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Effects of Disturbance on Population Dynamics of Selected Taxa in the Rocky Intertidal Zone of Channel Islands National Park, California

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Abstract. Changes in abundance following experimental, accidental, and natural disturbance of several rocky intertidal organisms were documented by biannual monitoring at the Channel Islands. During the last 10 yr, information on dominant cover was collected from permanent plots at 14 stations around Santa Barbara, Anacapa, Santa Rosa, and San Miguel Islands. While abundances of most organisms remained stable, there were differences between sites. Experimental trample and scrape plots at Anacapa showed slow recovery in the mussel (*Mytilus californianus*) and rockweed zones (*Pelvetia fastigiata/Hesperophycus harveyanus*). Accidental clearings by grounding of vessels or buoys at Santa Barbara Island showed rapid recovery. A natural influx of sea stars (*Pisaster ochraceus*) at Santa Rosa Island caused dramatic declines in the mussel population there. A mass mortality of black abalones (*Haliotis cracherodii*) was documented. We observed a parkwide decline of more than 90% from 1985 population numbers. While withered and weak abalone were frequently observed, no direct cause for the mass mortality was found.

Keywords: California Channel Islands; rocky intertidal; monitoring; black abalone; *Haliotis cracherodii*; algae; disturbance.

Introduction

Intertidal areas provide a glimpse into the marine world of our oceans and the interesting plants and animals that live there. Tidepools also provide a convenient look at the health of the marine ecosystem. Organisms of the rocky intertidal are subject to a variety of potential perturbations, including oil spills, vessel groundings, water pollution, harvest, and overuse (trampling) by people. Understanding the responses of intertidal organisms to disturbance is important to management of the resources.

The causes of variation in the species composition, abundance, and distribution of rocky intertidal organisms are complex and not well understood. A good review of the literature relevant to the causes of spatial and temporal patterns in the rocky intertidal can be found in Foster et al. (1988).

Undisturbed tidepools are unfortunately rare in southern California and the value of this resource was recognized as one of the special features mentioned in the enabling legislation for Channel Islands National Park. Long-term ecological monitoring of the rocky intertidal is one aspect of the marine monitoring program at Channel Islands National Park. The goals of the program are (1) to monitor trends in population dynamics, (2) to determine the normal limits of variation, (3) to discover abnormal conditions, (4) to provide remedies for management problems, and (5) to measure the success of management actions. The program itself is not designed to answer all the questions or to identify causes of all the problems, but rather to identify that there are questions or problems that need answers. The overall purpose of monitoring is to make recommendations to park management that may include further research into a problem (Davis et al. 1994, this volume).

Following the recommendations of Littler (1978), and the establishment of Channel Islands National Park in 1980, a monitoring design was developed in 1982 at Anacapa Island by VTN Oregon (VTN Oregon, Inc. 1983). Part of the original design included experiments to study the impacts from visitation. In 1985, the monitoring was expanded to other islands by park marine biologists, consulting with J. Engle. There are currently 14 permanent sites on Santa Barbara, Anacapa, Santa Rosa, and San Miguel Islands (Richards and Davis 1988).

The purpose of this paper is to describe changes in population dynamics of selected intertidal organisms following experimental, accidental, and natural disturbances.

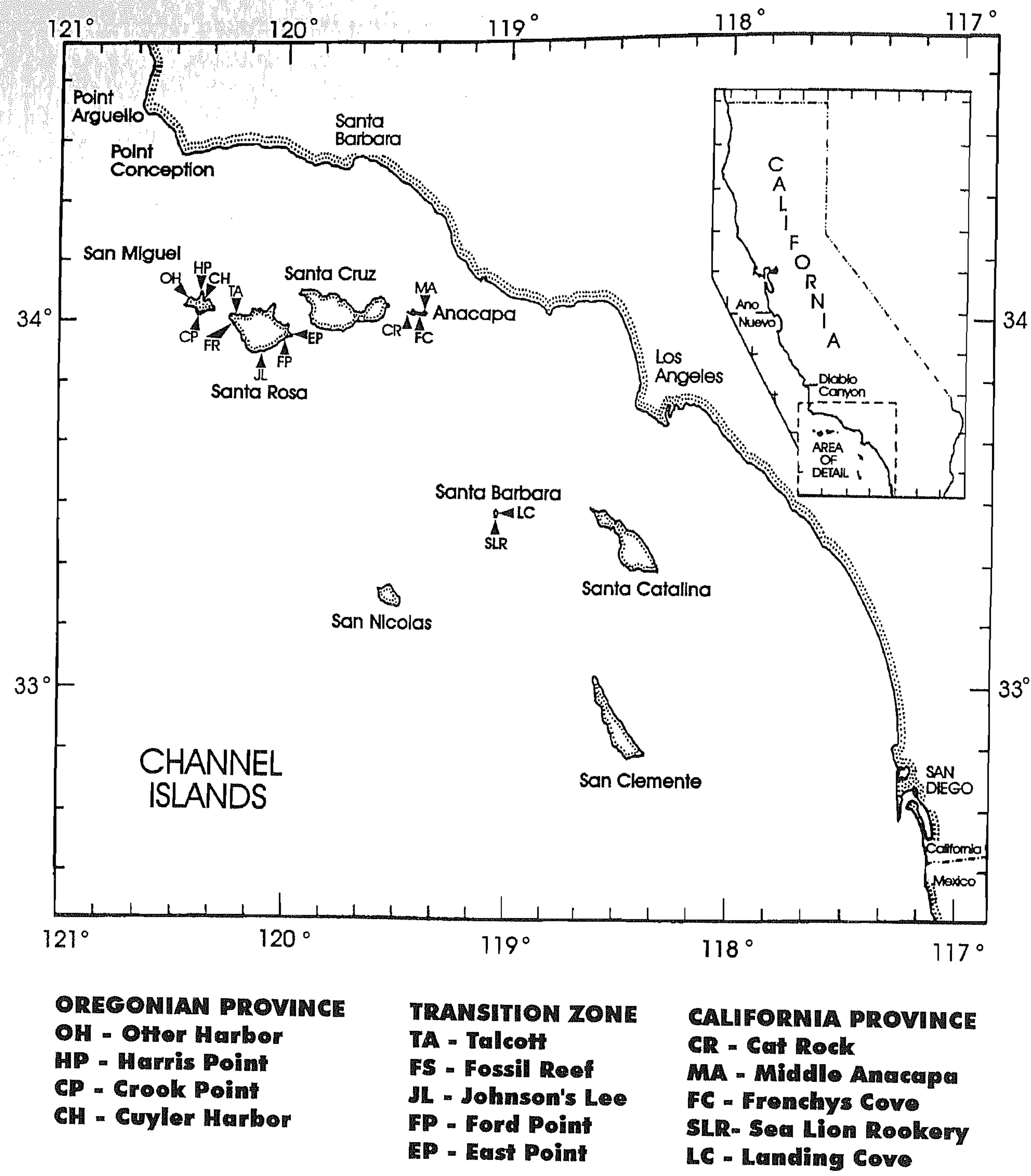

Figure 1. Location of rocky intertidal monitoring sites in Channel Islands National Park.

Study Sites

The 5 islands in Channel Islands National Park (Santa Barbara, Anacapa, Santa Cruz, Santa Rosa, and San Miguel) lie along the transition zone between 2 major biogeographic provinces (Murray et al. 1980; Seapy and Littler 1980). Warm water in the Californian Province dominates at Santa Barbara Island and extends northward during El Niño years. Cooler, nutrient rich waters of the Oregonian province characterize the northern islands.

The locations of the permanent monitoring stations in Channel Islands National Park are shown in Figure 1. Study sites were chosen to provide a variety of rock type and exposure. Ease of accessibility was taken into account, as was potential visitor use and past studies. Monitoring stations at Cuyler Harbor and Crook Point on San Miguel Island were located at sites used in the Southern California Baseline Study (Littler and O'Brien 1978; Littler and Martz 1979). The Santa Barbara Island Landing Cove site is near Cave Canyon (Seapy and Littler 1976) but provides a more workable intertidal bench.

Methods

Rocky intertidal monitoring at Channel Islands National Park was designed as part of a long-term program (Davis 1989). Specific rocky intertidal protocols are described in Richards and Davis (1988).

Three sites were established on Anacapa Island in 1982 by VTN Oregon, Inc. under National Park Service (NPS) contract. Other sites were established on Santa Barbara, San Miguel, and Santa Rosa Islands in 1985, and black abalone monitoring plots were added to Anacapa at that time. Additional sites were established on Santa Rosa Island at East Point and Talcott in 1986, and at Fossil Reef, on the southwest corner, in 1988 (Fig. 1).

Photoquadrats were used to monitor changes in percent cover of plants and animals at each site by recording the dominant cover at 100 points within each quadrat. At all 14 sites, 5 50- x 75-cm plots were established in each of 4 zones characterized by mussels (*Mytilus californianus*); acorn barnacles (*Balanus glandula*, *Chthamalus fissus*, or *Tetraclita rubescens*); turfweed or red algal turf (*Endocladia muricata* or *Gigartina canaliculata*); and rockweeds (*Pelvetia fastigiata/Hesperophycus harveyanus*). Photoquadrats were permanently established at each station by marking corners of the plots with small patches of marine epoxy on the rock surface. Quadrats were chosen on the basis of high cover of the dominant species in each zone, preferably with a relatively flat field for photographs. Slides (35 mm) were taken each spring and fall with Ektachrome 100 film in a Nikonos camera with 2 strobes mounted on a PVC frame. Cover determinations were either made in the laboratory by projecting the slide onto a grid pattern of 100 points, or in the field, using a frame with cross strings creating 100 intersections.

At Cat Rock on Anacapa Island, 9 plots within each of 4 zones were established, divided between trampled, scraped, and control treatments. Trampled plots were treated by walking up and down on the 50- x 50-cm plot 500 times at the start. Scrape plots were treated by scraping 50- x 50-cm areas to remove most of the organisms; only crustose coralline algae remained.

Black abalone, *Haliotis cracherodii*, population dynamics were monitored in plots at 11 sites, though East Point, Santa Rosa Island was monitored somewhat differently and data for that site are not presented here. Permanent plots ranged from 1 to 11 m² to accommodate aggregations of 30–100 abalones. Size frequency determinations were made each spring and fall by measuring maximum shell length of all abalones within each plot. Measured abalones were marked with a lumber crayon to avoid double or missed counts. Once populations dwindled to very low levels, timed searches for live abalones over the entire site were also employed. Shell counts were made at several sites on beaches that accumulated shells. Shells were removed after counting.

Owl limpets, *Lottia gigantea,* were monitored at 4 sites. At Otter Harbor and Crook Point on San Miguel Island, owl limpet size and density were measured within 3 of the abalone plots. In 1988, 5 circular, 0.5-m radius plots were established at Johnson's Lee and at Ford Point on Santa Rosa Island, within the main limpet zone.

Monitoring seastars (mostly *Pisaster ochraceus*) presented challenges because of their relatively low numbers and scattered distribution. Seastars were counted whenever they occurred within abalone plots; however, Crook Point was the only site to consistently have seastars inside plots. Transects were established where reasonable numbers of seastars were found and where the transects could be consistently relocated. Transects were of different sizes because of differing site topography: 10 x 1 m at Harris Point, San Miguel Island; 10 x 2 m at Johnson's Lee, Santa Rosa Island; 30 x 6 m at Fossil Reef, Santa Rosa Island; and 16 x 1.5 m at Landing Cove, Santa Barbara Island. Timed searches were used at a few sites and may be a useful method to determine relative abundance at sites with low densities, though actual density information cannot be obtained this way.

Results

Santa Barbara Island—accidental disturbances

The percent cover of organisms occupying most of the space within the photoquadrats remained remarkably stable with some notable exceptions. For example, at Landing Cove, 2 unexpected events allowed us to follow recruitment and succession in 2 different zones. In September 1985, a barge being used in the construction of the Santa Barbara Island pier was grounded on the intertidal shelf where the turfweed quadrats were located, clearing quadrats 323 and 324. The clearing was complete, with even the top layer of rock removed in some areas. Quadrats were relocated by triangulation. In October 1985, algal coverage in both plots consisted

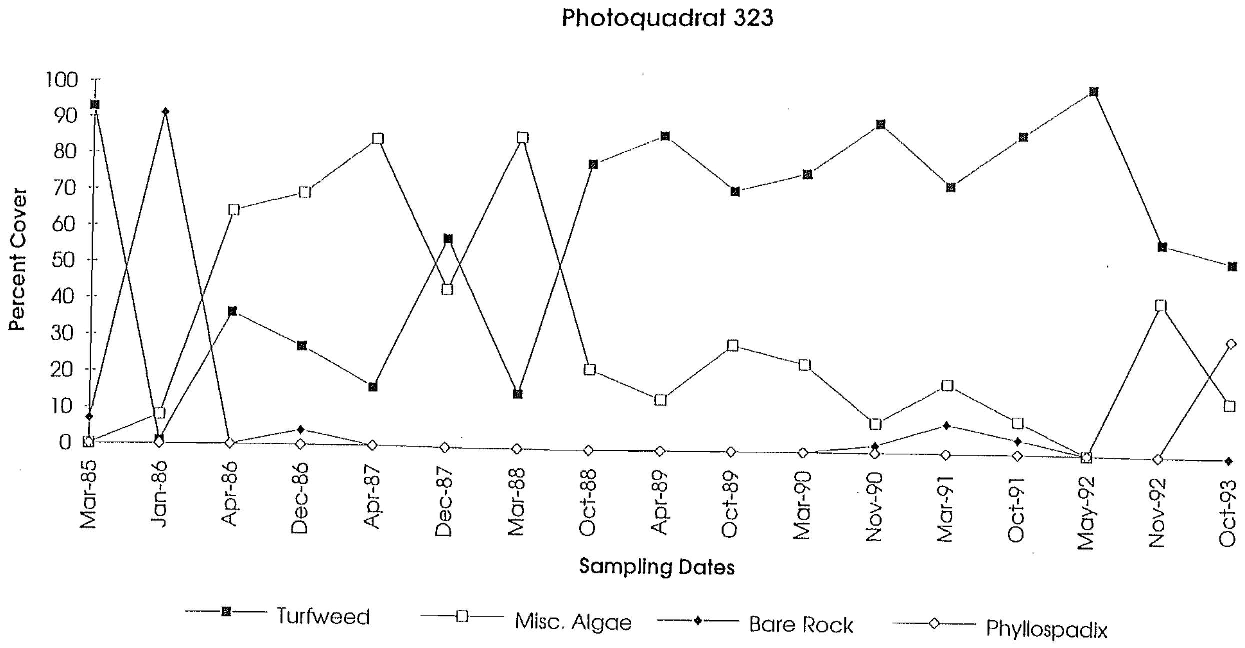

Figure 2. Percent cover of selected organisms in photoquadrat 323 within the turfweed zone at Landing Cove, Santa Barbara Island.

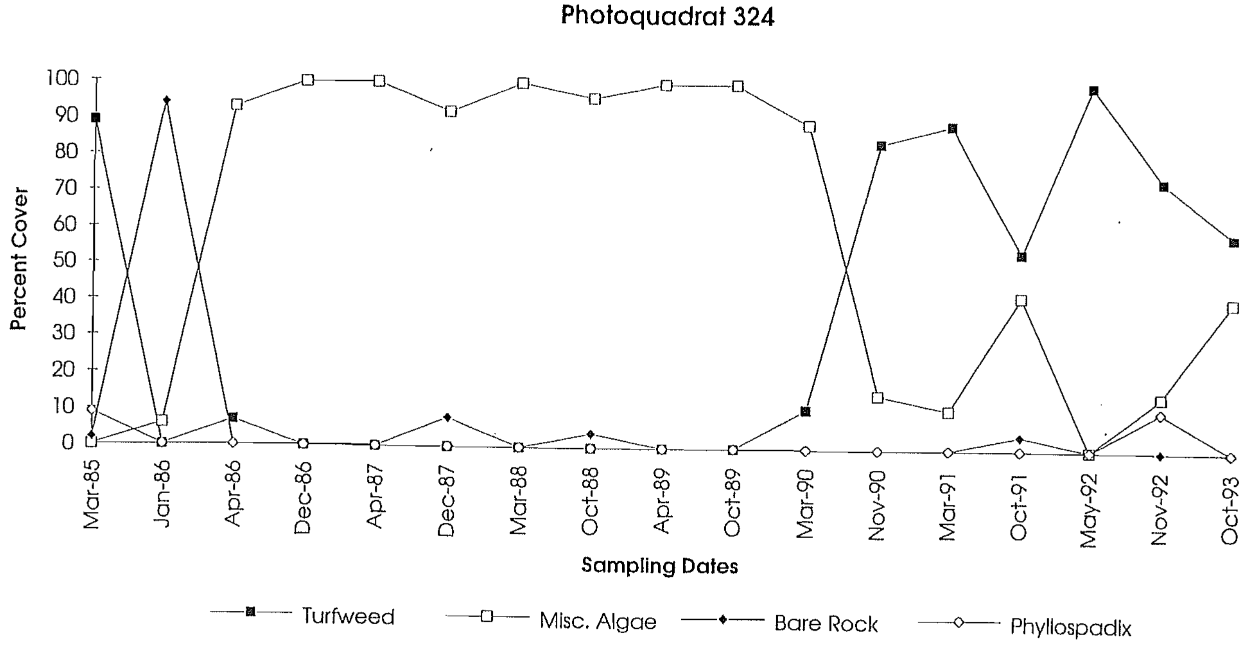

Figure 3. Percent cover of selected organisms in photoquadrat 324 within the turfweed zone at Landing Cove, Santa Barbara Island.

mostly of diatom film, with a few small plants of *Ulva* sp., and *Colpomenia* sp. In January 1986, the first sampling after the incident, both quadrats were mostly bare rock (Fig. 2). A small amount of the *Gigartina canaliculata/Gelidium sp./Pterocladia sp.* turfweed was present in quadrat 323 by April 1986. Turfweed regained dominance of the substrate in quadrat 323 by October 1988. Surfgrass *(Phyllospadix scouleri)* invaded the quadrat in 1992 and increased in cover in 1993.

Quadrat 324 is slightly lower in the intertidal and was more heavily damaged. Recovery of red algal turf in quadrat 324 was somewhat different than in 323 (Figs. 2 and 3). Miscellaneous algae (mostly *Egregia menziesii* and erect coralline algae) dominated through the first half of 1990. In 1993, *Egregia* still grew just outside quadrat 324. Species composition within quadrats 323 and 324, 6 mo and 6 yr after disturbance are presented in Table 1. Species composition of these quadrats in 1992 was typical of all the plots in that zone. *Gigartina canaliculata* and *Gelidium/Pterocladia* dominated the zone, while other species occurred sporadically. Within some undisturbed quadrats, *Phragmatopoma californica* formed a base, over which the algae grew. The undisturbed quadrats remained fairly stable, but an average of the 5 quadrats reflects the clearings in the 2 damaged plots (Fig. 4).

Storm waves during fall 1985 were strong enough to tear out planks on the newly constructed pier. A mooring buoy broke loose and grounded on the intertidal rocks, damaging quadrats 326 and 327 within the mussel zone. The overall area damaged was about 5 x 5 m, though somewhat patchy, with about 60% bare rock. Nearly 50% of both photoquadrats were left bare. Mussel cover dropped from about 70% to 30% in the affected quadrats

Table 1. Species composition of turfweed plots at Landing Cove, Santa Barbara Island, California, 6 mo and 6 yr after the plots were damaged by a barge grounding.

April 1986	May 1992
Quadrat 323	Quadrat 323
Colpomenia peregrina	*Bossiella* sp.
Gigartina canaliculata	*Corallina vancouveriensis*
Gigartina leptorhyncus	*encrusting coralline algae*
Gelidium/Pterocladia	*Gastrocolonium coulteri*
Laurencia sp.	*Gelidium/Pterocladia*
Rhodoglossum affine	*Gigartina canaliculata*
	Gigartina spinosa
	Haliptylon gracile
	Microcladia coulteri
	Odonthalia floccosum
	Plocamium violaceum
	Prionitis lanceolata
	Rhodoglossum affine
Quadrat 324	Quadrat 324
Ulva sp.	*Ceramium* sp.
Cladophora columbiana	*Corallina vancouveriensis*
Codium fragile	*Cryptopleura* sp.
Coplomenia peregrina	*Gastrocolonium coulteri*
Egregia menziesii	*Gigartina canaliculata*
Sargassum muticum	*Gelidium/Pterocladia*
Erythrocystis saccata	*Gratelupia* sp.
Gastrocolonium coulteri	*Laurencia* sp.
Gelidium/Pterocladia	*Odonthalia floccosum*
Gigartina spinosa	*Prionitis lanceolata*
Laurencia sp.	*Rhodoglossum affine*

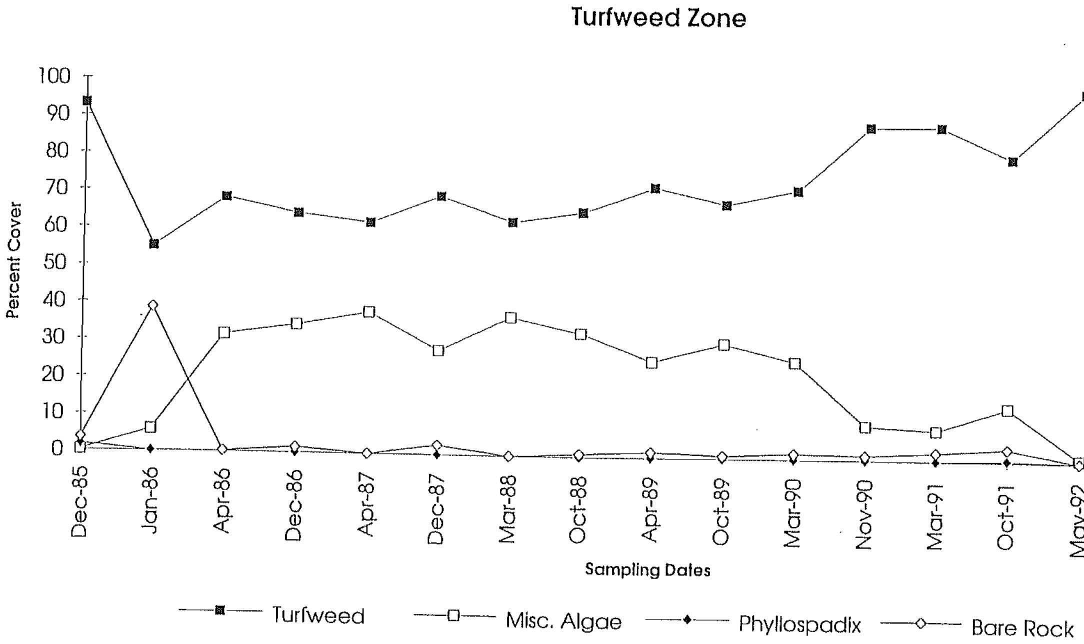

Figure 4. Percent cover of selected organisms in the turfweed zone at Landing Cove, Santa Barbara Island.

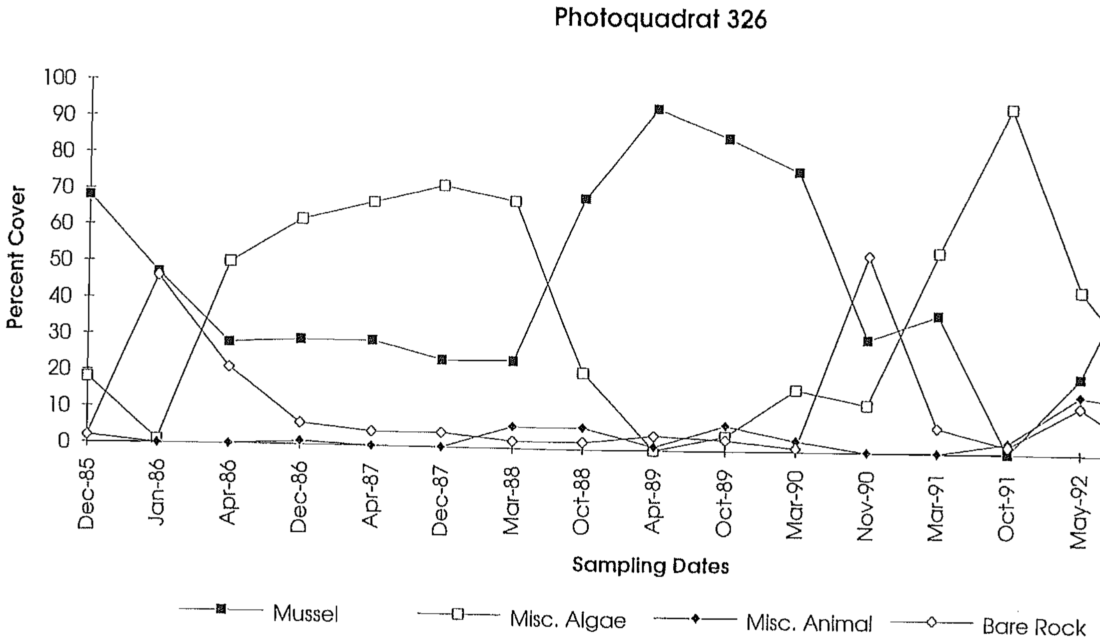

Figure 5. Percent cover of selected organisms in photoquadrat 326 within the mussel zone at Landing Cove, Santa Barbara Island.

(Figs. 5 and 6). Mussel cover remained unchanged for 4 yr until rapid colonization in 1989 returned mussel cover to pre-disturbance levels of more than 70%. Declines in the mussel cover occurred in several of the quadrats in 1990 and 1991. These may have been caused by an increase in the predatory sea star *Pisaster ochraceus*, whose densities peaked in October 1989 (Fig. 7). In 1993, mussel cover in quadrats 326 and 327 reached 98% and 88% respectively, though mussel densities declined in other quadrats.

Rockweed and barnacle zones at Landing Cove were unaffected by the disturbances and exemplify relatively stable conditions over the same period (Figs. 8 and 9). This pattern of stability over time was typical of most other sites.

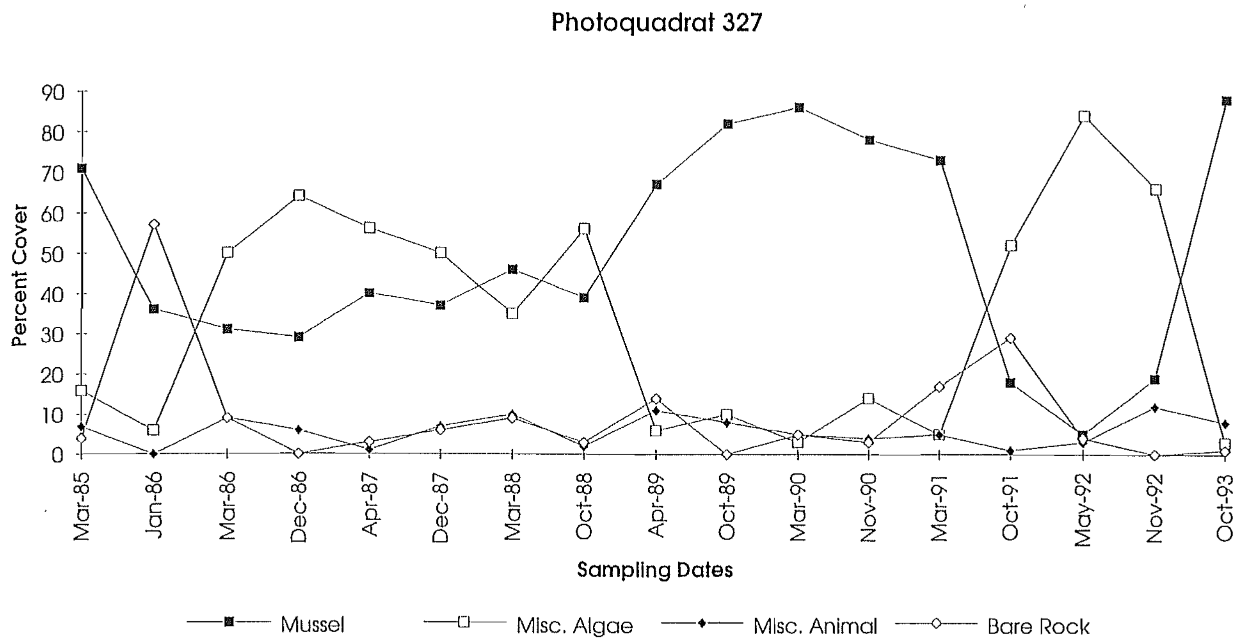

Figure 6. Percent cover of selected organisms in photoquadrat 327 within the mussel zone at Landing Cove, Santa Barbara Island.

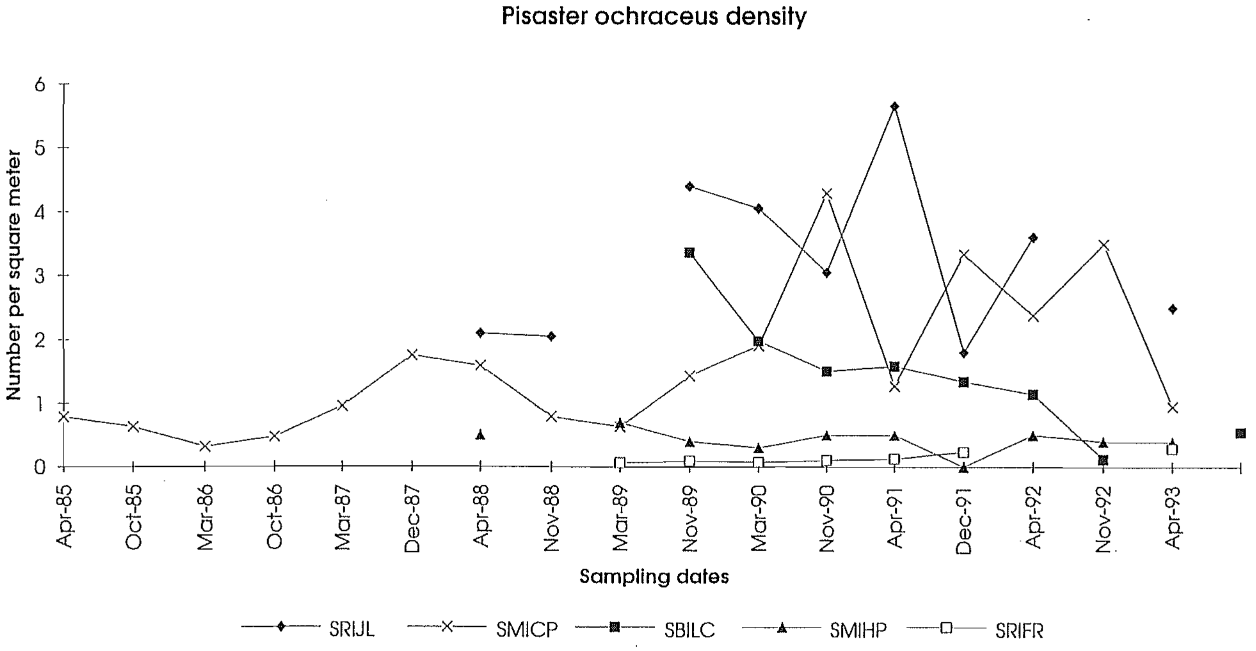

Figure 7. Density of seastars (*Pisaster ochraceus*) at Johnson's Lee and Fossil Reef, Santa Rosa Island; Crook Point and Harris Point, San Miguel Island; Landing Cove, Santa Barbara Island.

Anacapa Island—experimental disturbances

Experimentally scraped quadrats in the mussel zone at Cat Rock on Anacapa Island indicated a much slower rate of recovery than accidental clearings at Landing Cove on Santa Barbara Island (Fig. 10). After 10 yr, scraped quadrats did not recover to the pre-treatment mussel cover of 25%. The mussel zone at Cat Rock did not have large areas dominated by dense patches of *Mytilus californianus* as at Landing Cove. Rather, the mussels occurred in small patches with more algae and acorn barnacles occupying the rock surface.

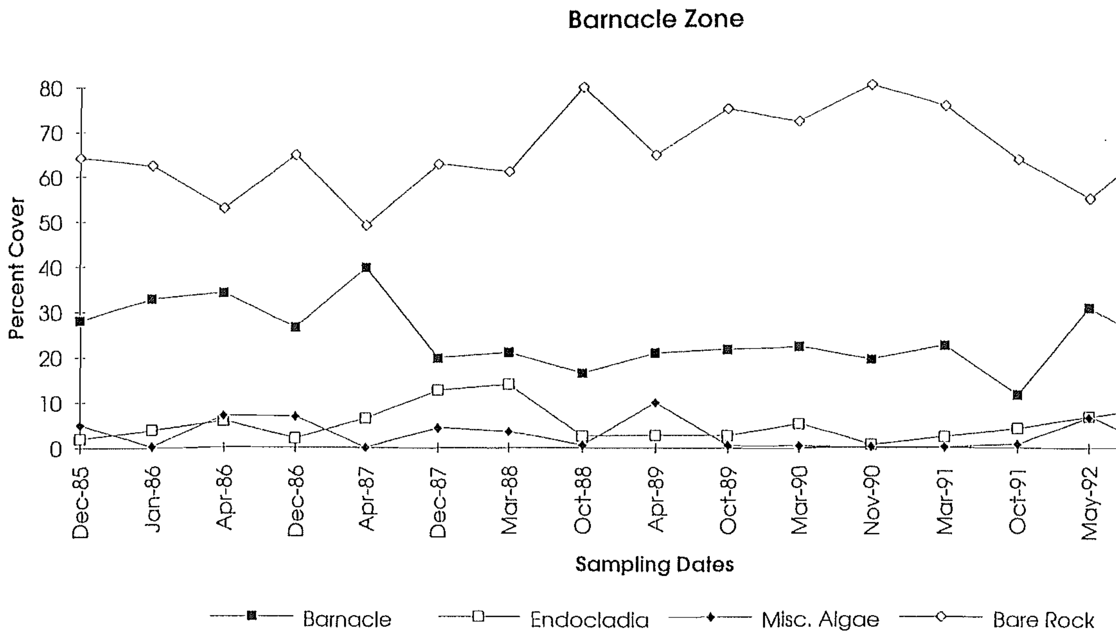

Figure 8. Percent cover of selected organisms in the acorn barnacle zone at Landing Cove, Santa Barbara Island.

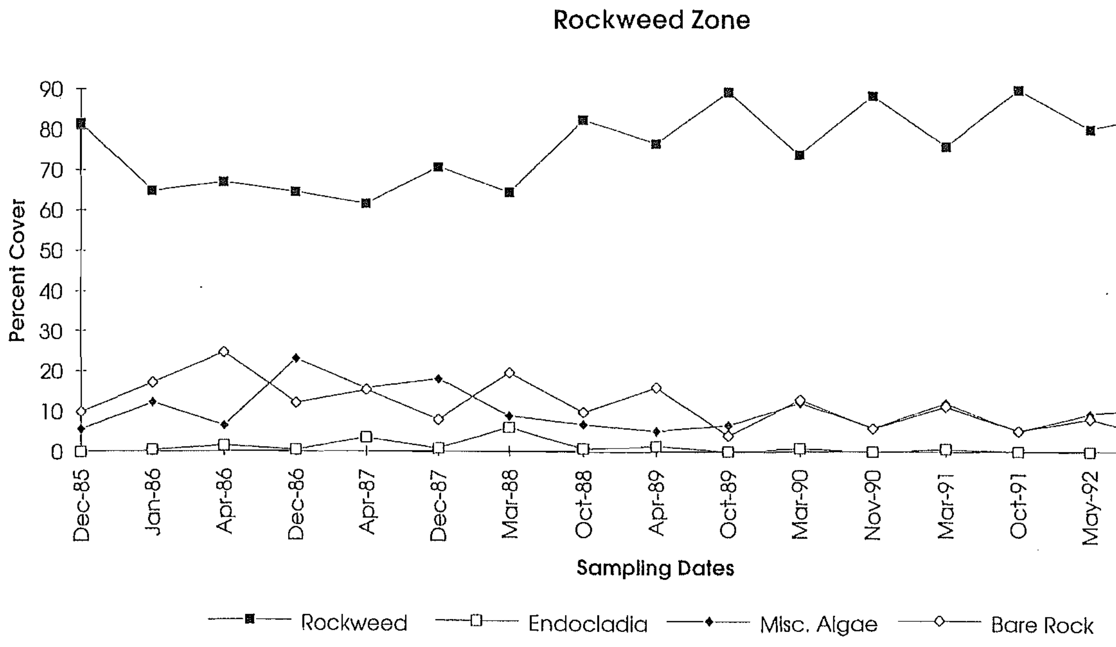

Figure 9. Percent cover of selected organisms in the rockweed zone at Landing Cove, Santa Barbara Island.

Rockweeds were also slow to recover from scrape experiments (Fig. 11). Rockweeds covered less than 30% of the substrate in scrape quadrats in 1993, compared to 60% in the controls and 80% in scrape quadrats before treatment. Rockweeds in trampled quadrats were also reduced to lower levels than pre-treatment and did not recover in 10 yr. The 30% rockweed cover in the scraped plots after 10 yr was matched in some of the scraped barnacle plots. *Hesperophycus harveyanus* is the dominant rockweed in barnacle zone plots, while *Pelvetia fastigiata* dominates rockweed quadrats slightly lower in the intertidal.

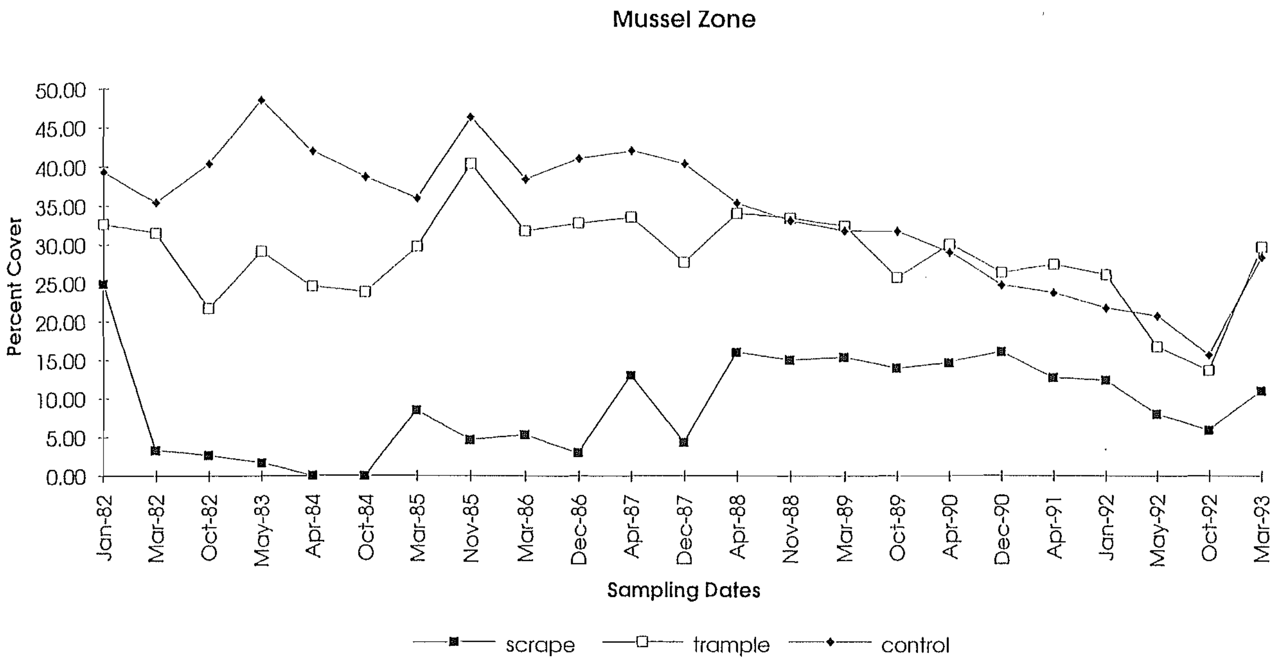

Figure 10. Percent cover of mussels (*Mytilus californianus*) after experimental treatments in photoquadrats at Cat Rock, Anacapa Island.

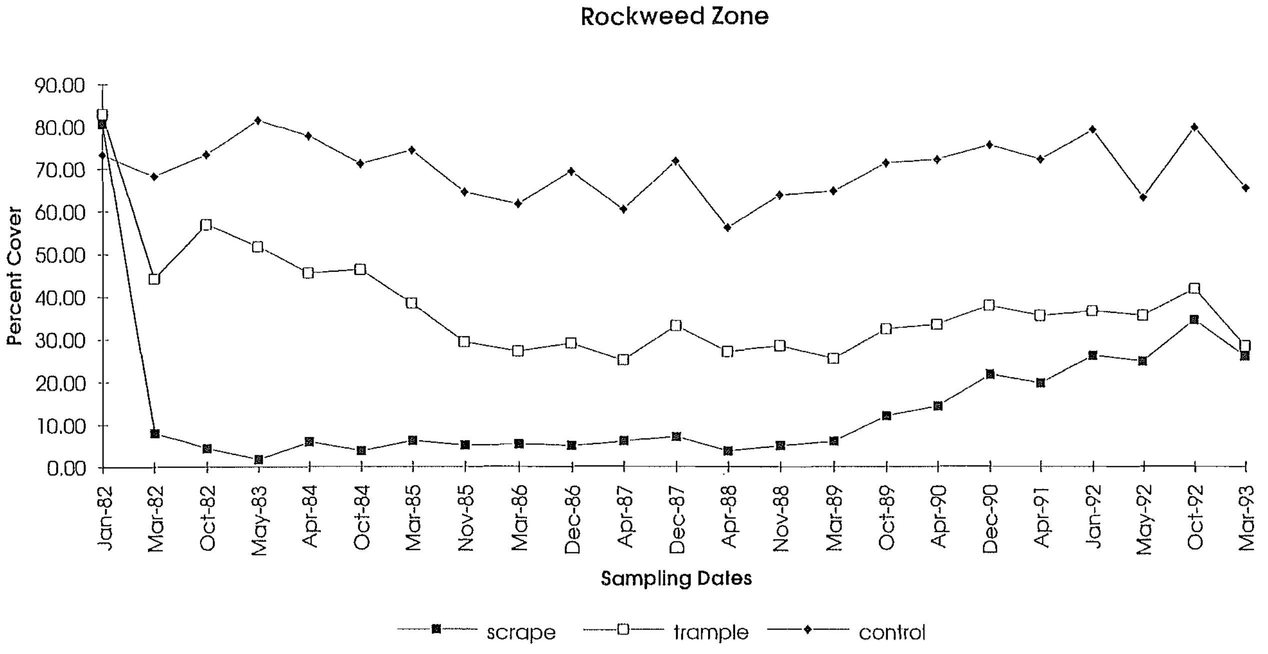

Figure 11. Percent cover of rockweeds (*Pelvetia fastigiata/Hesperophycus harveyanus*) after experimental treatments in photoquadrats at Cat Rock, Anacapa Island.

Acorn barnacles recovered within months from both scrape and trample treatments. *Endocladia muricata* also recovered quickly from the treatments. The warm waters of the 1983–1984 El Niño appeared to have a greater impact on *E. muricata*, reducing it to very low levels in all quadrats (Fig. 12). Recovery was back to pre-El Niño levels by 1986.

Santa Rosa Island—natural disturbance

Near the end of 1987, *P. ochraceus* densities increased dramatically at Johnson's Lee. At the same time, *M. californianus* densities began to decline in the mussel zone quadrats (Table 2). *P. ochraceus* densities peaked in early 1991 (Fig. 7). By that time, mussel densi-

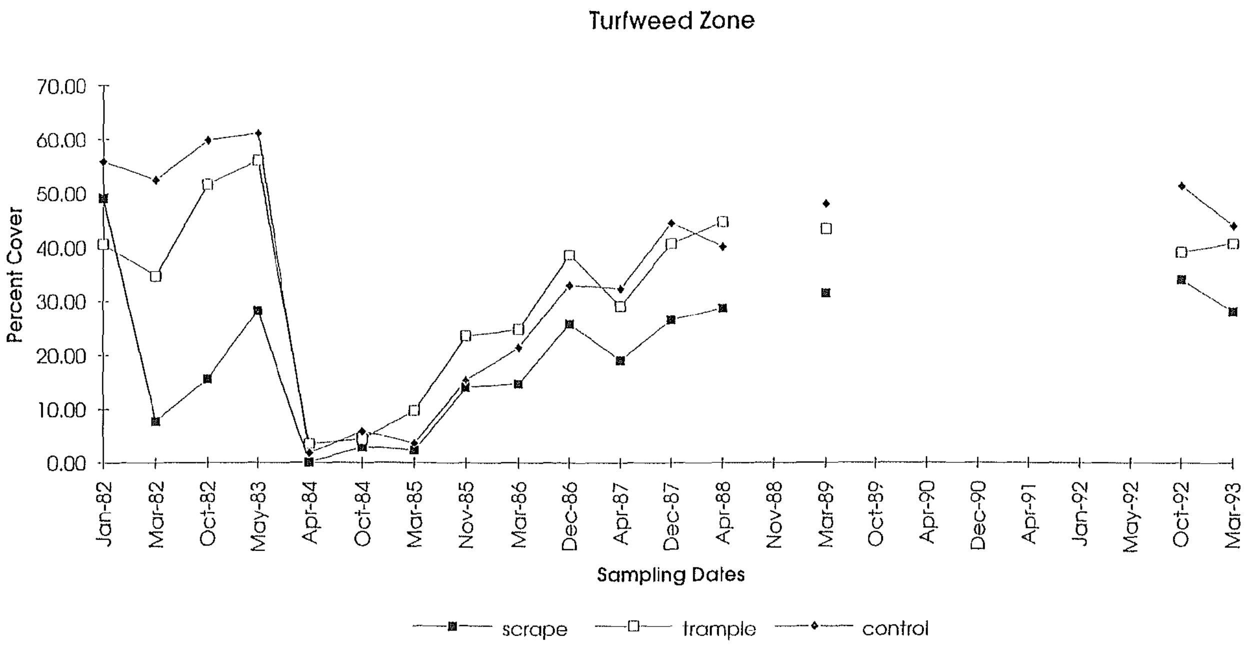

Figure 12. Percent cover of turfweed (*Endocladia muricata*) after experimental treatments in photoquadrats at Cat Rock, Anacapa Island.

ties neared 0 on the lower intertidal shelf. Mussel densities did not decline in 1 plot on a higher shelf where *P. ochraceus* were rare. *Anthopleura elegantisima* and *Phragmatopoma californica* (indicated as miscellaneous animals) and *Corallina vancouveriensis* (indicated as miscellaneous algae) increased in abundance in the absence of mussels and dominated the quadrats in the mussel zone (Table 2).

Black abalone

Black abalone populations at the islands collapsed during the late 1980s (Richards and Davis 1993). Only 10% of the 1985 black abalone population present at all sites remained in 1992 (Table 3). By 1993, only sites on San Miguel Island had appreciable black abalone populations. Densities in individual plots reached as high as 125 m^2 at Johnson's Lee in 1986. In spring 1993, only 17 abalones were found during a 30-min search of the Johnson's Lee site. Though black abalone monitoring only began in 1985, it was apparent by late 1986 that populations at several sites along the south side of Santa Rosa and Anacapa Islands were rapidly declining. Moribund abalones were found that were moderately to severely shrunken, often discolored with a bluish-green hue. This condition was termed Withering Syndrome (WS) and gained attention from federal and state agencies as well as from concerned fishermen (Davis et al. 1992; Haaker et al. 1992).

Other mollusks were apparently unaffected by WS. Giant owl limpets were found in densities as high as 60 m^{-2}, though typically much lower. Populations tended to remain stable at most sites through the period in which black abalone populations crashed (Fig. 13). Owl limpets at Crook Point, San Miguel Island, declined within the abalone plots but none of the symptoms of WS were observed.

Discussion

Following the barge grounding at Landing Cove in 1985, disturbed quadrats in the red algal turfweed zone were quickly covered by algae. *Ulva* sp. and *Colpomenia peregrina* are both relatively weedy algae and so it was not surprising to find them rapidly colonizing the disturbed quadrats. *Egregia menziesii* and *Gigartina spinosa* quickly colonized damaged areas. *Gigartina canaliculata* was able to regain dominance in the quadrats within 3–5 yr, slightly longer than the recovery Sousa (1979) found in boulder fields north of Santa Barbara. Stability of the damaged plots seems to be more tenuous than in undamaged plots, though fluctuations in *G. canaliculata* cover occurred in all quadrats in 1992 for unknown reasons.

There is an interesting competitive interaction between mussels and *Egregia*. Mussels occur only above a sea level about –30 cm, presumably the upper limit of where sea stars, and lobsters feed and where *Egregia* and *Halidrys dioica* dominate.

In contrast to the recovery of mussel plots at Landing Cove, Santa Barbara Island, experimental clearings at Cat Rock on Anacapa Island exhibited only minimal recovery.

Table 2. Percent cover of selected organisms in the five mussel zone photoquadrats at Johnson's Lee, Santa Rosa Island, California.

		Mussel	Bare Rock	Barnacle	Misc. Algae	Misc. Animal
Dec 1985	Average	68.41	17.10	2.41	3.62	7.44
	Std Dev	15.91	8.86	1.82	4.16	10.48
Apr 1986	Average	70.60	13.20	2.40	1.00	12.80
	Std Dev	13.72	6.22	1.14	1.73	13.14
Nov 1986	Average	68.80	14.80	0.80	3.00	12.60
	Std Dev	17.50	10.40	1.30	4.12	15.63
Mar 1987	Average	78.00	14.60	1.20	0.40	5.80
	Std Dev	12.55	10.11	2.17	0.89	7.66
Nov 1987	Average	63.73	19.64	1.80	8.62	6.21
	Std Dev	9.94	7.64	1.30	7.27	7.09
Mar 1988	Average	61.00	30.40	0.00	4.00	4.60
	Std Dev	14.00	14.29	0.00	3.24	4.98
Dec 1988	Average	60.00	29.60	0.40	4.60	5.40
	Std Dev	15.25	15.77	0.55	4.56	4.51
Mar 1989	Average	53.60	37.40	0.20	2.60	6.20
	Std Dev	16.82	18.27	0.45	2.79	7.46
Dec 1989	Average	52.60	33.60	0.20	8.40	5.20
	Std Dev	19.45	15.14	0.45	10.83	4.09
Mar 1990	Average	56.00	34.20	0.00	4.60	5.20
	Std Dev	22.85	22.33	0.00	5.55	3.27
Jan 1991	Average	40.80	45.00	0.60	6.80	6.80
	Std Dev	26.79	23.85	1.34	10.16	5.50
May 1991	Average	30.60	36.20	0.40	27.40	5.40
	Std Dev	16.43	20.20	0.89	32.01	3.97
Nov 1991	Average	8.00	42.60	0.20	37.60	11.60
	Std Dev	12.67	21.66	0.45	20.33	12.99
Mar 1992	Average	5.80	30.80	1.00	39.40	23.00
	Std Dev	12.42	20.44	1.41	22.78	26.93
Mar 1993	Average	10.00	34.00	1.00	35.33	19.67
	Std Dev	17.32	26.00	1.73	27.59	23.07
Jan 1994	Average	10.80	14.60	1.20	14.60	58.80
	Std Dev	16.28	2.68	0.00	14.50	34.57

Table 3. Average density of black abalone (per square meter) in fixed plots, 1985–1992.

	Season and Year[a]															
	S 1985	F 1985	S 1986	F 1986	S 1987	F 1987	S 1988	F 1988	S 1989	F 1989	S 1990	F 1990	S 1991	F 1991	S 1992	F 1992
Californian Province																
Cat Rock	27.4	24.4	19.1	17.2	15.2	9.8	6.3	3.1	2.2	0.8	0.3	0.2	0.1	0	0	0
Middle Anacapa	74.2	77.5	68.7	56.4	42.3	13.7	7.8	3.4	0.9	0.5	0.1	0.2	0.2	0.2	0.2	0
Santa Barbara Island	9.2	8.6	10.4	8.7	10.1	9.5	8.8	2.8	1.3	0.4	0.2	0.1	ND[b]	0	< 0.1	0
Transition Zone																
Ford Point		34.7	28.2	25.5	13.0	4.5	1.7	1.0	0.7	0.3	0	0.2	0	0	0	0
Johnson's Lee		52.8	63.1	57.2	51.6	32.7	24.1	18.6	15.6	6.5	4.6	1.4	0.8	0.5	0.5	0.2
Talcott				14.5	14.7	12.6	13.8	12.8	11.4	9.1	7.6	3.7	2.5	1.8	1.2	0.4
Fossil Reef								29.2	26.9	17.9	9.3	5.8	2.1	1.8	1.2	0.3
Oregonian Province																
Harris Point	17.4	21.4	18.6	23.2	19.0	19.3	16.1	22.4	17.2	20.2	18.5	15.1	15.3	14.9	14.5	16.0
Otter Harbor	33.3	33.5	28.5	29.8	28.5	31.3	27.2	28.8	26.7	27.4	27.7	24.2	14.8	7.3	5.0	2.9
Crook Point	47.0	37.4	38.1	30.2	27.7	22.9	21.2	16.6	15.4	15.0	11.6	13.3	11.3	8.2	4.5	1.8

[a] S = Spring (March–April); F = Fall (October–December).

[b] No data.

(Richards and Davis 1993)

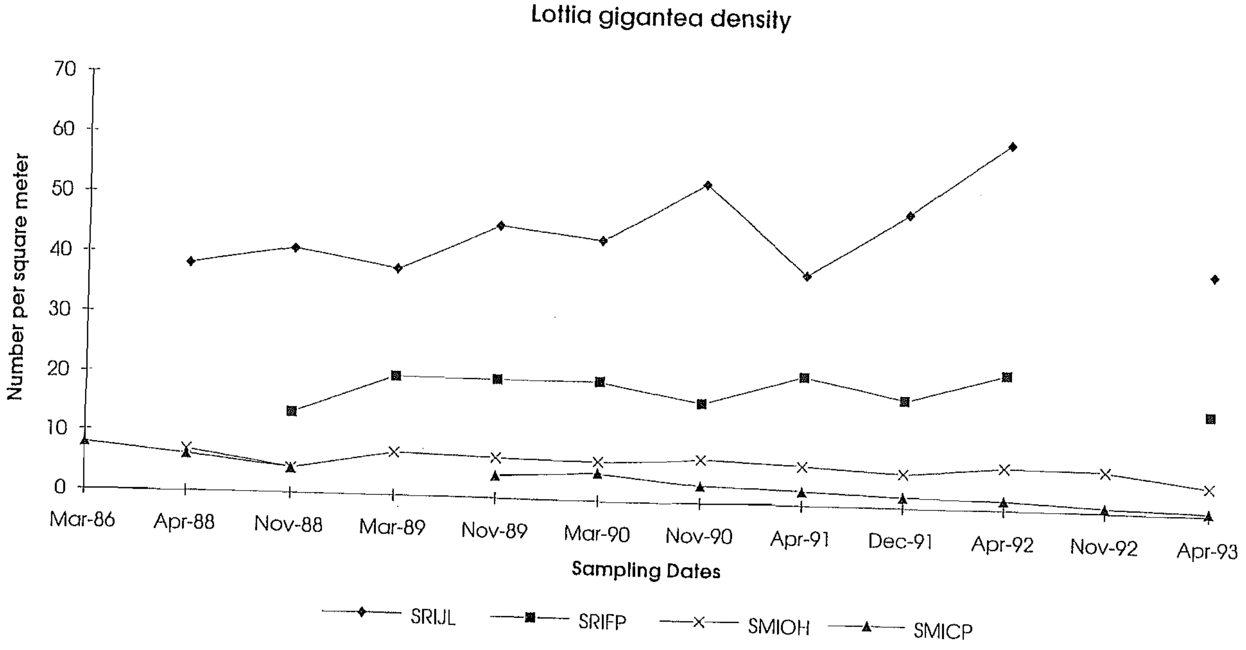

Figure 13. Density of owl limpets (*Lottia gigantea*) at Johnson's Lee and Ford Point, Santa Rosa Island and Otter Harbor and Crook Point, San Miguel Island.

These 2 sites varied considerably in the mussel density, even before clearing. Additionally, mussel densities declined in 1992 in all quadrats (control and cleared) at Cat Rock, Anacapa Island, while recruitment of mussels at Landing Cove, Santa Barbara Island, was generally high. Sea stars were rare at Cat Rock, and there were no other obvious predators, though lobsters were common subtidally in the area.

Rockweeds grow from perennial holdfasts that allow the plants to recover quickly from defoliation. However, when the holdfast is damaged, recruitment of new plants appears to be slow. Experimental clearings in the rockweed zone recovered to only one-third of the pre-treatment densities after 10 yr. Experimental trampling showed rockweed to be susceptible to foot traffic, with about a 30% decrease in cover after trampling. The 2 different treatments showed that rockweed densities had no influence on the rate of recovery.

Any mass mortality is disturbing, especially when it involves a dominant species such as black abalone. It is even more frustrating for managers when the cause of the mortality is unknown. The presence of both moribund animals and legal-size abalones in the remaining populations led us to rule out fishery harvest as the cause of the decline. The size structure of surviving populations differed between the southern islands, where large animals were typically the last survivors, and the northern islands, to where the fishery shifted as the southern population declined (Richards and Davis 1993). The search for the cause of the mass mortality, led to the discovery of a coccidian parasite in the kidneys of abalones, but no direct correlation between WS and the degree of coccidian infection was found (Friedman 1991). Experimental feeding of abalones gave no support to a starvation hypothesis (Haaker et al. 1992), though elevated water temperatures do seem to have a negative influence on survival (Steinbeck et al. 1992). Speculation about the cause of WS continues though no cause has yet been found (Lafferty and Kuris 1993; Richards and Davis 1993). In response to the population decline documented in this program, California Department of Fish and Game established a statewide harvest moratorium on black abalones in September 1993.

Abalones require a minimum density to reproduce successfully, so we would expect that it will be many years before the black abalone population regains its former high level of abundance. Bare rocks formerly occupied by abalones are now covered by other organisms such as sand castle worms *(Phragmatopoma californica)*, which may hinder abalone recruitment.

Through this monitoring program, we are gaining valuable information about the natural variability of the rocky intertidal communities. We are also gaining information on rates of recovery from disturbance. A crucial value of this monitoring program is the demonstrated ability to detect changes in the community, and to direct efforts to investigate the causes. We can better manage the resources if we have adequate baseline information about variability and natural disturbances.

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Natural History of Mainland and Island Populations of the Deep Water Elk Kelp *Pelagophycus* (Laminariales, Phaeophyta): How Many Species?

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Abstract. The elk kelp, *Pelagophycus porra* (Leman) Setchell (Phaeophyta, Laminariales) is endemic to the coastal waters of southern California and northwestern Baja California, Mexico. This species grows at a depth of 20–50 m depth, often along the seaward margins of *Macrocystis pyrifera* beds. Suites of morphological characters (stipe and holdfast dimensions, number and texture of blades) are consistently correlated with habitat: exposed, rocky substrate on the mainland vs sheltered, soft substrate on the leeside of the Channel Islands. These morphs have been recognized as separate species in the past, but are currently considered to be ecological variants of a single, phenotypically plastic species. Studies to date have focused exclusively on the biology of the "sheltered" morph at Santa Catalina Island. Our studies of the distribution of *Pelagophycus* document extensive beds of the "exposed" morph off the mainland and identify for the first time populations of this morph in the California Channel Islands. Our data on growth rates, phenology and longevity of the "exposed" morph off Point Loma reveal substantial differences when compared to those on the "sheltered" morph reported in the literature. While the latter have been shown to be annuals, we find that the Point Loma population is composed of perennial plants. We report inconclusive results from a reciprocal transplant experiment and discuss the question: Are the "sheltered" and "exposed" forms expressions of habitat-specific phenotypic variation in a single species, or do they represent separate species?

Keywords: California Channel Islands; *Pelagophycus*; Laminariales; Phaeophyta; systematics; kelp; demography; biogeography; growth; morphology; phenotypic variation.

Introduction

The elk kelp, *Pelagophycus porra*, is a giant brown kelp found forming dense groves in deep water or cast ashore on the coasts of southern California and Baja California, Mexico, and Santa Catalina, San Clemente and Santa Cruz islands in the California Channel Islands (Dawson 1962; Parker and Dawson 1964; Parker and Bleck 1965). Despite its great size, abundance and unusual habitat, *P. porra* is poorly understood. After reviewing the systematic and nomenclatural history of the genus and records of its geographical distribution, we present the results of the first demographic study of a mainland population at Point Loma, California, and a reciprocal transplant experiment between island and mainland populations; we also report new information on the distribution of *Pelagophycus* in coastal waters of the Channel Islands and of the mainland in the southern part of its range.

We offer an account of the natural history of this genus as a context for further studies to re-evaluate the question: Should populations of *Pelagophycus* that are distinct on the basis of morphology, demography and ecology be recognized as separate species? We propose 2 alternative hypotheses: (1) that *Pelagophycus* is represented by a single, phenotypically plastic species with a wide range of morphological responses to, and broad tolerances of, distinctly different habitats; and (2) that *Pelagophycus* comprises 2 species that can be described as distinct on the basis of morphological, demographic and ecological differences.

Nomenclatural History of *Pelagophycus*

Pelagophycus was recognized by early mariners as an aid to navigation long before it was described by botanists. Because of the buoyancy conferred by their large pneumatocysts, plants dislodged by storms from mainland populations typically floated out to sea. Anson's expedition in the early 1740s reported: