thus the date of collection will be given.

The results will be presented in sections for each of seven regions. First, the most southerly region of Isla de los Estados and the southern Argentine Tierra del Fuego will be described and compared to the nearby Chilean habitat studied by Santelices and Ojeda (1984a, b). Second, sites from the southern fjords will be described, as will experiments done at Isla Carlos III.

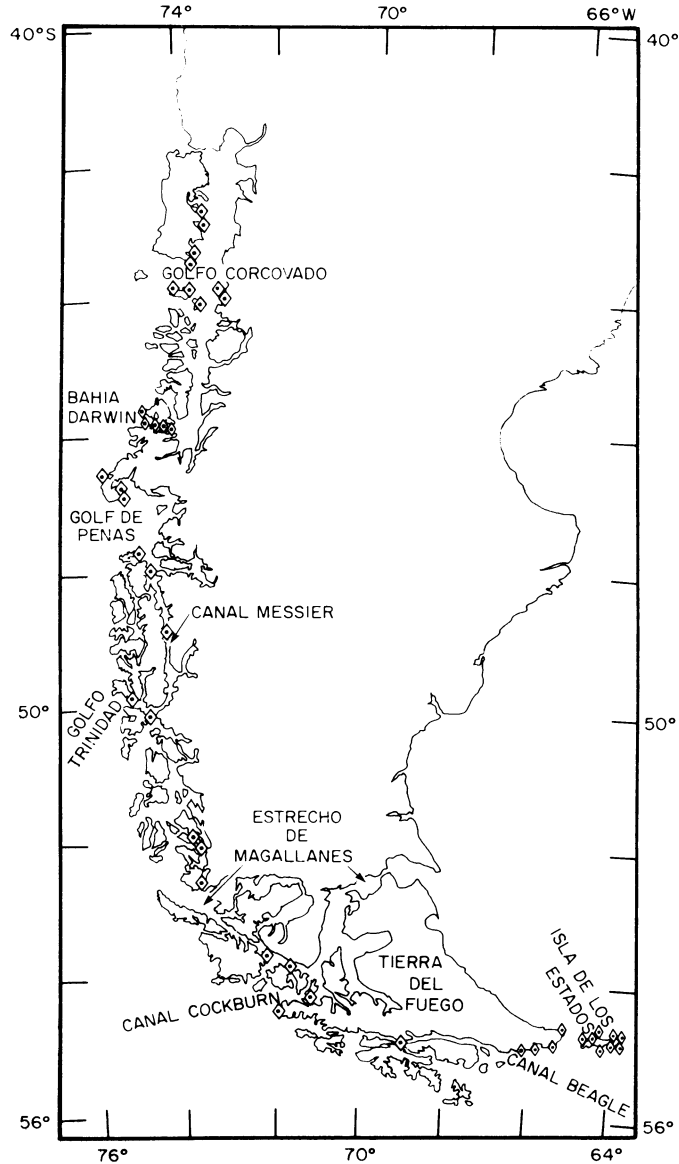


FIG. 1. Map of southwestern South America. Stations are indicated by diamonds. The actual coordinates for each site are recorded in the tables.

Third, descriptive and experimental results from the semiexposed Isla Knocker near the mouth of Golfo Trinidad will be presented, followed by (fourth) summaries of descriptive work from the protected inner areas of Golfo Trinidad and Puerto Edén. Then (fifth) descriptive and experimental work in the Golfo de Penas region will be presented, followed by (sixth) similar studies in the Bahía Darwin area. Finally (seventh), descriptive surveys from Golfo de Corcovado will be presented and compared to the Moreno and Sutherland (1982) work from Valdivia. The relatively rare lithodid crabs might be predators of urchins, and their occurrence was noted.

Isla de los Estados and Southern Tierra del Fuego

This area was visited 4–14 May 1973. Many of the kelp forests were very large, covering areas of many hectares to several square kilometres. When there is a continuous rocky substrate available, *Macrocystis* is zoned between *Lessonia vadosa* in shallow water and *L. flavicans* in deeper water (Searles 1978). The actual depths at which these transitions occurred varied from site to site; in many cases the respective densities of *L. vadosa*, *Macrocystis*, and *L. flavicans* were relatively high and all had very thick canopies. Because of very limited time at each station, we focused on the *Mac-*

TABLE 1. Mean densities (\pm SD) of sea urchins and *Macrocystis* at Isla de los Estados (Bahía Crossley to Puerto Lasserre on the north side; Puerto Back to Isla Alexander on the south side) and Argentine Tierra del Fuego (all other sites). All transects were done in May 1973, and each covered an area of 50 m².

Location	Depth (m)	Urchin density (no./m ²)				Macrocystis density (no./m ²)		Mean holdfast diameter (cm)	Proportion detached
		<i>Loxechinus</i>	<i>Arbacia</i>	<i>Pseudechinus</i>	<i>Austrocidaris</i>	Juvenile	Adult		
Bahía Crossley	6	0.12	0*	0	0.12	0	0.2	35	0.22
54°47.5' S, 64°42' W	6	0	0	0	0.20	0	0.14	40	0.29
Semiexposed	11	0.24 \pm 0.66	0	0	3.78	0	0.36	42	0.17
Isla Colnett	15	0	0.05	0.10	0.12	0.44 \pm 0.86	0.14	36	0.14
54°43.8' S, 64°13.9' W	15	—*	—	—	—	0.56 \pm 1.25	0.10	31	0
	10	1.98	0	2.42	0	0.68 \pm 1.00	0.44	23	0.14
	10	—	—	—	—	0.24 \pm 0.69	0.42	27	0.05
Bahía Colnett	15	0.13	0	0.19	0.08	0.04	0.30	37	0.10
54°42' S, 64°20' W	15	—	—	—	—	0	0.36	43	0
Bahía San Antonia	15	0.08	0	12.9	0.16	0.11	0.18	27	0
50°44.4' S, 64°30.8' W	15	—	—	—	—	0	0.30	41	0
Puerto Cook	10	—	—	—	—	0.18 \pm 0.44	0.16	50	0
54°44' S, 63°59.8' W	15	4.4	0	0	0.02	0.12 \pm 0.36	0.08	44	0
Puerto Lasserre									
54°43.9' S, 63°51.6' W	8	6.9	0	0.06	0.52	0	0.14	52	0.28
Puerto Back									
54°46.8' S, 63°53.3' W	14	0.08	0	0	0	0	0.14	28	0
Puerto Vancouver	11	0.18	—	—	—	0	0.16	23	0
54°47.3' S, 64°04.4' W	13	2.4	—	—	—	1.4 \pm 1.36	0.20	24	0
	13	3.68 \pm 8.3	—	—	—	1.1 \pm 1.32	0.24	23	0.25
Isla Alexander	11	4.18 \pm 4.6	0.1	0.25	0	0.14 \pm 0.57	0.64	24	0
54°50' S, 64°23.8' W	14	2.44 \pm 3.2	0	0.02	0	1.04 \pm 1.26	0.26	28	0
Bahía Valentín	6	2.88 \pm 4.1	—	—	—	3.2 \pm 3.5	1.66	12	0.13
54°54' S, 65°29' W	6	2.84 \pm 4.4	—	—	—	2.0 \pm 1.8	1.76	15	0.14
	11	6.16 \pm 9.5	0.04	0.2	0.04	0	0.12	41	0
	12	0.74 \pm 1.7	—	—	—	0	0.32	37	0
Bahía Sloggett	6	11.2	0	0.02	0.12	0	1.18	12	0
55°01' S, 66°23.6' W									
Bahía Thetis	11	—	—	—	—	2.5 \pm 2.15	0.66	16	0.2
54°38.2' S, 65°13.3' W	14	0.18	2.1	0	0.06	7.78 \pm 4.2	2.02	12	0.13

* 0 means species was searched for but not found; — means no search.

rocystis zone, and no transects were run in the *Lessonia* zones. Competition-induced zonation seemed an obvious hypothesis, but it could not be tested because no return visits were planned. Santelices and Ojeda (1984b) removed *L. vadosa* and demonstrated that it restricts the *Macrocystis* distribution from shallow water at the nearby Isla Navarino, Chile. While four species of sea urchins were observed regularly, there was very rarely any indication of sea urchins grazing healthy plants; rather, urchins were found in crevices and holdfasts, where they appeared to eat drift algae, benthic diatoms, and perhaps small encrusting animals. Table 1 presents the densities of sea urchins and adult and juvenile *Macrocystis*. The mean holdfast diameters show that many of the plants were large relative to other areas, and the proportion of adult plants detached from the substratum suggests that this is a major source of mortality in these areas. It is clear that some areas have much more recruitment than other areas; this appeared to be correlated with the amount of light penetrating the surface canopy.

The kelp forests in the Colnett area averaged from 100 to 700 m wide by 2 to 5 km long. The *Macrocystis* was replaced by *Lessonia flavicans* at a depth of \approx 18 m, at which point the substratum became dominated by small cobbles which may allow the buoyant *Macrocystis* to drift away. There were many large patches (to 10 ha) in which almost all of the *Macrocystis* fronds were covered with small bivalves (perhaps *Gairmardia trapezina*, C. Moreno, personal communication) and predatory asteroids (mostly *Anasterias* and *Diplasterias* spp.) which had climbed onto the kelp to eat the bivalves. The kelp forests between Bahía San Antonio and Puerto Lasserre were 200–500 m wide (in depths of 5 to 25 m) and followed the coastline for many kilometres. In this area, too, there were many large patches of kelp plants being sunk by encrusting bivalves and predatory asteroids.

The south side of Isla de los Estados was much more exposed to the prevailing waves from the Westwind Drift, and the *Macrocystis* forests tended to be in the protected bays. In some of the protected bays such as

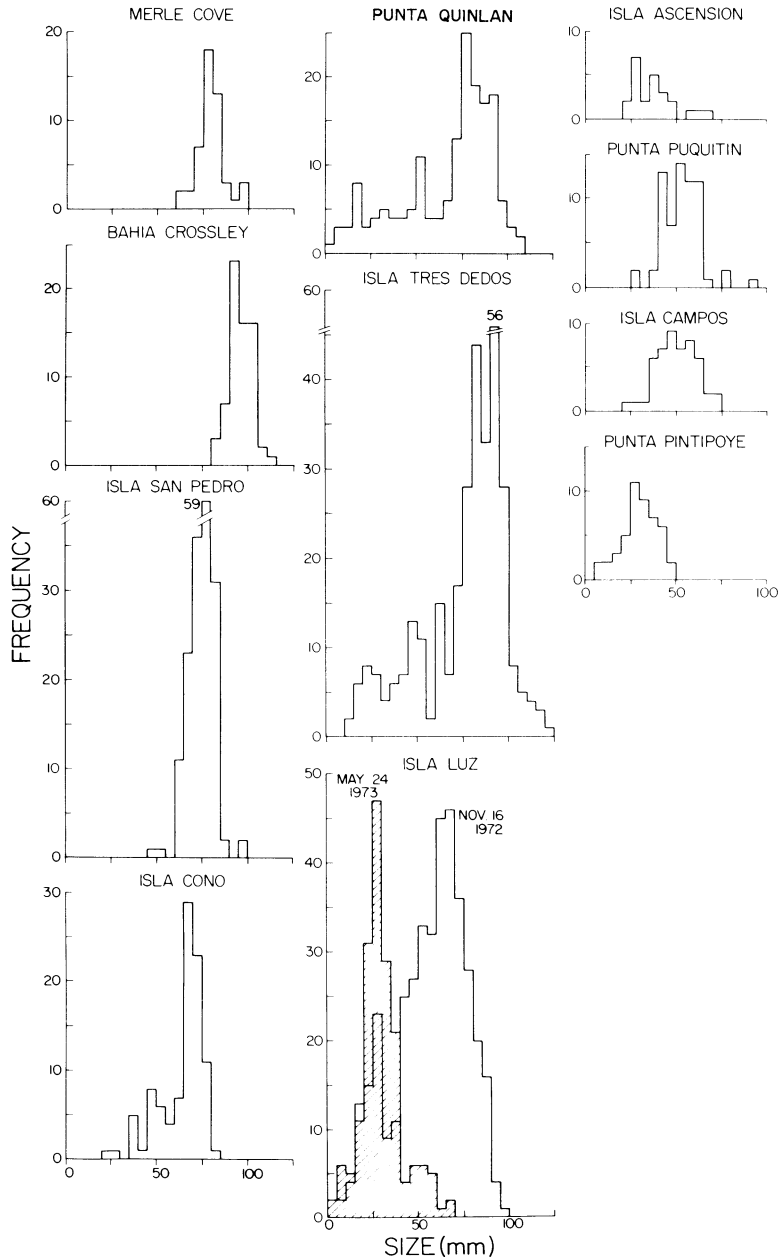


FIG. 2. Size-frequency histograms of test diameters of *Loxechinus albus* at different localities. Isla Cono (46°35' S, 75°31' W) was very exposed to prevailing surge and waves; Merle Cove (54°47' S, 64°0.4' W) and Bahia Crossley (54°48' S, 64° 42' W) were on Isla de los Estados and were semiexposed to swells; Isla San Pedro (47°43' S, 78°53' W) in the southern part of the Golfo de Pena was exposed. Punta Quinlan (45°24' S, 74°08' W), Isla Tres Dedos (45°18' S, 74°33' W) and Isla Luz (45°27' S, 73°56' W) were in the Bahía Darwin area; Isla Tres Dedos was exposed, Punta Quinlan moderately exposed, and Isla Luz protected from oceanic swells. However, Isla Luz was exposed to strong tidal currents which eliminated sedimentation. The hatched histogram represents urchins which appeared in the November 1972 urchin clearing area. Finally, Islas Ascension and Campos and Puntas Puquitin and Pintipoye were all in the semiexposed Golfo Corcovado area; the small test sizes indicated that these *Loxechinus* populations apparently had both been fished and had experienced some recruitment.

Puerto Vancouver there were areas with dense populations of *Loxechinus albus* (to 131 individuals/m² in one exceptional area) which had apparently grazed off all the macroalgae. In one such area in Merle Cove, haphazard 1-m² quadrat samples averaged 16.2 *Lox-*

echinus/m² (*N* = 20 samples), in another area the density was 12.0 *Loxechinus*/m² (*N* = 10), and in one patch the density was 70 *Loxechinus*/m² (*N* = 8). In all such areas there were essentially no macroalgae. The data in Table 1 were taken in healthy *Macrocystis* forests.

TABLE 2. Size and abundance of *Macrocystis* in southern fjords, at sites relatively protected from oceanic waves. Data are means \pm 1 SD.

Location	Depth (m)	Area surveyed (m ²)	<i>Macrocystis</i> density (no./m ²)		Holdfast diameter (cm)	No. stipes per plant	Proportion adults detached
			Juvenile	Adult			
Cta Awaia Kirrh 55°0' S, 69°02.2' W	11	50	0	0.56	19	6.4 \pm 6.8	0.25
Canal Ocasión 54°33.4' S, 71°59.7' W	5	50	0.34 \pm 0.82	0.32	23	13.9 \pm 8.7	0.06
	5	50	0	0.18	16	9.8 \pm 5.0	0.78
Punta Valparaíso 54°22.2' S, 71°21.7' W	6	50	0.28 \pm 0.61	0.44	17	9.5 \pm 8.3	0
	9	50	0.02	0.94	22	10.9 \pm 8.1	0
Bahía Campana 53°56' S, 70°49' W	5	100	0.08	0.26	38 \pm 14.0	7.3 \pm 4.9	0.20
	10	50	0.08	0.06	32 \pm 2.9	3.0 \pm 2.3	0
Isla Carlos III* 53°39.4' S, 72°14.8' W	5	100	0.19	0.21	28 \pm 13.2	9.0 \pm 7.3	0.08
	10	100	0.15	0.16	19 \pm 12.7	9.3 \pm 6.8	0.06
	10 (a)	100	0.54	0.35	17 \pm 5.6		0.13
	10 (b)	100	0.41	1.27	10 \pm 7.8		0
Isla Hunter 52°01.5' S, 73°13.3' W	5	100	0.03	0.43	16 \pm 6.0	9.7 \pm 5.4	0
	10	100	0	0.21	14 \pm 7.9		0

* (a) and (b) were the same transects in October 1972 and May 1973, respectively. The first three sites were visited in May 1973; the last three sites (except b) were done in October 1972.

Strong unimodal size frequency data skewed to the larger size classes in Merle Cove (Fig. 2) suggest that there is little successful recruitment and/or low survivorship of very young urchins.

The kelp forests studied along the southeastern part of Tierra del Fuego (Bahía Valentín, Sloggett, and Thetis) were similar to those along the north side of Isla de los Estados. The kelp forests were 500 m to 1 km wide and often followed the coastline for many kilometres. In one part of Bahía Valentín a patch of kelp 200 \times 500 m had been sunk by bivalves and asteroids. These kelp forests were only a few kilometres from the area studied by Castilla and Moreno (1982), Moreno and Jara (1984), and Santelices and Ojeda (1984a, b), and appeared essentially identical to their kelp forest. In all the kelp forests we visited in this area, there was a considerable amount of drift algae resulting from entanglement mortality and the sinking of kelp plants from heavy encrustation. Except for the Puerto Vancouver area, there was no evidence that *Loxechinus* overgrazed macroalgae.

Southern fjords

The main characteristic these sites have in common is that they are in areas relatively protected from oceanic waves. Table 2 gives the locations and summarizes the *Macrocystis* transects taken at these sites. The most striking aspect of the *Macrocystis* in most such protected sites was that they appeared brittle and unhealthy; in most cases the blades were almost entirely on the surface with relatively rare subsurface blades. Because of the lack of waves and surge to move them about, dense surface accumulations of blades intercept most of the light, and the subsurface areas are relatively dark. More important, most plants in these very protected areas appeared not reproductive, as sori on spo-

rophylls were rare. The first three sites were visited in May 1973.

Awaia Kirrh is the only site visited in the Beagle Channel. It is a protected site with heavy sedimentation on the plants and substratum. In the top 3–4 m there was a dense (2.6 individuals/m²; SD = 0.9; N = 10 quadrats) band of *Lessonia vadosa*. The shallower (6 m) *Macrocystis* were a little more dense and smaller (0.7 plants/m² and 15 cm holdfast diameter; N = 10 quadrats) than they were on the 11 m deep transect (densities 0.56 individuals/m² and 19 cm mean holdfast diameter; N = 28 quadrats). The 11 m deep transect had a relatively high (25%) proportion of detached plants. The *Macrocystis* were zoned between the *Lessonia vadosa* (3 m) and *L. flavicans* (16 m). The abrupt transitions suggest that the zones are maintained by interspecific competition for light. Finally, three divers recorded only two *Loxechinus* despite the fact that the substratum had an estimated 70% cover of loose fronds and other drift algal material; clearly food does not limit the *Loxechinus* population at this site.

We studied a small (100 \times 300 m) kelp forest in the very protected Canal Occasión where there was also much sedimentation on the algae and on the substratum. The *Macrocystis* were relatively shallow (mostly < 6 m) and most lacked subsurface fronds. Many *Macrocystis* had settled on fragile worm tubes and lifted off the substratum to float on the surface; most plants were tangled with each other or with drifting plants. Again, there was low fertility: 3 out of 31 and 5 out of 41 plants had well-developed sporophylls in two brief surveys of attached plants. Interestingly, many of the young plants which had become detached and floated to the surface had much more sporophyll material than the much larger attached plants. Presumably this is because the entire detached plant was near or on the

surface where it received proportionally more light. The two transects for this site (Table 2) were positioned to contrast two areas with different *Macrocystis* densities, sizes, recruitment, and proportion of detached plants. The percentage of detached plants (78%) is extremely high, and here resulted from settlement on unstable worm tubes. From ≈ 6 to 20 m there were very large *Lessonia flavicans*; most were > 2 m tall and 2 m wide. Below 20 m there was a forest of sea whip gorgonians and crinoids (1.2 individuals/m²; $N = 20$ 1-m² quadrats). No *Loxechinus* were seen.

The Punta Valparaíso site differs from the previous two sites because we observed a moderate current, no sedimentation, and a relatively heavy cover of understory red algae (58% cover; $SD = 16$; $N = 10$ quadrats at 11 m). The *Macrocystis* appeared much healthier and most were reproductive. Three divers recorded only 25 *Loxechinus*, all deep within crevices. Four *Lithodes antarctica* were observed; after one of these crabs was injured, > 25 myxinid hagfish appeared almost instantly to eat it.

The Bahía Campana site was visited in October 1972; it is in protected water with a fine silt covering the algae and substratum. The kelp forests covered an area of ≈ 400 m² and were in depths of 1–13 m. All the plants seemed to be rather young; only one had fertile sporophylls. Many of the plants had heavy settlements of bivalves on their fronds. The asteroid *Diplasterias brandti* was common ($\bar{X} = 1.6$ individuals/m²; 50-m² transect) and was consuming bivalves on the bottom and in the kelp fronds. *Loxechinus albus* was present and was observed consuming attached *Macrocystis*, but the urchins were rare and did not appear to affect the *Macrocystis* population. A few small lithodid crabs were seen.

One of the largest kelp forests observed in this area was at Punta Ballena, Isla Carlos III, in October 1972. The floating canopy covered an area of 80×200 m in depths of 1 to 15 m; there were isolated *Macrocystis* plants to depths of 20 m. From depths of 12 to 25 m there was a rather dense forest of *Lessonia flavicans* (0.7 individuals/m²; $N = 100$ 1-m² quadrats). The *Lessonia* plants were uniformly ≈ 2.5 m tall and each of their fronds shaded an area of 3–5 m². The distribution of the *Lessonia* on the transect was remarkably even; this and the large sphere of influence of these large plants suggests an hypothesis that this *Lessonia* population is limited by intraspecific competition for light, and that it similarly restricts the deeper distribution of *Macrocystis*. *Loxechinus* were not conspicuous, but 121 were collected in a 4×5 m area; four of these were observed eating *Macrocystis* sporophytes and three were observed eating *Lessonia* haptera.

The dense canopy cover of the small kelp bed at Punta Ballena suggested the hypothesis that the growth and recruitment of *Macrocystis* and understory species was limited by competition for light. To test this hypothesis we established, on 27 and 28 October 1972,

two almost adjacent 4×25 m plots in the middle of the kelp forest in depths of 4–7 m. Both plots were marked with floats and tagged nails. All the *Macrocystis* plants more than a few centimetres tall were removed from one plot by prying loose the holdfasts, while all the *Macrocystis* in the control plot were measured and tagged.

Upon returning on 18 May 1973 we found the kelp forest slightly larger (100×300 m). The experimentally cleared plot was a jungle of 391 adult *Macrocystis* plants plus 113 younger plants. Thus the mean *Macrocystis* density was > 5 plants/m². There was a total of 891 stipes or a mean density of almost 9 stipes/m². This recruitment and growth occurred during the 7 mo of austral summer. In addition there were three large plants which obviously had drifted into the clearing where they became entangled long enough for their haptera to become reattached; one of these reattached drifters was one of the tagged plants from the nearby control plot. Finally the cleared patch had a much heavier cover of understory algae, particularly *Gigartina skottsbergia*. Photographic measurements of the percent understory cover in 10 0.25-m² quadrats in the cleared and control plots showed a significantly ($P \leq .01$; arcsine-transformed data) higher cover in the cleared patch than in the control plot (24 vs. 2% covers, respectively).

The control plot in May 1973 looked much the same as the rest of the kelp forest, thus giving credibility to the growth and survivorship experiments. Of the 35 adult plants tagged on 26 October, seven were entangled by drift plants, and of these, two had all their stipes ripped off, and two more had lost most of their stipes and were senescent and near death. The remaining three plants had lost many stipes, but were still attached and healthy. One tagged plant had drifted about a metre and become reattached, as had the one that drifted into the experimental clearing. In addition to the plants affected by drift plants, 4 of the original 35 plants appeared to have lost in intraspecific competition for canopy space and light, because they had only a few old brittle fronds, no holdfast growth, and a net loss of stipes. Of the remaining 24 plants plus the 3 entangled but unharmed plants, the mean holdfast area increased from 238 to 463 cm², a mean increase of holdfast area of 130%.

Isla Hunter was visited on 22 October 1972. It is a protected site with a flushing current; in many ways it is similar to Punta Valparaíso. Mussels (mostly *Aulacomya ater*) extend from the intertidal to ≈ 5 m deep, covering an estimated 80% of the hard substratum. The mussels were being eaten by *Diplasterias brandti* and *Lithodes antarctica*, which were abundant (> 30 seen by two divers). The relatively high abundance of *Lithodes* was interesting, particularly because they appear to be effective predators on mussels and other invertebrates.

While no transects were taken, we also visited Punta

Dashwood (52°24' S, 73°39.7' W) and Estrecho Collingwood (51°52' S, 73°43.6' W) on 19 May 1973. Punta Dashwood had a small kelp forest growing over a virtual 100% cover of mussels, *Aulacomya ater*, which in turn were being eaten by asteroids and *Paralithodes*. The *Macrocystis* settled on mussels and occasionally smothered and killed them and floated free, but in most cases the lateral growth of the *Macrocystis* haptera was sufficiently fast to keep the plant anchored. The Estrecho Collingwood site was similar but seemed to have a higher current and fewer *Macrocystis*.

Summarizing, these semiprotected sites were characterized by dense canopies, relatively high amounts of drift and, usually, sedimentation. There was evidence of canopy competition for light, but sea urchins were rare and were never observed overgrazing the kelps.

Isla Knocker area, Golfo de Trinidad

Isla Knocker is semiexposed to the strong oceanic swells coming into the Golfo de Trinidad. The substratum is very clean with no sign of sedimentation. The intertidal is dominated by a conspicuous band of the large *Durvillaea antarctica*. The *Macrocystis* population occurs on the exposed side of the island in a shallow (3–5 m) belt, zoned between the *Durvillaea* above and the sea urchin *Loxechinus albus* below. Table 3 records the densities of sea urchins and *Macrocystis* from 50-m haphazardly placed belt transects taken from different locations around the small island. This site differs from previous sites because sea urchins at high densities were obviously overexploiting the kelps. *Loxechinus albus* was the only sea urchin species observed eating *Macrocystis*; the *Arbacia dufresnei* and *Pseudechinus magellanicus* were not definitely seen feeding, but appeared to be subsisting on drift, diatoms, and possibly very small sporophytes. The transects which did have *Macrocystis* were taken from the exposed side of the island where the strong surge appeared to keep *Loxechinus* from exploiting the kelps along a shallow ledge. While this was not documented in the transect records, the *Macrocystis*-free transects were dominated by 90–100% cover of encrusting coralline algae with patches of *Codium* and *Desmarestia* spp., the latter covering 10 to 15% of the area. It is interesting to note that *Codium* and *Desmarestia* also occur in urchin-dominated areas at Amchitka Island, Alaska (Dayton 1975a; P. K. Dayton, *personal observation*). This urchin-coraline pavement was a classic example of sea-urchin-dominated barren grounds (Lawrence 1975). Within the small kelp forest there was a sparse understory of red (*Plocamium*, *Rhodomyenia*, *Gigartina*, and a *Delesseriaceae*), green (*Codium* and *Ulva*), and brown (*Desmarestia* and *Dictyota*) algae.

The distribution of the intertidal *Durvillaea* may also be influenced by *Loxechinus* grazing. The largest and probably oldest individuals of *Durvillaea* occurred highest in the intertidal zone, but there seemed to be

a very effective recruitment all the way to the lower limit of the population, where *Loxechinus* were seen grazing young plants and fronds from the larger plants above. This hypothesis gains support from the observation of *Durvillaea* extending to >2 m depth on an exposed vertical wall where the oceanic swell appeared to reduce the effectiveness of the *Loxechinus* foraging. The following *Durvillaea* data were obtained from the protected side of the island by intertidal work during low tide and by the removal experiments discussed below. The *Durvillaea* along the upper margin of its distribution had a sparse density (estimated at 2.5 individuals/m²) of relatively large plants (mean holdfast diameter 18.2 cm; SD = 8.0; N = 10 plants) and no juveniles. In contrast, the adults in the lower intertidal were denser (estimated at 4.4 individuals/m²) and had smaller mean holdfast diameters averaging 8.9 cm (SD = 3.0; N = 10 plants), but in this zone there were at least another 20 juveniles/m². There was a band of *Loxechinus* ≈ 1 m below the *Durvillaea*; 10 0.25-m² quadrats taken in this band had a mean of 18.2 *Loxechinus* each (SD = 6.8). It was apparent that these *Loxechinus* were foraging up toward the intertidal during neap tides or calm seas; many had fragments of *Macrocystis* and *Durvillaea* and some were holding pieces of *Durvillaea* still attached to the holdfast above.

Durvillaea/Loxechinus removal experiments

It was obvious from these data and from observations in several other areas around Isla Knocker that *Loxechinus albus* occurred in high densities and actively foraged on macroalgae, especially *Durvillaea* and *Macrocystis*. The luxuriant *Durvillaea* population existed in an intertidal refuge. In most places the *Macrocystis* was entirely absent from urchin-coraline pavement, which seemed to be an ideal macrohabitat. When *Macrocystis* did occur, it was in areas where the wave exposure apparently reduced the foraging efficiency of the *Loxechinus*. The *Macrocystis* appeared to be young plants existing in a fugitive situation in the dynamic buffer zone between *Durvillaea* and *Loxechinus*. This hypothesis was tested with two sets of removal experiments. On the lee side of the island the *Durvillaea* were removed from a 4 × 5 m area; no *Loxechinus* were removed because it was apparent that they were foraging actively and would quickly invade a removal area. There were no *Macrocystis* in the area, but the *Loxechinus* were observed feeding on drift *Macrocystis*. On the exposed side the *Durvillaea* were removed from a 4 × 3 m area. Below the *Durvillaea* removal zone there was a band of *Macrocystis* (Table 3). Below the *Macrocystis*, the *Loxechinus* were removed from an approximately 3 × 7 m ridge surrounded by sheer walls and a sand barrier which might inhibit *Loxechinus* immigration. After only one low tide on a partially sunny day, the coralline understory below the *Durvillaea* was badly bleached and the re-

removal area changed from red to a conspicuous white patch; this is reminiscent of the obligate understory of Dayton (1975b). In each experimental treatment an adjacent undisturbed area was surveyed as a control. There was an isolated *Lessonia nigrescens* plant adjacent to the *Durvillaea* removal site on the protected side of the island. The transects and removal experiments were done 30 and 31 October and 1 November 1972.

When we returned at the end of the austral summer on 20 May 1973, we observed dramatic differences between the removal treatments and the adjacent controls. In both intertidal *Durvillaea* removal areas an almost 100% cover of *Macrocystis* extended as high into the intertidal as the *Durvillaea* used to grow. In a shallow but wetter depression in this intertidal *Durvillaea* removal zone there were a few large (> 2 m long) *Macrocystis* and *Durvillaea*. Interestingly, the barnacle zone above the *Durvillaea* removal area had significantly (t test: $P \leq .01$) more barnacles than on the adjacent control. This may result from the whiplash of the massive *Durvillaea* fronds interfering with barnacle recruitment; this hypothesis is supported by the observation that the larger, probably more vulnerable *Elminius* are more strongly affected than *Chthamalus*. Within the upper *Durvillaea* removal area there were also more *Mytilus* and *Perumytilus* and a dense cover of understory algae, including an almost 90% cover of *Iridaea*, *Polysiphonia*, *Ballia*, *Rhodoglossum*, *Chaetangium*, *Plocamium*, *Ceramium*, and *Colpomenia*. The intertidal understory composition changed in the mid-intertidal clearing as *Scytosiphon* and *Adenocystis* took over $\approx 70\%$ of the cover, the rest of the space being occupied by *Chordaria*, *Cladophora*, *Spongomorpha*, *Bryopsis*, *Ulva*, and *Codium*. These algae occurred in the control area, but were very rare, together occupying <5% of the cover compared to 90% under the *Macrocystis* and *Durvillaea* in the *Durvillaea* removal site. The lower intertidal removal plot had to be evaluated by diving; the understory algae appeared similar but were not recorded. Five 0.25-m² quadrats recording *Macrocystis* and *Durvillaea* recruits were taken at each of five lower intertidal levels, starting at ≈ 0.3 m above MLW and extending to ≈ 0.5 m below MLW; Fig. 3 shows the increased *Macrocystis* settlement in the *Durvillaea* removal experiments. The control area had no *Macrocystis* and no *Durvillaea* which appeared small enough to have been recruited during the summer. *Lessonia nigrescens*, apparently recruiting from the single individual, were relatively common within 3 m of the adult plant, and seemed to reflect limited spore dispersal (Dayton 1973) into the cleared area.

Due to very limited time, quadrat count data were not taken from the exposed *Durvillaea* removal site. However, the algae were removed from 0.25-m² quadrats and were separated and weighed. All such data are very low estimates because a great deal of material was

TABLE 3. Mean densities of sea urchins and *Macrocystis* at Isla Knocker, Punta Alert (49°52.8' S, 75°13.3' W), 30 October–1 November 1972. Sites were semiexposed to strong oceanic swells. No detached *Macrocystis* were observed.

Depth* (m)	Density (no. individuals/m ²)				
	<i>Loxechinus</i> †	<i>Arbacia</i>	<i>Pseudechinus</i>	<i>Macrocystis</i>	
				Adult	Juvenile
4	1.88	0.16	0.22	0	0
6	11.56	0	0	0	0
7	1.12	0	0	0	0
5	6.96	0.46	0	0	0
4	5.72	0.22	0	1.30	0
3	1.04	0	0	0.48	7.00
6	1.72	0.10	0	0.06	1.64
5	1.50	0.06	0	1.36	6.00
3	0.84	0	0	1.54	4.00
3 ^a	11.2	14.0	0	0	0
7 ^a	2.8	12.2	0	0	0
13 ^a	8.4	4.2	0	0	0
7	2.2	0.04	0.40	0	0.14
4 ^b	6.1	0.13	0.50	0	0.12
5	4.72	0.50	0	0	0
3	1.04	0	0	0.56	0

* All transects were 50 m² except (a) which were 20 m² and (b) which was 30 m².

† *Loxechinus* densities in the lower intertidal *Macrocystis* zone were 1.4/m², and 1 m below it were 38.4 and 44.8 individuals/m² (N of each = 10).

lost while being collected in the heavy surge over the intertidal habitat. Two such quadrats from the upper intertidal zone had 41 and 36 *Macrocystis* with respective lumped masses of 1250 and 870 g. The same quadrats had 1 and 7 *Durvillaea* respectively, weighing 95 and 980 g. Two quadrats from the mid-intertidal zone had 45 and 26 *Macrocystis* (720 and 995 g, respectively) and 7 and 6 *Durvillaea* (361 and 695 g). Four 0.25-m² quadrats from the lower intertidal zone had 13, 23, 22, and 30 *Macrocystis* (350, 500, 536, and 845 g, respectively) and 24, 9, 2, and 6 *Durvillaea* (505, 625, 75, and 155 g, respectively). Incidentally included in the collections were *Ballia*, *Rhodomenia*, *Griffithsia*, *Lophurella*, *Gigartina*, and several Delesseriaceae red algae, *Desmarestia*, *Lessonia*, *Codium*, and *Heterosiphonia*. The control area had no *Macrocystis* and very few understory plants.

The *Loxechinus* removal experiment at Isla Knocker produced dramatic results (Fig. 3); the area had a thick growth of *Dictyota* and 79 *Macrocystis*; of the *Macrocystis*, 21 had fronds to the surface and 19 had fertile sporophylls. Before the urchins were removed the area had no macroalgae. The control reef had no macroalgae. Ten 1-m² quadrats were placed in each of six depths on the control reef. The mean *Loxechinus* density was 32.4 individuals/m² (SD = 10.6) at 3 m, 13.9 (SD = 11) at 5 m, 12.0 (SD = 8.4) at 6 m, 21.0 (SD = 20.2) at 8 m, 6.5 (SD = 6.8) at 10 m, and 0.7 (SD = 0.8) at 12 m. Thus even though some *Loxechinus* may have moved from the control to the treatment area, enough remained in the control to maintain an urchin-coraline

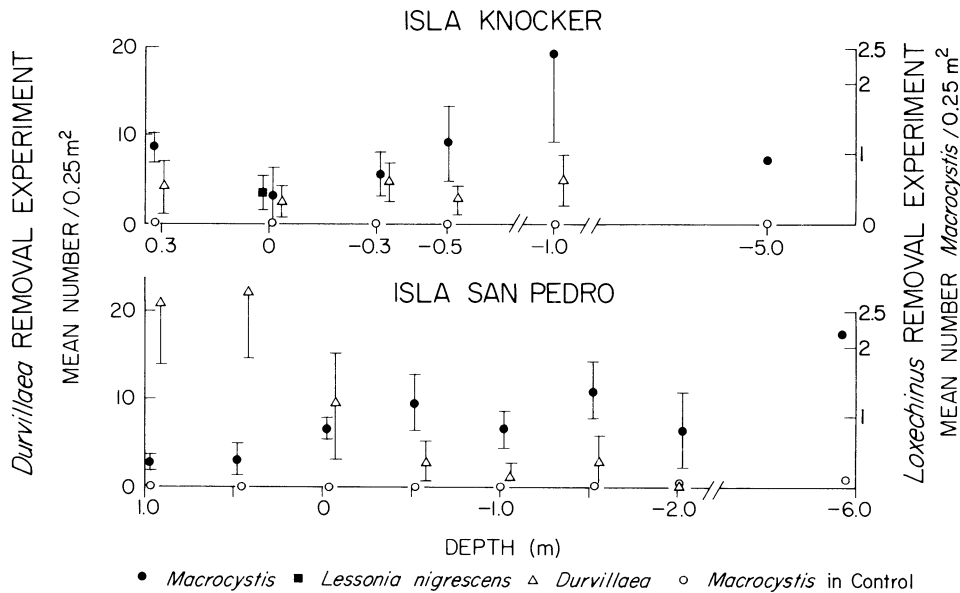


FIG. 3. Effects of *Durvillaea* removal (left) in the intertidal (+1 to -1 m) and *Loxechinus* removal (right) in the subtidal (-1 to -6 m) on kelp recruitment between 1 November 1972 and 20 May 1973. The data are mean (± 1 SD) number per 0.25 m², except for the *Macrocystis* at -5 and -6 m depths, which are number per square metre.

barren which dramatically contrasted with the lush algal growth on the experimental reef.

Summarizing, this area appears to be a classical urchin-barren (Lawrence 1975, Hagen 1983) with *Macrocystis* occurring opportunistically between intertidal *Durvillaea* and deeper *Loxechinus* which do not forage much into shallow water, presumably because of the severe wave exposure. *Durvillaea* removal experiments allowed an upward invasion of *Macrocystis*, a heavy cover of other algae and an increased recruitment of barnacles in higher zones. A *Loxechinus* removal allowed a downward extension of *Macrocystis* and understory algae. Fertile *Macrocystis* occurred in *Durvillaea* and *Loxechinus* removal areas, demonstrating that these are acceptable *Macrocystis* habitats but for the biotic restrictions.

Golfo Trinidad to Puerto Edén

All three sites in this area were visited in early November 1972. The Bahía Tom transects (Table 4) were east of Isla Vallack on shallow granite ridges which run through a sandy-cobble bottom. There was a moderate amount of sedimentation and small patches of *Loxechinus* and other urchins. The densities of *Loxechinus* were relatively low and most of them were consuming only drift *Macrocystis*, which was plentiful. Many of the cobbles had large clumps of *Desmarestia*.

The *Macrocystis* morphology in this protected habitat is very different: many fronds, apparently healthy with active growth tips, simply lie along the bottom with no indication of any pneumatocysts. (A similar morph has been observed in New Zealand by Moore

[1943] and Gerard and Kirkman [1984].) The growth tips also were unusually wide; one measured 80 cm across only 20 cm from the tip. The juvenile plants were almost square; for example, one small plant was 8 × 9 cm and another was 11 × 12 cm. The nonfloating but healthy stipes came from normal *Macrocystis* holdfasts, but none of at least 50 of these prostrate *Macrocystis* had any sporophyll material. The transects (Table 4) were taken from granite ridges on the other side of a headland exposed to a longer fetch. Here most of the plants had vesicles and normal floating canopies. The short (10 × 1 m) transect at 3 m depth was placed haphazardly and missed the kelp plants which were there; however, 15 holdfasts near the transect were evaluated: they had a mean diameter of 10.3 cm (SD = 4.6); 53% were fertile and 4 were being damaged by *Loxechinus* eating the stipes. The 2- and 5-m transects were placed in areas with relatively young and uniform plants, of which only two were recorded as being severely grazed by *Loxechinus*. The deeper transects were over a silty, relatively bare substratum; the few plants seen were large but seemingly senile. We returned to the site in May 1973 and found more obvious signs of *Loxechinus* grazing in patches, but otherwise the area appeared similar.

The Isla Stratford was interesting because there is a small, somewhat enclosed bay with *Durvillaea* growing in the intertidal zone and a subtidal urchin-barren zone. The *Loxechinus* density immediately below the *Durvillaea* was 26.4 individuals/m²; (SD = 9.5; N = 10 quadrats). Fifteen 1-m² quadrats at 1.5 m depth had a mean of 8.3 (SD = 3.29) *Loxechinus*/m²; at 3.0 m depth,

3.9 (SD = 2.44); at 4.5 m depth, 1.1 (SD = 1.23); and at 5.5 m depth, 1.5 (SD = 1.41) *Loxechinus*/m². But the area immediately around a corner to the east was somewhat more protected and had a sparse population of *Macrocystis* being eaten by *Loxechinus* (transects in Table 4 were done here). The few adult plants had *Loxechinus* in their holdfasts and in the stipes, but in shallow water there was a relatively heavy recruitment of juvenile *Macrocystis* between 1 and 4 m tall. When we returned in May 1973, all the *Macrocystis* were gone and the old transect areas had become an urchin-barren. There were a few *Macrocystis* in the low intertidal area.

Both the Bahía Tom and Isla Stratford sites had relatively large numbers of lithodid crabs; they were often on the kelp fronds, where they seemed to be eating encrusting animals. The Isla Stratford site had large clumps of benthic mussels (*Aulacomya ater*) extending as deep as 12 m.

The substratum and plants at Puerto Edén were covered with a great deal of silty sediment: there were no *Loxechinus* seen in our transects. The *Macrocystis* grew as deep as 12 m, but the main kelp forest started at 8 m and became extremely dense at 2 m (Table 4). These were relatively large plants and the kelp forest was almost too thick to swim through. An interesting asteroid predator, *Solaster regularis*, was unusually abundant here. There were 6 *Solaster* on the 8-m transect and 17 on the 4-m transect: of these 83 and 59%, respectively, were feeding on asteroids plus one *Pseudochinus*. The abundant crinoids in the area had an extremely effective swimming escape response to *Solaster*.

Golfo de Penas region

Isla Scout is at the northern end of Canal Messier. It was visited on 5 November 1972. The heavy cover of *Durvillaea* suggested that the site was moderately exposed to waves; the *Macrocystis* seemed restricted to relatively shallow water where there were patches of *Loxechinus*-coralline pavement and patches of kelp with only scattered *Loxechinus* (Table 5). The *Loxechinus* distribution below the kelps was also patchy with some extreme densities of >100/m², but in non-urchin areas there was a 100% cover of *Desmarestia*, *Dictyota*, *Ulva*, *Hymenena*, *Gigartina*, and juvenile *Macrocystis*. There was a highly visible layer of fresh water from 1 to 3 m at the surface (see Pickard 1971). The *Macrocystis* fronds appeared healthy, but there were few *Loxechinus* in the freshwater depths. As in most other areas, there were many small lithodid crabs on the bottom and in the kelp fronds.

Isla San Pedro is located in the south part of the Golfo de Penas. The study area was near the lighthouse. There was a thick band of *Durvillaea* in the intertidal, and most of the subtidal substratum is an urchin-barren zone with 10 to >100 *Loxechinus*/m²; 30 1-m² quadrats averaged 41.3 *Loxechinus*/m² (SD = 14.7).

Some small lithodids were seen at this site. Isla San Pedro is somewhat more exposed than Isla Knocker and had a small, shallow (<5 m depth) kelp forest. The transects in Table 5 were taken in the kelp forest or immediately adjacent to it, in November 1972.

Durvillaea and *Loxechinus* removal experiment

Durvillaea and *Loxechinus* removal experiments similar to that at Isla Knocker were established. The removal was done by divers at high tide; the waves prevented the removal of a thin strip of large *Durvillaea* at the topmost levels; otherwise, *Durvillaea* was removed from a 3 × 5 m area, and the *Loxechinus* were removed from a small 1–3 m deep reef at ≈3 m depth. The *Loxechinus* removal area had no sand barrier, but the bottom of the reef had sheer walls which we hoped would reduce immigration in what appeared to be a very surgy area.

When we returned on 22 May 1973, we found that the *Macrocystis* had invaded both the *Durvillaea* and *Loxechinus* removal areas. Fig. 3 demonstrates the high recruitment of both *Macrocystis* and *Durvillaea* across the rather broad *Durvillaea* removal area. The *Durvillaea* control area had a very thick cover of *Durvillaea* which impeded our survey. No small *Macrocystis* were seen, but it was not possible to evaluate whether or not there was *Durvillaea* recruitment in the control. The *Loxechinus* removal ledge was similar to that at Isla Knocker, in that there was a strong downward invasion of *Macrocystis* into the *Loxechinus* removal area. Furthermore, 25 of the 47 plants had large sporophyll bundles. In this case, the *Loxechinus* had returned in large numbers and were all over the lower parts of the *Macrocystis* plants. It appeared as though the *Loxechinus* had eaten many small *Macrocystis* and were rapidly killing the adults, because we saw at least six holdfasts from which all the stipes and sporophylls were removed. Interestingly, the adjacent control ledge seemed to have fewer *Loxechinus* and seven small (1–3 m tall) *Macrocystis*. It appeared as though some of the *Loxechinus* had abandoned the control reef to invade the experimental reef where the *Macrocystis* were growing.

Isla Cono is a small island in the mouth of Bahía San Andres outside the Tres Montes Península north of the Golfo de Penas. It was the southernmost area we visited with a conspicuous *Lessonia nigrescens* zone. Isolated *Lessonia nigrescens* did occur far to the south (indeed, almost one-third of the plants in the *Durvillaea* zone on a highly exposed islet in the mouth of the Golfo Trinidad were *L. nigrescens*), but here it occupied a large, distinct intertidal zone, and it appeared to have displaced *Durvillaea* into a thin, higher level zone (see Santelices et al. 1980). On the lee side of Isla Cono the *L. nigrescens* disappeared and was replaced by *Durvillaea*.

There was a kelp forest of ≈100 × 400 m in the lee

TABLE 4. Mean densities (\pm SD) of sea urchins and *Macrocystis* in the Golfo Trinidad region. All sites are well protected from wave action. All transects were done in November 1972.

Location	Depth (m)	Area surveyed (m ²)	Urchin density (no./m ²)			Macrocystis density (no./m ²)
			<i>Loxechinus</i>	<i>Arbacia</i>	<i>Pseudechinus</i>	Juvenile
Bahía Tom 50°11.25' S, 74°47.9' W	3	10	1.6 \pm 1.6	0.6 \pm 1.3	1.9 \pm 4.5	0
	2	50	1.0 \pm 3.1	0*	2.2 \pm 6.1	0.8
	5	50	0.8 \pm 2.0	0.2 \pm 3.0	3.1 \pm 5.0	0.2
	11	100	0.1	0	0.2	0
	14	100	0.02	0	0	0
Isla Stratford 50°11.5' S, 74°47.9' W	3	25	7.0 \pm 5.7	4.8 \pm 8.5	0	10.5 \pm 8.1
	6	100	0.5	0.5	0	8.3
	5	30	5.2	0	0	0
	3	17	15.6	0	0	0
	2	15	33.2	0	0	0
Puerto Edén 49°09.8' S, 74°26.2' W	8	50	0	0.92	0.2	0
	4	50	0	0.20	0.1	0
	2	50	0	0	0	0.64

* 0 means species was searched for but not found; — means data not collected.

side of the island. The transects (Table 5) were run on the largest ledge with kelp plants; these sites were chosen for the heavy kelp and are not representative of the generally thinner kelp forest. Most of the habitat was of large boulders 2–5 m in diameter. Most of the boulders in the area were dominated by *Loxechinus* (20 to >100 individuals/m²) and coralline algae, but there were boulders with various combinations of *Loxechinus* and kelp densities, always inversely correlated.

Several experiments were attempted on 8 November 1972. Thirty kelps on five large boulders were individually tagged to measure growth. The mean holdfast diameter was 8.9 cm (SD = 4.7), and the mean stipe number was 3.5 (SD = 1.8); all the plants were fertile. The *Loxechinus* were removed from five different boulders with relatively high (30–80 individuals/m²) *Loxechinus* densities. Finally, we thought that the asteroid *Meyenaster gelatinosus* stampedes *Loxechinus* from rocks (Dayton et al. 1977), so we placed *Meyenaster* on three boulders with similar *Loxechinus* densities. Bad weather forced us into more protected areas of the Golfo de Penas, and when we returned 3 d later, the *Meyenaster* were still on the same rocks and the *Loxechinus* density was reduced by almost half.

When we returned to Isla Cono on 23 May 1973, a very strong surge prevented accurate assessment of the tagged plants. It appeared, however, that they had suffered \approx 50% mortality and had very little net growth. The urchin removal and *Meyenaster* addition experiments effectively removed *Loxechinus*, and algae carpeted the boulders. With the exception of one *Meyenaster* addition boulder adjacent to a boulder with *Macrocystis*, none of the urchin removal boulders which were >30 m from other *Macrocystis* acquired *Macrocystis*, but they did have 100% covers of *Dictyota*, *Gigartina*, and other unidentified red algae. *Macrocystis* may not have invaded these latter boulders because the effective spore dispersal is limited (see Dayton et

al. 1984). All of the control boulders maintained their *Loxechinus* populations and continued as urchin-coraline pavements.

Table 5 also presents the data collected on 9 and 10 November in the protected areas of the northern Golfo de Penas. Isla Waller had a small (50 \times 200 m) kelp forest along a very shallow ledge. Here the *Loxechinus* seem less effective in shallow water, perhaps because the surge and abundant *Meyenaster* knock them off the rather steep walls of the reef. The kelp forest on Isla Baja is on large boulders isolated from each other by a sand substratum. Many of the boulders had high densities of *Loxechinus* and others had few *Loxechinus* and dense growths of kelps. The two transects in Table 5 were across the largest boulders we could find with *Macrocystis*, and are not representative of what appeared to be dynamic and interesting boulder-to-boulder dispersal relationship between the urchins, *Meyenaster*, and kelps. Experiments similar to those of Isla Cono were established, but we were not able to return.

Roca Logan (46°48.47' S, 75°15.87' W), at the entrance to Puerto Barroso, had a fringing *Macrocystis* forest between 1 and 5 m depths. These were older plants interposed among patches of *Loxechinus* which appeared to maintain a barren ground in deep waters while occasionally concentrating on *Macrocystis* in shallow water. In several instances dark brown holdfasts from which the stipes had long since been lost were growing new stipes.

Most of the sites in the Golfo de Penas region had large urchin-coraline pavement barren zones. *Durvillaea* were conspicuous in the southerly sites but appeared to be replaced as the intertidal dominant species in the northern Isla Cono site by *Lessonia nigrescens*. Removal experiments again demonstrated that *Durvillaea* and *Loxechinus* can restrict the distribution and abundance of *Macrocystis*. Because *Loxechinus* has effective behavioral defenses to the asteroid *Meyenaster*

TABLE 4. Continued.

<i>Macrocystis</i> density (no./m ²)	Mean holdfast diameter (cm)	Mean no. stipes per plant
Adult		
0	—*	—
0.4	13.8 ± 6.4	10.1 ± 7.7
0.5	15.8 ± 5.5	10.2 ± 12.9
0.1	—	—
0.1	—	—
0.08	15.0 ± 4.2	—
0.01	—	—
0	—	—
0	—	—
0	—	—
0.32	—	—
0.78	—	—
3.4 ± 8.1	15.8 ± 6.7	—

gelatinosus, *Meyenaster* does not effectively reduce the *Loxechinus* density; however, it does stampede the urchins from large boulders, allowing algae a temporary refuge. This *Loxechinus-Meyenaster*-algae relationship was seen in several areas with large boulders and was demonstrated experimentally at Isla Cono. Similar relationships have been reported in the North Pacific by Schroeter et al. (1983) and Duggins (1983).

The urchin and *Macrocystis* densities for the Bahía Darwin area are presented in Table 6. All the described data in this area were collected in November 1972. *Loxechinus* size frequency data are in Fig. 2. The areas around Isla Tres Dedos and Isla Auchilu had very high densities of *Loxechinus*; the data on Table 6 represent dives in several areas as the RV *Hero* moved about unsuccessfully searching for a kelp forest. The three transects which had *Macrocystis* are not representative, as we searched many kilometres for those few patches of kelp. There was highly significant negative correlation ($P < .001$) between kelps and urchins in quadrats with and without kelps on the transects. The adult *Macrocystis* were young plants, probably <1 yr old, and were all on the edges of ledges where strong waves appeared to reduce the efficiency of the *Loxechinus* foraging. *Lithodes antarctica*, many in mating pairs, were common here.

The most interesting observation was the perfect association of young *Macrocystis* (from blade stage plants to those 2–3 m tall) with large clumps of *Desmarestia ligulata*. A total of 620 young *Macrocystis* were seen on the transects and elsewhere, and all were growing among clumps of *Desmarestia*. We never saw *Loxechinus* eating *Desmarestia*, and it was apparent that the *Loxechinus* did not move into an area swept by

TABLE 5. Mean densities (±SD) of sea urchins and *Macrocystis* in the Golfo de Penas region. Data were collected in November 1972.

Location	Depth (m)	Area sur- veyed (m ²)	Urchin density (no./m ²)			<i>Macrocystis</i> density (no./m ²)		Mean holdfast diameter (cm)
			<i>Loxechinus</i>	<i>Arbacia</i>	<i>Pseude- chinus</i>	Juvenile	Adult	
Isla Scout 47°57.5' S, 74°40.5' W Semi exposed	3	50	2.5	—*	—	13.3 ± 5.6	2.8	12.1 ± 5.4
	5	50	6.8 ± 8.2	6.0 ± 5.9	0*	33.4 ± 14.8	2.9	8.5 ± 4.7
Isla San Pedro 47°43.2' S, 74°53.3' W Very exposed	3	50	—	—	—	13.8	3.9	—
	10	20	7.6 ± 4.6	—	—	0	0	—
	4	30	1.2	0	0	0	1.6	—
	5	30	3.4	0.4	0	0	0	—
	11	30	4.7	1.1	0.5	0	0	—
Isla Cono 46°35.3' S, 75°30.6' W Very exposed	1	10	—	—	—	31.0 ± 18.6	5.5 ± 2.3	7.9 ± 3.7
	3	10	—	—	—	38.4 ± 14.2	4.4 ± 2.1	9.6 ± 10.8
	6	50	0.06	1.2	2.4	8.8 ± 4.0	0.4 ± 1.1	10.7 ± 3.7
	10	50	0.08	0.92	2.7	2.3 ± 3.0	0.5 ± 1.4	10.6 ± 5.5
	5	50	0.6 ± 3.2	4.1 ± 5.0	1.1 ± 2.0	1.7 ± 4.6	1.1 ± 1.3	—
	2	10	0	0	0	0	3.0	8.6 ± 4.6
Isla Waller 46°48.4' S, 75°15.8' W Protected	3	50	1.1 ± 1.8	0.1 ± 3.0	0	0	4.1 ± 3.5	—
	5	30	3.6	1.2	1.7	3.7	0.7	15.3 ± 7.5
	8	30	6.0	5.1	3.1	0.9	0.1	19.3 ± 6.4
Isla Baja 46°43.0' S, 75°15.2' W Protected	5	30	2.2	2.6	0	0.9	0.1	13.7 ± 1.5
	6	30	4.1	2.3	0	0.8	0	—

* 0 means species was searched for but not found; — means no search.

TABLE 6. Mean densities (\pm SD) of sea urchins and *Macrocystis* in the Bahía Darwin area. All data were collected in November 1972.

Location	Depth (m)	Area surveyed (m ²)	Urchin density (no./m ²)			<i>Macrocystis</i> density (no./m ²)		Mean holdfast diameter (cm)
			<i>Loxechinus</i>	<i>Arbacia</i>	<i>Pseudochinus</i>	Juvenile	Adult	
Isla Tres Dedos 45°18.2' S, 74°33.3' W Exposed	5	30	3.2	2.1	1.8	0.3	0.03	14
	6	30	3.5	1.8	1.7	0.6	0.03	13
	5	16	40.4	1.8	0*	0	0	0
	2	15	6.3	4.3	3.5	0	0	0
	2	15	7.0	4.2	3.3	0	0	0
	3	5.25 ^a	101	—*	—	0	0	0
Isla Auchilu 45°20.6' S, 74°33.3' W Exposed	5	4.0	40.4	1.7	0	0	0	0
	6	50	—	—	—	11.5 \pm 8.2	0.9	14.7 \pm 5.3
Canal Unicornio 45°24.3' S, 74°15.8' W Protected	6	3.75 ^a	9.16	0	0	0	0	0
	3	50	—	—	—	4.7 \pm 39	10.4 \pm 7.0	10.5 \pm 6.8
	6	10 ^b	10.0	2.4	50.4	0	0	0
	5	10 ^b	68.9	64.0	29.6	0	0	0
	3	10 ^b	1.2	5.2	0	0	0	0
	6	50	—	—	—	0.7	0.4	12.0 \pm 7.1
	7	25	24.8	6.1	45.6	0	0	0
	3	2.5 ^a	0	1.2	5.2	0	0	0
Punta Quinlan 45°23.5' S, 74°08.0' W Moderately exposed	5	2.5 ^a	68.8	4.0	29.6	0	0	0
	6	2.5 ^a	10.0	2.4	50.4	0	0	0
	5	50	—	—	—	1.0 \pm 1.2	1.8	9.8 \pm 5.6
	10	30	7.7	16.8	6.8	0.5	0.3	6.0
	4	50	—	—	—	1.4 \pm 1.8	1.8	12.6 \pm 7.9
	5	10	16	13.2	17.2	0	0	0
	6	50	12.5	2.2	0.1	0.42	0.7	19.3 \pm 7.8
	9	3.75 ^a	7.7	16.8	8.0	0	0	0
	8	2.75 ^a	16	13.2	5.2	0	0	0
	2	2.75 ^a	91.6	17.2	12.6	0	0	0
	3	2.75 ^a	76	4.0	16.4	0	0	0
	5	2.75 ^a	60	2.4	14.4	0	0	0
	6	2.75 ^a	33.2	2.4	14.4	0	0	0
	8	2.75 ^a	6.8	18.8	20.0	0	0	0
9	2.75 ^a	0	3.2	7.2	0	0	0	
Isla Luz 45°27.2' S, 73°55.6' W Protected	4	50	2.1	—	—	1.4 \pm 1.8	1.4 \pm 1.8	12.6 \pm 7.9
	5	50	2.0	0.3	0.08	0.4	0.7	19.3 \pm 7.8
	2	2.75 ^c	73.6	27.2	26.8	0	0	0
	3	2.75 ^c	79.2	13.6	13.2	0	0	0
	5	2.75 ^c	57.2	23.6	36.4	0	0	0

* 0 means that the species was searched for but not found; — means no search.

^a Data were collected from 0.25-m² quadrats.

^b A vertical transect down a gentle slope; data are means of 10 0.25-m² quadrat samples, extrapolated to 10 m².

^c Samples taken from the urchin removal experiment site; data are means of 10 0.25-m² quadrat samples, extrapolated to 1 m areas.

Desmarestia fronds. Presumably the *Loxechinus* avoid the sulfuric acid-laden *Desmarestia* fronds (Schiff 1962).

The first transect in Table 6 was from a small island at the entrance to Canal Unicornio. There was an extremely thick kelp population along the top of a shallow ridge. There were scattered urchins, but no counts were possible because the kelp was so thick. Three 5 \times 1 m transects below the kelp recorded high densities of urchins and no kelp. There were scattered *Macrocystis* with light recruitment, again associated only with the presence of *Desmarestia*. The other samples were taken \approx 1 km inside Canal Unicornio; the area was much more protected and there was a considerable amount of drift kelp and, while not quantified, the phenomenon in which *Desmarestia* creates an refuge for young

Macrocystis was conspicuous in an otherwise widespread urchin-barren. We also saw many lithodid crabs.

The Punta Quinlan area had thick patches of kelp along several broken reefs in depths of 3–13 m. These patches were too thick to swim through and sample. Transects were done in adjacent areas and a striking negative relationship between the *Loxechinus* and *Macrocystis* was observed. The *Desmarestia*-*Macrocystis* association was especially pronounced.

Desmarestia, *Macrocystis*, and *Loxechinus* removal experiments

Isla Luz was similar but more exposed to tidal currents. There were several small islands and ridge systems with different associations of kelps, urchins, and

TABLE 7. Effects of reciprocal *Macrocystis* canopy and *Loxechinus* removal experiments at Isla Luz on *Macrocystis* survival and growth from 14 November 1972 to 24 May 1973.

Treatment	<i>Macrocystis</i>		Increase (mean \pm SD)		Comments
	Survivors	Total	Holdfast diameter (cm)	Number of stipes	
<i>Loxechinus</i> removal with canopy present	20	26	5.5 \pm 3.2	5.1 \pm 3.2	...
Canopy removal with <i>Loxechinus</i> present*	7	35	0	0	<i>Loxechinus</i> density went from \approx 12.0 to 26.9 individuals/m ²
<i>Loxechinus</i> and canopy removal		50	13.8 \pm 6.2	12.6 \pm 3.0	...
Control: canopy and <i>Loxechinus</i> present	6	12	0	0	<i>Loxechinus</i> density increased from \approx 10.0 to 30.5 individuals/m ²

* Thirty-five small plants not removed with canopy plants.

Desmarestia/*Macrocystis*. Three types of experiments were done at this site on 14 November 1972. In each case adjacent untreated areas were evaluated as controls.

First, the hypothesis that the *Desmarestia* acts as an "acid broom" to prevent the *Loxechinus* from eating the small *Macrocystis* was tested by removing the *Desmarestia* clumps from a 5-m² area while leaving the small *Macrocystis*. The area was surveyed 48 h later; within this brief period of time, \approx 40 *Loxechinus* moved into the clearing and killed at least 100 small (<0.5 m) *Macrocystis* and were eating the fronds and haptera of 10 larger (1–2 m tall) plants. This fast response negates the null hypothesis of no *Desmarestia* effect. When we returned on 24 May 1973, there were no large *Desmarestia*; it is an annual plant which appears to recruit in the spring and die out by late summer. But the old *Desmarestia* removal area was dominated by *Loxechinus* and coralline algae, whereas the control area from which no *Desmarestia* had been removed had 15 fertile and 21 young *Macrocystis* plants; all were being heavily grazed by *Loxechinus*. These data indicate that *Desmarestia* can act to at least delay the *Loxechinus* grazing long enough for some *Macrocystis* to germinate and reproduce.

In the second experiment all the *Loxechinus* were removed or smashed in an entire "valley" between two subtidal reefs. The total area was 20 \times 10 m and it varied in depth from 2 to 6 m. The two 50-m Isla Luz transects (Table 6) went through this area and describe the urchin and *Macrocystis* abundances. Half of this urchin removal area and half of the control had the canopy plants removed in order to evaluate the growth rate of different sized *Macrocystis* plants with and without canopies in the presence or absence of *Loxechinus* predation (Table 7). When the *Loxechinus* were removed but the canopy left intact, there was 77% survivorship of the canopy plants (the mortality appeared to result from reinvading urchins), a mean holdfast growth of 5.5 cm, and a mean stipe-number increase of 5.1. When the canopy but not *Loxechinus* was re-

moved, there was only 20% survivorship and no growth because the urchins were heavily grazing the remaining plants. In the joint *Loxechinus*-canopy plant removal experiment, 72 adult plants were replaced by 87 plants, of which 50 were measured and found to have mean holdfast growth of 13.8 cm and stipe increase of 12.6. The control area had 50% survival of large plants. The six plants that died still had their holdfast tags, and it was clear that they had been killed by urchins. The six survivors were being grazed by many *Loxechinus*; there was no recruitment or growth in the control. In summary, the canopy may have reduced recruitment and growth of new *Macrocystis* sporophytes as well as interfering with growth and survival of extant plants. But the *Loxechinus* grazing seemed to be the most important factor in the habitat.

A third experiment was the removal of *Loxechinus* from a small 2 \times 5 m ledge which was an urchin-barren, as opposed to the above experiments, which were originally in an existing kelp forest. The results were similar to those of the same experiment elsewhere in this paper in that the plot acquired a reasonably high kelp density (4.2 individuals/m² from 10 photo quadrats). Probably half of these plants had some sporophyll material. Here again, the *Loxechinus* had reinvaded the plot (9.0 *Loxechinus*/m²; SD = 3.4; N = 10 photo quadrats) and there were no conspicuous understory species. But there were no macroalgae in the control area, and it was clear that the *Loxechinus* eliminate the macroalgae.

Summarizing, the *Loxechinus*-dominated barren ground was the principal feature over most of this area. While *Meyenaster gelatinosus* are relatively common here (Dayton et al. 1977), no boulder situations were observed where they might allow a temporary algal refuge from sea urchins. However, a similar temporary algal refuge from *Loxechinus* was observed in clumps of *Desmarestia ligulata*. In this case, the urchins seem to avoid the area swept by *Desmarestia* fronds, presumably because the *Desmarestia* contain sulfuric acid (Schiff 1962). This supposition needs verification, be-

TABLE 8. Mean densities (\pm SD) of sea urchins and *Macrocystis* in the Golfo de Corcovado region, the only surveyed area that was inhabited by people. All data collected in November 1972. *Pseudechinus* was present but not recorded.

Location	Depth (m)	Area surveyed (m ²)	Urchin density (no./m ²)		<i>Macrocystis</i> density (no./m ²)		Mean holdfast diameter (cm)
			<i>Loxechinus</i>	<i>Arbacia</i>	Juvenile	Adult	
Isla Camiao 43°54.7' S, 73°15.5' W	2	50	16.2	—*	4.3 \pm 3.0	4.7	11.1 \pm 3.6
	5	50	25.6 \pm 3.9	—	2.4 \pm 1.3	1.5	9.0 \pm 4.5
	6	20	21.0 \pm 4.7	—	21.0 \pm 2.1	0.3	8.0 \pm 5.2
	6	50	0.9 \pm 1.5	—	1.9 \pm 1.3	1.5	10.0 \pm 6.0
	6	50	1.0 \pm 2.2	—	3.2 \pm 2.8	2.7	11.4 \pm 4.2
Isla Marta 43°48' S, 74°0.1' W	5	50	14.4 \pm 18.8	—	5.7 \pm 4.1	2.7	15.5 \pm 9.7
Punta Puquitin 43°50' S, 73°47' W	6	20	2.1 \pm 1.5	0*	11.0 \pm 5.2	3.6 \pm 2.0	—
	7	20	2.4 \pm 2.2	0	7.0	5.6 \pm 5.5	—
	6	20	1.5 \pm 2.1	0	11.0 \pm 5.2	3.6 \pm 2.0	—
	8	20	1.5 \pm 2.0	0	19.8 \pm 9.4	8.7 \pm 3.6	—
Canal Puquitin	7	30	12.0	6.7	3.4 \pm 2.6	0.7	16.7 \pm 5.6
	8	30	6.8	3.5	2.8 \pm 2.3	0.4	14.3 \pm 6.3
Isla Ascension	6	50	10.0 \pm 5.9	3.2 \pm 2.3	7.0 \pm 8.4	1.5	11.5 \pm 8.5
	6	50	26.9 \pm 8.6	4.1 \pm 1.9	4.6 \pm 4.1	1.4	14.5 \pm 5.8
	7	50	26.2 \pm 9.8	1.4 \pm 1.8	6.5 \pm 8.8	1.7	9.3 \pm 6.6
Isla Campos 43°54.2' S, 73°39.3' W	13	30	4.5 \pm 1.4	30.6 \pm 3.4	12.8 \pm 5.1	0.3	14.3 \pm 11.7
	10	30	9.4 \pm 2.5	23.2 \pm 4.4	20.2 \pm 16.5	0.4	13.9 \pm 6.8
Isla San Pedro 43°22.5' S, 73°41' W	6	20	61.8	5.4	0	0	—
Isla Acui† 42°55.3' S, 73°26.7' W	5	30	0	0	22.7 \pm 13.2	1.4 ^a	21.9 \pm 8.3 ^c
	7	50	0	0	8.9 \pm 4.2	3.0 ^b	19.2 \pm 7.8 ^c
Punta Leibun† 42°46.9' S, 73°30.3' W	7	25	0	0	4.2 \pm 2.7	3.8 ^d	16.5 \pm 10.9 ^c
	7	25	0	0	7.9 \pm 5.1	6.24 ^e	17.1 \pm 11.7 ^c

* 0 means species was searched for but not found; — means no search.

† The plants at Isla Acui and Punta Leibun were on a sand substratum. ^a 21% and ^b 23% were detached at Isla Acui. ^d 48% and ^e 33% were detached at Punta Leibun. ^c Despite the fact that they were all 1st-yr plants, their holdfasts have wide flat morphs and the diameters are abnormal.

cause *Strongylocentrotus* spp. in the North Pacific will eat *Desmarestia* (Cowen et al. 1982; A. Ebeling, G. Irvine, *personal communication*). The *Desmarestia* are annual plants that disappear by late summer, but by that time many of the associated *Macrocystis* are able to reproduce. This relationship was conspicuous in many habitats and experimentally demonstrated at Isla Luz. Other experiments at Isla Luz demonstrated *Macrocystis* canopy inhibition and the ability of *Loxechinus* to maintain barren zones.

Golfo de Corcovado and Isla Chiloé

This region differed from all the others because it was inhabited by people, and the *Loxechinus* seemed to have been fished when we visited in November 1972. The Isla Camiao site was a large, young (no plant looked much over a year old) kelp forest in shallow water between the small, exposed Isla Camiao and the large Isla Refugia. There were fishing camps in the vicinity. Table 8 indicates some transects at Isla Camiao with high densities of *Loxechinus*, but these means are inflated by a few dense patches; furthermore, while systematic size frequency data were not taken, all the *Loxechinus* appeared much smaller than elsewhere (Fig. 2). The young adult *Macrocystis* were usually very dense

with considerable mutual entanglement; in most cases there was a very heavy recruitment of *Macrocystis*.

We did one intertidal experiment at Isla Camiao in November 1972 in which we clipped the stipes off the *Lessonia nigrescens* holdfasts to test whether it competitively excludes *Durvillaea* from part of the intertidal zone (Santelices et al. 1980). Seven 1-m² quadrats had a mean of 4.9 *Lessonia*/m² (SD = 2.5); the mean holdfast diameter of 11 *Lessonia* was 20.1 cm (SD = 5.4). Here again the articulated coralline algae behaved as an obligate understory (Dayton 1975b), as they turned white after only one low tide. Unfortunately, heavy waves prevented a quantitative analysis on our return in May 1973, but it was clear that *Durvillaea* had strongly invaded the cleared area. Elsewhere, and in the controls, *Durvillaea* occurred only as a thin upper zone above the *Lessonia*, but the *Durvillaea* had recruited into the *Lessonia* removal plot. Santelices et al. (1980) concluded that *Durvillaea* is less able to withstand wave shock; my incomplete experiment suggests that *Lessonia* may also be a stronger competitor.

The Isla Marta to Isla Campos sites were in shallow, moderately exposed sites in the opening to the Golfo de Corcovado. The *Loxechinus* at these sites also seemed to have been recently fished because their den-

sities usually were low (but patchy) and there were many small and juvenile kelps growing over relatively wide areas. This is a dynamic area, obviously susceptible to storm damage, yet exhibiting recruitment of both *Loxechinus* and *Macrocystis*.

Isla San Pedro is near the southwest tip of Isla Chiloé. It had a pronounced urchin-barren ground from 6 to 20 m depth; the transect in Table 8 is from the top of the urchin zone; in depths shallower than 6 m, there is a rapidly declining population and mean size of *Loxechinus* (P. K. Dayton, *personal observation*). We observed fishermen here and it appeared as though all these areas were subject to free-diving human exploitation of *Loxechinus*, which seems to disappear in depths shallower than 6–8 m.

The Isla Acui and Punta Lelbun sites were sand bottom areas without urchins. Here the *Macrocystis* certainly seemed to constitute annual, ephemeral kelp forests. All the *Macrocystis* were weakly attached or completely detached and tangled (28% of 298 adult plants surveyed were drifters entangled with other plants). Even a moderate storm would eliminate most of the plants.

Finally, in October 1972, we made a few dives courtesy of V. Gallardo, E. Furet, and V. Ohme in Bahía Concepción near the University of Concepción marine laboratory near Tumbes. Here the habitat seemed similar to that described by Moreno and Sutherland (1982). Because of heavy fishing, sea urchins were rare, and there were patchy but very high densities of *Tegula* spp. and other gastropods, as well as asteroids *Stichaster* and *Meyenaster* (see Dayton et al. 1977). The gastropods, mostly *Tegula atra*, *T. quadricostata*, and *Monodonta nigerrima*, occurred in densities averaging at least 50 individuals/m²; in areas where drift algae occurred, there were several hundred individuals per square metre. In such areas the *Loxechinus* occurred at densities of 0.4–1.5 individuals/m² and there were no kelps. Moreno and Sutherland report that the gastropods do not overexploit *Macrocystis* but do eat other algae and drift; these observations are entirely consistent with ours. The few *Macrocystis* we saw were regenerating from old holdfasts; V. Gallardo, E. Furet, and V. Ohme (*personal communication*) reported that these plants produced kelp forests by late summer.

DISCUSSION

Distribution and abundance of Macrocystis

The main focus of this paper is the influence of the sea urchin *Loxechinus albus* on the distribution and abundance of *Macrocystis pyrifera* throughout much of its broad range in the southeast Pacific. The kelp forests in the Isla de los Estados and Tierra del Fuego region are large and apparently stable. Here the vertical local distribution of *Macrocystis* is limited by availability of suitable rocky substratum and perhaps by competition in shallow water with *Lessonia vadosa*

(Santelices and Ojeda 1984a) and in deeper water with *L. flavicans*. In common with observations of Castilla and Moreno (1982) and Santelices and Ojeda (1984a, b), sea urchins in this area were almost never seen overgrazing algae and then only in the relatively protected Puerto Vancouver-Merle Cove area. The two main mortality sources for *Macrocystis* were entanglement with drift algae and the heavy settlement of bivalves on the kelp fronds. At Point Loma near San Diego, California, drifting plants kill many other plants. In several southern South American areas >20% of the plants were detached and drifting. This is high by some California standards, because 10% is unusually high at the Point Loma kelp forest (Dayton et al. 1984). Judging from the Point Loma results the subsequent entanglement mortality in some of these Argentine sites may be >50% of the population. The relatively large areas of many hectares in which the *Macrocystis* plants were sunk by the mass of encrusting invertebrates appeared to be a patchy but potentially important source of mortality. This occurs very rarely in southern California, because various fishes have a fast switching response and usually eat the encrusting invertebrates before they sink the kelp fronds (Bernstein and Jung 1979). Such fishes seem entirely absent from the South American habitats (Moreno and Jara 1984).

The distribution and abundance of *Macrocystis* in all the other sites was strongly influenced by the degree of exposure to waves, the grazing of the echinoid *Loxechinus albus* and, indirectly, the effects of human fishing of *Loxechinus*. The sites well protected from wave exposure usually were characterized by sparse populations of *Macrocystis* in which the individuals often appeared unhealthy with sparse brittle fronds, little apparent new growth, and few blades per frond. More important, most of the plants were nonreproductive. In sites exposed to strong currents and some wave action such as Punta Valparaíso, Isla Carlos III, or Puerto Edén, the plants were much healthier and robust and most were reproductive. In most of the protected sites there was a great deal of drift algae and sea urchins were rare, with no grazing impact on the kelps. However, many of the study sites were in more exposed areas where there were high densities of actively foraging *Loxechinus* which overgraze the kelps and maintain urchin-coraline algae "barren grounds" (Lawrence 1975). Several experiments demonstrated that in such areas, *Macrocystis* occurred only in a thin band above the deeper zone where *Loxechinus* was restricted by surge and waves. In most such cases the *Macrocystis* were demonstrated to be competitively restricted from the intertidal zone by competition with *Durvillaea antarctica*. In a few areas young *Macrocystis* were sheltered from urchin grazing by *Desmarestia ligulata*, which results in small ephemeral patches of *Macrocystis* occasionally surviving to reproduce. Finally, in the Golfo de Corcovado area it appeared that man had harvested the urchins and thus perhaps released the kelp popu-

lation from the grazing pressure long enough for the establishment of relatively large forests, which we observed in November. Hay (1984) documents similar community effects of human foraging. These kelp forests seemed susceptible to storm damage (see Moreno and Sutherland 1982, and Hall and Boraso de Zaixso 1979).

Habitat requirements of Macrocyctis

An important value of a broad geographical survey such as this is that it is possible to evaluate, at least in a comparative sense, the habitat requirements of a species. While quantitative physical data are lacking, it is clear from the abundance and size data that *Macrocyctis pyrifera* thrives in habitats semiexposed to wave action. Presumably because the holdfasts are susceptible to being dislodged, *Macrocyctis* is very rare and usually absent in the most exposed areas. However, areas where there are strong currents and/or surge seem to be the physiologically optimal habitat for *Macrocyctis*. In more protected areas where there is obvious sedimentation and little apparent water motion, the *Macrocyctis* fronds are usually brittle and the plants often nonreproductive. Finally, in the most protected sites in which we observed *Macrocyctis* growing, the plants sometimes even lacked flotation vesicles and the fronds simply lay on the substratum. It is interesting to note that most of these *Macrocyctis* grow much closer to shore than they do in California.

Why are the protected areas poor habitats for *Macrocyctis*? At least five untested hypotheses present themselves. First, the sedimentation may bury settled spores and gametophytes, and this plus scour in rare storms may kill the gametophytes and small sporophytes (Neushul et al. 1976, Deviny and Volse 1978, Dayton et al. 1984). Second, lack of water movement allows the floating fronds to accumulate on the surface without moving about enough to allow light through, thereby reducing light for understory fronds and blades, which tend to disappear in such habitats. This situation was fairly common and was associated with nonreproductive plants. Such a density-dependent relationship results in severe intraspecific competition for light, to the point that individual plants can be reproductively sterilized. Third, the lack of water motion may result in local nutrient depletion (Jackson 1977, Wheeler 1980a, b). Evidence for nutrient depletion such as more bleached fronds in the interior of a kelp forest was lacking, and the protected water kelp forests may be too small to be nutrient limited (Jackson and Winant 1983). On the other hand, fourth, the fjords themselves may become nutrient limited so that the plants will suffer irrespective of an edge effect. Finally, fifth, in the fjords, we occasionally saw cells of fresh water from rainfall, melting snow, and surface runoff; if they persist very long they may be an important if periodic source of stress to *Macrocyctis*. This last hypothesis was, at

least in part, negated by the observation of apparently healthy fronds growing through such freshwater lenses. It is important to realize that each of the above hypotheses has exceptions. If the hypotheses do, in fact, help explain the distribution and abundance of *Macrocyctis*, they must do so in a synergistic manner. More likely, other future ecological and physiological explanations will offer a more complete understanding.

Loxechinus and the realized niche of Macrocyctis

In many apparently optimal habitats between 44° and 52° S, *Macrocyctis* is prevented from realizing its fundamental niche (sensu Hutchinson 1957) by the severe grazing of *Loxechinus albus*. In other areas *Loxechinus* exists in lower densities or is absent altogether and does not affect the *Macrocyctis* population (see also Castilla and Moreno 1982, Moreno and Sutherland 1982, Castilla 1984, Santelices and Ojeda 1984b). Three other species of sea urchins were recorded, but were never observed to graze living kelps (Vasquez et al. 1984). Thus a basic question emerging from this paper is: Why does *Loxechinus albus* overgraze kelps and create urchin-coraline algae barren grounds in some areas and not in others? More specifically, what controls (1) the foraging behavior and (2) the density of *Loxechinus albus*?

Foraging behavior.—The *Loxechinus* foraging behavior is influenced mainly by the degree of wave surge and by hunger, as is seen for *Strongylocentrotus* spp. (Vadas 1977, Harrold and Reed 1985). *Loxechinus* often was observed to restrict its ambit in areas exposed to severe wave action. Such surge effects on the foraging of *Strongylocentrotus franciscanus* were reported to reach as deep as 12 m in central California (Lees and Carter 1972, Cowen et al. 1982). The surge effects on *Loxechinus* were somewhat more shallow, but there were areas with high densities of *Loxechinus* clustered at depths of 3–7 m at which they were less likely to be swept away. In such areas they ate drift algae and fronds of *Durvillaea* and *Macrocyctis* which were swept to them. This depth restriction caused by wave surge often resulted in a thin strip of *Macrocyctis*, zoned between the urchins below and the *Durvillaea* above. The removal of either resulted in an extension of *Macrocyctis*, thus negating the null hypothesis that *Macrocyctis* are physiologically restricted to the narrow zone. The importance of hunger is also well known to influence the behavior of sea urchins and eventually the formation of sea urchin grazing fronts irrespective of density (Lawrence 1975, for review of early literature and Dean et al. 1984, Ebeling et al. 1985 and Harrold and Reed 1985, for more recent literature). With regard to hunger, there was a considerable amount of drift algae in all the areas where there were large kelp forests (Castilla and Moreno 1982). In the Isla de los Estados and Tierra del Fuego sites the drift resulted from plant entangle-

ments and excessive encrustations which sunk and killed the fronds. In these areas *Loxechinus* was commonly seen but usually was not very abundant, and it was clear that they did not forage far for food (see Castilla and Moreno 1982, Santelices and Ojeda 1984b). In most of the protected areas, there was a great deal of drift, and *Loxechinus* often was rare. In most other areas where the *Loxechinus* were abundant, they foraged actively.

Loxechinus density.—There was a wide range of *Loxechinus* densities ranging from a complete absence in many protected sites to densities of >100 individuals/m². Clearly the dense populations of *Loxechinus* also were hungry, but almost all the patterns discussed in this paper were correlated with the density of *Loxechinus albus*. Even in the large kelp forests where there is abundant food, the *Loxechinus* population should, in principle, be capable of numerical increase to a density at which they do overgraze the kelps; this situation was observed in Merle Cove, Isla de los Estados. Thus, insights into the mechanisms regulating the density of *Loxechinus albus* are fundamental to any understanding of the organization of this community. In general, population dynamics are functions of emigration, immigration, recruitment, and survival of individuals. The areal scales in this paper are too large relative to the urchin ambits to be much modified by emigration or immigration. Thus the recruitment process refers to larval settlement, metamorphosis, and survival. While the sampling may have missed some small urchins, the skewed size-frequency distribution seems real and I hypothesize that low larval availability is an important factor related to the relatively low Isla de los Estados and Tierra del Fuego *Loxechinus* populations. These habitats are influenced by the circumpolar Westwind Drift currents, and the only source of *Loxechinus* larvae is from the Cape Horn Archipelago. Assuming that *Loxechinus* larvae are similar to other echinoids in spending four or more weeks in the plankton, the Westwind Drift would carry most of the larvae away, and the only recruitment into these habitats would come from eddies or areas where larvae are trapped. An attempt was made to test this hypothesis by sampling areas around Isla de los Estados where we thought larvae might accumulate, and contrasting such areas with more exposed areas. There was some support for the larval availability hypothesis, especially the high *Loxechinus* densities observed in the Merle Cove area where larvae might be expected to accumulate. However, a more rigorous test must include samples around Isla Wollaston and Cabo de Hornos, where I predict even lower urchin densities.

Loxechinus were rare in protected areas. Because they were relatively abundant in nearby but more exposed areas along the coast, the larvae should be expected to get into the protected coasts and fjords. Hypotheses for the absence of urchins in these areas include

possible larval sensitivity to the reduced salinities in many of these habitats (Pickard 1971; P. K. Dayton, *personal observation*) or unsuccessful settlement in areas with a high sediment load.

Finally, the abundance of adult sea urchins often is influenced by predation. An original objective of this project was to search for functional analogs of such northern hemisphere predators of urchins as sea otters (Estes and Palmisano 1974, Dayton 1975a, Duggins 1983), fishes and/or lobsters (Mann 1977, Tegner and Dayton 1981, Cowen 1983), crabs (Kitching and Ebling 1961, Bernstein et al. 1983), or asteroids (Mauzey et al. 1968, Paine and Vadas 1969, Rosenthal and Chess 1972). The only conspicuous predator of sea urchins seen in this study was *Meyenaster gelatinosus*, which occurred in abundance only north of Golfo de Penas. *Loxechinus*, however, has effective defense behaviors (Dayton et al. 1977) and *Meyenaster* only reduces *Loxechinus* densities on isolated boulders from which the urchins can be stampeded without immediate immigration. When the boulders are sufficiently isolated and large, this stampeding phenomenon can result in *Macrocystis* being released from *Loxechinus* predation long enough to recruit and survive to reproduce. It may be that other unseen fish or seabird predators exist, but *Lithodes antarctica* is another predator which may once have been important to *Loxechinus* populations. The *Lithodes* population is now much reduced by fishing (Compodonico 1981). We commonly observed small *Lithodes* eating asteroids, mussels, and on a few occasions, urchins. The king crab (*Paralithodes camtschatica*), a close northern relative, has been observed to eat sea urchins (D. Somerton, *personal communication*), and the preharvest lithodid populations in Chile may have exerted strong predation pressure on *Loxechinus*. In summary, however, these South American kelp communities do not seem to have predators capable of controlling *Loxechinus* populations, and while there are short-term cycles (Hall and Boraso de Zaixso 1979, Moreno and Sutherland 1982), I know of no evidence of long-term cycles resulting from disease (Miller and Colodey 1983, Scheibling and Stephenson 1984) or other catastrophe.

Recent geological history of South American kelp communities

Perhaps the most perplexing issue to come from this study relates to the apparent simplicity and instability of these kelp communities. To one experienced in the northeastern Pacific, these southeastern Pacific communities lack all of the stabilizing predatory relationships, such as effective predation on sea urchins, and picker fish which can remove encrusting invertebrates from kelp fronds (Bernstein and Jung 1979). Furthermore, the number of algal species is very much reduced from what one would see in similar habitats in the northeastern Pacific (B. Santelices 1980; P. K. Dayton,

personal observation) and the large number of species of small crabs, gastropods, fishes, nudibranchs, and other invertebrates so abundant in the north are much less conspicuous or are absent in these southeastern Pacific kelp habitats. The intertidal community is also very much less speciose and has species such as *Balanus laevis* and *Jehlius cirratus* which appear to be relict species occupying transition or unstable habitats (sensu Newman 1979a, b).

Except for the lack of stabilizing predation observed in the kelp forests, these observations and conclusions are subjective. Yet they are so persuasive that they merit mention. The only immediate hypothesis explaining what appear to be abundant "empty niches" is that the Pleistocene ice sheets occurring in periods of much lower sea levels scoured the coastal areas of southern South America (Vuilleumier 1971). Because the rocky habitats necessary for kelp communities tend to be restricted to portions of southern South America, many species in these shallow water communities may have gone extinct. The existing communities, then, may be composed of species which have invaded during the last few thousand years of the Holocene. This is consistent with the observation that the algal species are species which readily disperse by fragments of drifting reproductive material or by rafting on holdfasts, logs, or other material which could have come via the Westwind Drift. Floating algae such as *Macrocystis* and *Durvillaea* are especially good dispersers. Other invertebrate species such as the abundant sponge and compound ascideans and their predators have deepwater distributions and could have simply moved upward into the shallow coastal habitats as the ice retreated, in much the way some of the Antarctic benthic communities are speculated to have established themselves (Newman and Ross 1971, Dell 1972, Dayton et al. 1982). The isolation resulting from the eastern Pacific barrier to dispersal certainly seems effective.

ACKNOWLEDGMENTS

Rick Searles' companionship on both cruises, his friendship, help, and support over the years are gratefully acknowledged, as are his assistants, G. Leister and J. Brauner. They did all the algal identification for this paper. R. Rosenthal and L. Mahan on the first cruise and T. Antezana and E. Gomez on the second cruise were research assistants who participated in all the diving research; their careful and hard work in uncomfortable and difficult conditions is much appreciated. Without the help of the following Chilean colleagues, most of the work would have been completely impossible: K. Alveal, U. and J. Ohme, E. Furet, V. Gallardo, and R. Wilce and G. Conan who were in Chile at the time. Early encouragement, help, and advice from A. Ebeling, M. Neushul, W. North, J. McLain, and R. Lavenberg were very helpful and are much appreciated. I appreciate the extremely competent support of Captain P. Lenie and the crew of the RV *Hero*. I acknowledge with great appreciation the encouragement and support from F. Jara, B. Santelices, C. Moreno, P. Matrai, B. Mordida, J. Castilla, T. Antezana, K. Antezana, P. Bernal, and D. Rivera. I acknowledge and thank the following people for help in reading the manuscript: J. Barry, J. Castilla, R. Cowen, T. Dean, L. Deysher, A. Ebeling, J. Estes,

F. Jara, T. Klinger, P. Matrai, C. Moreno, W. North, B. Santelices, R. Searles, M. Tegner, and G. van Blaricom. I very much appreciate the comments by the two reviewers and J. Sutherland. This work was supported by the Polar Programs Division of the National Science Foundation; I especially thank the program manager (now retired) George Llano for all his years of encouragement and support.

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