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The differential effects of macroinvertebrates and fish on "turf" communities

Laur, David Ray, Ph.D.

University of California, Santa Barbara, 1990

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UNIVERSITY OF CALIFORNIA
Santa Barbara

The Differential Effects of Macroinvertebrates and Fish on "Turf" Communities

A dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Biology

by

David Ray Laur

Committee in charge:

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March 1990

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ACKNOWLEDGEMENTS

I am grateful to have participated in the long term sutidal research program in southern and central California under the guidance of Professor Alfred Ebeling. I would like to express my gratitude to Professor Ebeling for his intellectual leadership, encouragement, material support and wonderful friendship throughout the long and winding course of this work. The collaboration with his many excellent and productive graduate students and his colleagues throughout the university, the state and the country has been academically exciting and personally enjoyable.

I also want to thank the other members of my committee, Professors Michael Neushul, Larry Harris and Diane Eardley for their support, encouragement and their many helpful suggestions for improving the quality of this work.

I am indebted to the many-many people who have assisted in the field and laboratory work as well as those who offered valuable discussions and ideas. Asmund Bjordal, Malcolm Cook, Robert Cowen, Craig Fusaro, Linda Leum, Dana Rowley, Dale Sarver,Richard Bray, Langdon Quetin, Ralph Larson, Milton Love, Gordon Tribble, Charles Ebeling, Tom Dean, Steve Schroeter, Denise Breitburg, Bruce Harger, Jim Woesner, Richard Zimmer-Faust, Tod Pearsons, Jean Jenkins, Karen Light, Steve Norton, Rob Day, Lew Haldorson, Steve Hoffman, Gerry

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Wellington, Craig Osenberg, Gary Robinson, Peter Sale, Adrian Wenner, Bob Warner, Joe Connell, Allan Stewart-Oaten Dan Morse, and the kind and gentle Jan Ebeling.

I appreciate the technical assistance provided by Norm Lammer, Shane Anderson, Jim McCullagh, Floyd DeWitt,and Bob Fletcher.

I especially want to acknowledge the close work and friendship with Mark Hixon, Bob Rowley, Dan Reed, Alfred DuBois and Carolyn Darrow.

Finally, I am thankful to Kathryn Courtney, my good friend James Wright and my family for their love and support. My late father, Peter M. Laur for promoting my curiosity about nature, my mother, Joyce R. Laur for instilling the drive to achieve, my brother, Randy Laur for his steady approach to life and my sister, Susan B. Laur-Peters for her unconditional love. My grandmother Pearl Laur is the strong self taught naturalist that I love. To her and my family, I dedicate this work.

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ABSTRACT

The purpose of this research was to gain an understanding of how physical and biological factors interact to transform local reef communities to and from a kelp forest and a barren state.

Data on plant, sea urchin and fish densities indicate that two unusually sever winter storms in 1980 (Storm I) and 1983 (Storm II), had different effects on a Southern California kelp forest. Storm I removed all canopies of giant kelp. Denied their preferred diet of drift kelp, urchins emerged from shelters and in the lack of predators, they consumed most of the remaining algal turf. This caused a decline in fish (Embiotocidae) that eat small animals living in turf. Storm II reversed the process by eliminating exposed urchins and clearing rock surfaces for kelp settlement and growth, thus extensive canopies redeveloped by summer 1984.

A study of the microhabitat use and food habits of five surfperch (Embiotocidae) showed them to exploit small animal prey in benthic turf. Turf contained inorganic debris and "low value" food items which fish mostly rejected, and "high value" items (amphipods etc.) which they selected. Two species took careful bites and swallowed all items. The three others selected food by winnowing bites of turf in their mouth and spitting out the cast. All species preferred microhabitats with highest densities of valued food items. Due to the ability of urchins to overgraze kelp and turf to a barren state of bare rock and crustose coralline, laboratory and field experimental investigations of physical obstacles to urchin movement was undertaken. Both red (Strongylocentrotus franciscanus) and purple (S. purpuratus) urchins can negotiate sand using their oral spines, although purple urchins are more hesitant to do so. Starved red urchins transplanted to rock plots retreated to

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nearby crevices from where they ate attached kelp. Red urchins transported to sand plots with kelp present soon disappeared because individuals have difficulty holding and eating attached kelps on unconsolidated surfaces. In another experiment, red and purple urchins reached kelp on a rock ledge only by mounting an artificial ramp. In the absence of predator control, urchins can surmount most rock or sand barriers during periods of low water motion.

Observations of sea otter invasion of two rock reefs and predation on urchins showed contrasting outcomes. At one urchin-dominated low relief and barren reef, otter predation eliminated urchins as turf, kelp and sessile animals filled the space once dominated by urchins and crustose coralline algae. Similar changes occurred in urchin exclusion plots in an urchin barren ground at Naples reef in southern California where there are no otters. At a central California high relief reef not dominated by urchins and barrens, otter invasion and predation produced little change because urchins had not overgrazed the pre-otter reef. The organization of this reef was probably dominated by winter storm disturbance.

Results of caging treatments over several years in a barrens area as well as in kelp and turfed areas at Naples reef showed that urchin grazing is far more destructive to turf than is fish grazing. In the barrens area where urchins were exposed and actively grazing, differences in turf stands between urchin exclusion/total exclusion and fish exclusion/control plots were dramatic. In the kelp and turfed area urchin overgrazing was abated by the presence of drift kelp. Differences between grazing treatments and controls here were not significant and were overwhelmed by effects of season and year. Fish grazing was subtle and appeared only in the barrens area where they attacked and decimated any kelp sporophytes that recruited there.

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CHAPTER 1

GENERAL INTRODUCTION

During a four-year period of unusual weather ending with the El Nino, we observed events associated with the loss and regeneration of a typical kelp forest on Naples Reef, an offshore outcrop of shale covering 2.2 ha at a depth of 5-15 m off Santa Barbara (Ebeling et al. 1985). Over the past 70 years for which records exist, the area of forests in the Santa Barbara Channel has fluctuated far less than areas of other forests to the south because the Channel forests are protected by a "natural breakwater" of offshore islands diminishing the impact of storm swells from the south (North 1971). Yet in winter 1980, the greater area of these forests was lost during a rare episode of huge storm swells ("Storm I") coming from the northwest. The loss was unprecedented in historical record (M. Neushul, personal communication). A second such storm ("Storm II") three years later heralded the return of many of the rock-based kelp beds here. Our studies indicated that storm disturbance either initiated forest loss or catalyzed regeneration, depending on the disposition of kelp grazers (Harris et al. 1984).

Our explanation of kelp forest loss after Storm I is essentially complete. Powerful waves removed all of the giant kelp (Macrocystis pyrifera) canopy from Naples Reef and environs up to 6 km away. Hence, the large detrital accumulation of detached drift kelp disappeared.

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Detritus-feeding sea urchins Strongylocentrotus franciscanus and Strongylocentrotus purpuratus then emerged from shelters to find a new food source. Most of these adult urchins remained completely exposed both day and night because their numbers were not controlled by predators. The urchins safely moved out and consumed the remaining plant growth of understory kelp (mostly Pterygophora californica) and all new kelp recruits.

The effect of exposed but uncontrolled populations of urchins has been documented elsewhere as well (e.g., Mann 1977). Unexpected, however, was the increasing abundance of subtropical species of browsing fishes, most notably halfmoon Medialuna californiensis and opaleye Girella nigricans. Although switching to alternative sources of food, these fishes attacked the few isolated plants escaping the hungry urchins.

The general aim of my research was to investigate the process by which physical and biological factors interact to transform local reef communities between forest and barrens. The principal physical factor is disturbance by wave action due to severe storm swell, which was treated in our basic collaborative study (**Chapter 2**: Ebeling et al. 1985). Other work that I have initiated includes studies of potential biological factors. These involve grazing and browsing disturbances created by macroinvertebrates and fishes, and control of destructive sea urchin grazing by sea otters. Thus my studies included the following topics: the foraging behavior of members of a guild of

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surfperches that browse and glean small prey from algal turf (Chapter 3: Laur and Ebeling 1983); the environmental characteristics that influence destructive grazing by sea urchins (Chapter 4: Laur et al. 1986); and the mitigation of grazer effects by immigration of sea otters (Chapter 5: Laur et al. 1987).

These first four chapters thus provide background material for interpretation of my study of the differential effects of macroinvertebrate and fish grazing on benthic communities under different disturbance regimes (Chapter 6: manuscript). For this work I took advantage of of the outcome of a moderate storm disturbance which defoliated a small area of Naples Reef, leaving the rest in the preexisting condition of dense kelp forest and carpeting algal turf. I designed arrays of cages constructed to either exclude all large browsers and grazers, just macroinvertebrates, or just fishes. These arrays were deployed in two sites, forested and barrens (the defoliated area), to test the hypotheses of grazer effects indicated by Chapters 2-5: First, obvious effects are expressed only in the barrens where there is not enough plant detritus to satisfy the population of resident urchins and no extensive canopy of living kelp to disperse the browsing activities of fishes. Second, the major biological disturbance is due to macroinvertebrates, primarily sea urchins.

My results have generally corroborated these hypotheses and have suggested further research on effects of fish browsing which are now underway. It seemed likely that plants protected from urchins are

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destructively browsed only in the barrens. This is because fishes are attracted to isolated patches of plants that are not rendered inconspicuous by a thick forest.

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CHAPTER 2

SEVERE STORM DISTURBANCES AND REVERSAL OF COMMUNITY STRUCTURE IN A SOUTHERN CALIFORNIA KELP FOREST

INTRODUCTION

The frequency, magnitude, and scale of major storm disturbances may determine the structure of many kinds of natural communities, including those of marine reefs (Goreau, 1959; Connell, 1978; Paine, 1979). For example, Woodley et al. (1981) described hurricane-induced perturbations of a Jamaican coral-reef community: Large amounts of primary substrate were cleared and settled by new growths of sessile organisms, and change in community structure varied with degree of exposure to the full force of the waves. Such changes will persist only if the disturbance rate exceeds recovery time. Hence geographic differences in storm frequency may account for observed differences in the community structure (Goreau, 1959). However, in places where severe storms are rare such as Jamaica (Woodley et al., 1981) and southern California (Dayton and Tegner, 1984), the community may either undergo cycles of alteration and recovery (Connell and Sousa, 1983) or persist in the altered state if recovery time is long (Sutherland, 1981).

Recovery time of subtidal kelp forests in temperate waters may be delayed by grazing sea urchins if the urchins have neither adequate detrital food nor effective predator control. In a mature forest, most of the annual production of kelps forms a litter of detatched drift

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(Gerard, 1976). Urchins readily eat such drift (Vadas, 1977) and usually spare living plants wherever sufficient supplies are available (e.g., Rosenthal et al., 1974; Lowry and Pearse, 1973). If the forest is destroyed by severe storms or other agencies, the urchins may have no drift to eat (see Harrold and Reed, 1984). If uncontrolled by predators, disease, or water motion, the urchins will then move out over the reef to graze back new growth and form a 'barrens' covered with little more than crustose algae and patches of low turf (Lawrence, 1975). Urchins are able to remain in a barrens because they can subsist on little food (Ebert, 1967; Lang and Mann, 1976). This prevents recovery of the important detritus-based food chain (see Mann, 1982), which generates much of the small invertebrate prey that fish eat (Simenstad et al., 1978; Mann, 1977; Laur and Ebeling, 1983). Frequency-dependent foraging by sea otters (Enhydra lutris) effectively controls numbers of exposed, grazing urchins in dense kelp forests off the Aleutian Islands (e.g., Estes et al., 1978), Alaska (Duggins, 1980), and central California (Lowry and Pearse, 1973; Reed and Foster, 1984). Yet kelp grows abundantly off southern California where otters are absent and where exposed urchins occur abundantly in barrens patches (e.g., North, 1971; Leighton et al., 1966; Pearse et al., 1970; Tegner, 1980). Under such circumstances, kelp forests may be less resilient and occur more sporadically (North, 1971).

Hence, mature kelp forests and their productive detrital food chains may persist off southern California only because storms powerful

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enough to destroy them and eliminate drift kelp are rare here (see Dayton and Tegner, 1984). Once destroyed, however, forests without a source of drift may be slow to recover unless sea urchins are controlled (North, 1971; Wilson et al., 1980). Yet a storm strong enough to remove kelp may also remove urchins or alter their behavior, especially exposed individuals in barren areas (Cowen et al., 1982; Harrold and Reed, 1984). Thus the process may be reversible.

In our study, we show that two unusually severe storms, which surprisingly struck coastal southern California only three years apart, started reversible processes. The first storm initiated a process leading to deforestation of our study reef: Drift kelp was eliminated, hungry urchins left shelter, regrowth was grazed back, secondary production probably fell, and fish abundance declined. The second storm, of similar force, initiated the process of reforestation: Exposed urchins were decimated, kelp regrew, drift again accumulated on the bottom, and the detritus food chain was restored. We attribute much of this reversal in community form to marked changes in the behavior, distribution, and abundance of grazing sea urchins.

We documented this by monitoring four important components of the detrital food chain accounting for much of the obvious community structure at our study site: (1) kelps, both giant kelp Macrocystis pyrifera which forms a surface canopy, and the understory kelps Pterygophora california and Laminaria farlowii which rise less than 1 m off the bottom; (2) algal turf which houses many of the secondary

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producers such as small crustaceans, mollusks, and worms; (3) grazing sea urchins Strongylocentrotus purpuratus and S. franciscanus; and (4) epibenthic fishes in the surfperch family Embiotocidae which are the principal exploiters of small invertebrate prey living in the turf (Laur and Ebeling, 1983). Results of this monitoring and other work provide a unique view of a reef community as forest, as barrens, and in transition between the two conditions.

METHODS

We monitored densities of these four groups of organisms at Naples Reef, an isolated outcrop of shale located 1.6 km offshore about 23 km west of Santa Barbara, southern California (34 25'N, 119 57'W). The reef covers 2.2 ha, ranges in depth from 5 - 15 m, and consists of a series of rills and ridges running parallel to the coast (Ebeling et al., 1980). Regular observations were made during a 5 year span in 4 permanent transect sites marked NE, SE, M, and NM in Fig. 1D. This included intervals before and after the large storms of 1980 ('storm I') and 1983 ('storm II'). Two transect sites (NE, SE) were in an extensive stand of understory kelp over reef base. Substrate at the NE site was originally a mosaic of sand, cobble, and partly encrusted rock, but was scoured by storm I. Throughout most of the study the more protected SE site remained covered with sand merging with cobble. The two other transect sites (M, NM) were near the reef top at 7 - 8 m

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depth among crests and rills with high urchins densities, rich algal turf, and intense foraging by surfperch. Site M was in a rill; site NM was located along the north slope of the reef. Permanent 60 m transects of polypropylene rope had been anchored and maintained at sites NE and NM for fish censusing and other studies (see Ebeling and Laur, 1984). A similar transect was constructed at site SE for monitoring a persistent stand of understory kelp. At midreef site M, steel pins marked ends of a 13 m transect for measuring macroinvertebrate densities along the gently sloping side of a rill.

Since the study was opportunistic, we could not predesign all sampling, and had to extend new observations from previous ones made for other studies. Hence, not all monitoring was quantitative and not all measurements were made at each transect site. The state of the kelp forest before and after storms I and II was mapped from field notes and measurements made during reefwide surveys throughout the 5 year interval (Fig. 1). We feel that this is adequate because many changes were widespread and dramatic: for example, from a thick, continuous kelp forest to an exposed 'barrens'. At least once a season, we surveyed the reef and redefined limits of kelp stands and substrate type. We counted kelp-sporophyte recruits in 0.25 m^{-2} quadrats near our transect sites during times of maximum settlement. Water temperature was measured semi-weekly at the surface and 13 m depth during 1979-1981, but not during 1982, and irregularly during 1983.

Regular observations of plant cover and of sea urchin and fish

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densities were averaged per bimonthly interval. Percent understory kelp cover was estimated once every two months in 30 0.75 m^2 quadrats placed randomly along the NE transect both before and after storm I, and along the SE transects after storm I only. Similarly, we estimated algal turf cover in 15 quadrats along the NM transect before and after storm I. Sea urchin densities were measured 1 - 7 times within bimonthly intervals before and after storm I at transect site M and occasionally after storm I at NE. Since abundances of the two urchin species were strongly correlated ($r = 0.85$, $n = 69$, $P < 0.001$), we pooled densities for counts of total adults in a 13 x 1 m band delimited by a meter bar pushed along the side of a nylon line stretched between two pins. Surfperch densities were of total adult and subadult individuals of the 5 principal species inhabiting the reef (see Laur and Ebeling, 1983; Ebeling and Laur, 1984): Embiotoca jacksoni, E. lateralis, Hypsurus caryi, Rhacochilus toxotes, and Damalichthys vacca. We counted fish 4-10 times within bimonthly intervals (about weekly) along a transect line at site NM, tallying all individuals seen within a space estimated to be 3 m wide over the bottom and extending 1.5 m upward.

The litter of drift algae ('drift') was sampled at Naples and comparable reefs inshore about 6 km away. Unlike Naples, the inshore reefs were forested during the entire 5-year study period. Collected under dense stands of giant kelp, the inshore samples included drift from accumulations like those we saw (but did not sample) at Naples before storm I. Samples were taken by scuba divers stuffing as much

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algae as they could into net bags during 5 min swims out from midreef in random compass directions. Bags were weighed full and empty (to subtract the weight of the bag) when returned to the diving skiff.

RESULTS

Kelp forest and reef

Storms I and II initiated periods of kelp loss and resettlement at Naples Reef (Fig. 1). In summer 1979 before storm I, a large surface canopy of giant kelp covered the reef (Fig. 1A). It extended inshore, supported by holdfasts anchored to smaller reefs or even sand bottom (see North, 1971). Large fields of understory kelp, mainly Pterygophora californica with widely scattered individuals of Laminaria farlowii, covered much of the eastward reef base. Smaller stands extended southwestward or formed patches on top of the reef. Then for two weeks in February 1980, storm I generated waves that reached the extraordinary height of 6 m in the Santa Barbara Channel (wave height data estimated from ARCO oil platform Holly and provided by Craig Fusaro). This was more than twice the maximum wave height recorded during the previous 7 years (Harger, 1979). The powerful surge swept away sand, scoured off crusts of coralline algae, and broke off slabs of shale to create large areas of bare rock ('new surfaces'). Water motion removed all canopies of giant kelp from Naples Reef and environs. Most holdfasts from which stipes had been torn eventually

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died. The nearest surviving kelp forest was more than 6 km away. Yet the sturdier stipes of Pterygophora endured about reef base to grow new blades during spring 1980. This produced a new understory canopy unshaded by surface kelp. Kelp sporophytes recruited mostly to new surfaces in densities of about 50 m^{-2} (n = 22). However adult sea urchins soon left refuges in cracks and crevices to graze back the new growth.

Continued grazing by sea urchins eliminated most of the remaining stands of macroalgae. This process was well underway by fall 1980 (Fig 1C). By then urchins had stripped the reef of new kelp sporophytes and most vegetative regrowth, primarily of understory kelps anchored to continuous rock surfaces. The only surviving field of understory kelp was at site SE. Here the sandy substrate seemed to deter a long front of large red sea urchins (Strongylocentrotus franciscanus) advancing from the north. However, even the SE kelp stand was eliminated in spring 1981 (Fig. 1D). A gathering front of red urchins suddenly invaded the previously inviolate area of sandy substrate to destroy the whole stand (about 1 ha) within a month (24 March - 25 April). The community remained in this barren condition until spring 1983.

Following benign seasons of 1981 and 1982, the winter storm series of 1983 (storm II) was also unprecedented in magnitude (see Dayton and Tegner, 1984). Waves again reached 6 m or more in height. The powerful surge created extensive new surfaces on Naples Reef, the first since 1980. [Measured during a 50 min dive, 31 scars from detatched shale

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slabs averaged 1.3 m ± 1.0 (S.D.) in breadth, about the same as scars produced by storm I. Sand and rock scoured even larger areas.] Populations of exposed urchins on the elevated parts of the reef were decimated. Only those individuals sheltering in deeper water about reef base were spared in substantial numbers. Kelp sporophytes recruited to most reef areas (Fig. 1E), but in densities more than 10 times greater on new surfaces than on old (Harris et al., 1984). Sporophytes averaged 558 m^{-2} on new surfaces at transect site M (Harris et al., 1984) and 518 ± 600 (S.D.) on similar surfaces at NM (n = 28, 0.25 m^2 quadrats placed haphazardly on new surfaces in June 1983). Thus in spring 1983, most of the reef and surrounding base supported a dense canopy of new kelp sporophytes some 5-40 cm tall (Fig. 1E). Individuals of Pterygophora outnumbered those of Macrocystis by about 10:1. Enough plants survived the following calm summer and winter to produce well-developed surface and understory canopies in spring-summer, 1983, the first in the area since 1979 (Fig. 1F). Kelp stands were destroyed only in the few places where adult red urchins were still abundant and could assemble as fronts near new surfaces. At site NM (Fig. 1E, F), for example, urchins had consumed all sporophytes by mid August, 1983. Surviving the storm in deep refuges, these urchins soon formed fronts and moved upslope to graze back all stands of young kelp and most algal turf before fall.

Water temperature varied yearly as well as seasonally (Fig. 2). Relative to typical seasonal values measured during 1979 - 1981, both

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surface and 13 m temperatures decreased as usual during the spring upwelling period of 1983, but then reached unusual highs during summer and fall 1983.

Algal drift

Loss of giant kelp eliminated the main source of algal drift (Table 1). Before storm I, benthic accumulations on Naples Reef resembled those under inshore forests. Detatched Macrocystis made up the greatest portion by far, followed by understory kelps and other brown algae, and small amounts of foliose red algae. After storm I, algal drift dropped to less than 100 g per sample and contained little or no kelp, as compared to more than 3 kg of mostly Macrocystis collected under a persistent forest at an inshore reef about 6 km away. Drift algal abundance at Naples remained low throughout the barrens period. As noted above, kelp recruitment was high at Naples following storm II, and the young forest began producing substantial amounts of drift by fall 1983. Reflecting forest structure, this new supply included noticeable amounts of an early arriving, fast growing species of non-laminarian brown alga, Desmarestia spp., as well as abundant kelp. In and about refuges sea urchins held various bits and pieces (80% of 100 pieces examined were held by one or more urchins). By August 1984, drift again reached amounts typical of summer accumulations under a mature kelp forest (Table 1).

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Sea urchin density and understory kelp cover

Sea urchin densities varied with conditions imposed by the two storms (Fig. 3, top). Before storm I, densities of exposed (countable) urchins of both species at transect site M averaged 7.9 - 14.2 m^{-2}, with purple urchins (Strongylocentrotus purpuratus) outnumbering red urchins (S. franciscanus) by 3:1. The transect was on the sloping side of a rill, however, and we could see (but did not count) clusters of individuals sheltering in crevices and under boulders above and below the slope. After storm I, densities of exposed urchins doubled from March 1980 at the start of the barrens period to over 23 m^{-2} in 1981, as the ratio of species densities remained 3:1. Since thorough searches revealed far fewer sheltering urchins, the increase probably reflected an emergence of individuals that had been hiding before (see Russo, 1979; Harrold and Reed, 1984). Then after a series of smaller storms during fall-winter 1982-1983, densities fell to nil with storm II in 1983. During 1983-1984 the few adult immigrants sought shelter under boulders at rill bottom.

Disruptions in normal seasonal cycles of understory kelp cover were related to increased densities of exposed sea urchins (Fig. 3, top). Although understory cover was measured at a different transect site (NE) than urchin densities (M), the relation was generally robust and held reefwide. Before storm I at site NE, the understory canopy had undergone its usual seasonal cycle of thinning from more than 50% cover

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in summer to about 15% cover in winter (Fig. 3, top). We saw few urchins at site NE then, and no plants had been grazed. The abrupt decline in cover in spring and summer 1980 occurred as large red urchins appeared, formed fronts, and consumed the plants. Storm II reduced urchin densities at site NE from 3.2 ± 0.5 (S.E.M.) m^{-2} ($n = 5$ haphazardly placed transects) to 0.3 ± 0.1 ($n = 4$), after which kelp recruited abundantly to the area (Fig. 1D). By comparison, large red urchins counted separately at site M were reduced from 5.6 ± 0.5 m^{-2} ($n = 20$ counts from Sept. 1980 to storm II) to 0.4 ± 0.1 ($n = 23$).

Continued understory cover at transect site SE indicated that, without urchin grazing, conditions favored kelp growth after storm I (Fig. 3, top). Ungrazed during 1980, understory kelp at site SE underwent a full seasonal cycle of thinning and regrowth of blades after storm I. Urchins eventually invaded the sandy site and eliminated plants in spring 1981. There was no subsequent kelp recruitment to this area, which retained its sand cover throughout the study.

Turf cover and surfperch density

Embiotocid surfperch densities correlated strongly with turf cover at transect site NM (Fig. 2, bottom; $r = 0.80$, $P < 0.001$, $n = 21$). Before storm I, both varied seasonally, increasing during the spring and summer. Both fell during the barrens period between storms I and II, then increased after storm II though not to previous maxima. The site no longer attracted the abundance of surfperch recorded before

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storm I. The abrupt decline in turf cover after June 1983 occurred as fronts of urchins grazed their way up the slope at this site (Fig. 1E, F). Before this, however, cover of turf and of understory kelp appeared controlled by the same reefwide processes.

DISCUSSION AND CONCLUSIONS

The two large storms marked periods of disappearance and reappearance of a kelp forest. However, this reversal of community form was related less to the frequency of storm disturbance than to the magnitude and scale of initial effects coupled with the frequency of biological disturbance by grazing sea urchins. The storms affected one part of the community directly and another part indirectly (see Foster, 1982; Cowen et al., 1982). The reversal occurred because direct effects of storm I were indirect effects of storm II and vice versa: Storm I (1980) destroyed kelp, which altered the feeding behavior of urchins; storm II (1983) decimated urchins, which allowed successful recruitment of kelp.

After storm I (Feb. 1980), new kelp plants appeared during spring and early summer when nutrient and light levels favor plant recruitment and growth (e.g., Dean and Deysher, 1983; Harger, 1979). However, nearly all were eaten by sea urchins, which had presumably emerged from rocky hiding places once located near accumulations of drift kelp and smaller amounts of other algae. Urchins are known to alter their feeding behavior from quietly sheltering and holding drift to moving

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about and grazing live plants when drift food is unavailable (Dean et al., 1984 and references therein; Harrold and Reed, 1984). At Naples the change was manifest as an apparent doubling of urchin densities at our regularly monitored midreef site (Fig. 3), as we were able to see and count the previously hidden individuals.

This high density of exposed sea urchins probably exceeds that at which living plants can survive in the absence of drift. Red urchins (Strongylocentrotus franciscanus) are larger and more active than purple urchins (S. purpuratus). Leighton et al., (1966) concluded that algae can recolonize successfully among urchins whose densities are not much more than 1 red urchin or 10 purple urchins m^{-2}, much less than we observed at midreef. Presumably, either species could have prevented plant recolonization here because purple urchins outnumbered red urchins by 3:1. Even at the deeper and flatter site along reef base (Fig. 1, NE) understory kelp cover was completely destroyed where the ratio was only 0.5:1 and red urchins were fewer ($\bar{x}$ = 3.2 m^{-2}) than at midreef (5.6) before storm II. Furthermore, the grazing power of red urchins may be underestimated if it is based only on densities of dispersed or stationary individuals. Such individuals may become more destructive when they aggregate as dense, moving fronts (Dean et al., 1984).

A comparison of kelp cover trends indicates that seasonal regrowth after storm I would have been normal but for urchin grazing. Having durable holdfasts and stipes (Reed and Foster, 1984), understory kelp

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plants grew new blades after Storm I, but were devoured by red urchins at site NE during May-August 1980. Yet the process was delayed for almost a year in adjacent site SE whose sandy substrate may have temporarily discouraged urchin movements (see Breen and Mann, 1976; Tegner and Dayton, 1977).

Dispersed over the whole reef, moving and grazing adult sea urchins may have prevented any large-scale recruitment of kelp and other algae between storms. Urchins ate most living plants because the accumulation of drift kelp and other algae was nil. They survived in the open because they could subsist on alternative foods and had few predators (see introduction). In the absence of sea otters, the large California sheephead fish Semicossyphus pulcher (Cowen, 1983) and spiny lobster Panulirus interruptus (Tegner and Levin, 1983) may control urchin numbers. Yet sheephead abundance at Naples Reef was probably far less than that needed to control exposed urchins (Cowen, 1983), and lobsters were overfished and rare (personal observations).

Even though storm II created as much or more disturbance as storm I, it had the reverse biological effect on the reef community. Dense stands of kelp sporophytes appeared on new rock surfaces bared by the storm. Plant settlement was unusually heavy, despite an uncertain source of propagules and the presumed limited dispersal distance of kelp spores (see Dayton, 1973; Anderson and North, 1966). Wave action decimated the population of urchins because most individuals were foraging in the open and exposed to the full force of the surge.

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Without grazing urchins, the young kelp plants survived and grew. Also, an initial cover of early arriving, fast growing filamentous brown algae (Ectocarpus and Giffordia spp.) may have protected young kelp plants from grazing fish (Harris et al., 1984). The kelp understory soon reached pre-disturbance (1979) levels of percent cover.

Although the density of kelp recruits was more than 10 times greater after storm II than after storm I, the lack of kelp regrowth after storm I was more likely due to grazing urchins than to recruitment limitation. Wherever they survived storm II, urchins were fully capable of destroying even the densest stands of young kelp. For example, urchins that had survived under boulders within a surge shadow below site NM soon moved upslope to eliminate sporophytes that had recruited heavily to extensive new surfaces there.

Reefwide, kelps survived despite an El Nino intrusion of warm, nutrient-poor water that has persisted since winter 1982-1983 off coastal southern California (Fiedler, 1984). As also observed off San Diego some 300 km to the south (Dayton and Tegner, 1984), however, water cooled to usual levels in spring 1983 indicating a strong pulse of upwelling and nutrient enrichment. This and intermittant shoaling of the thermocline during the summer may have supplied plants with the nutrients required for canopy regrowth in spring 1984 (see Harger, 1979; North et al., 1982). Understory kelps and lower fronds of giant kelp may have been nourished from time to time by nutrient-rich water below the thermocline. They grew new blades or fronds during the spring

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upwelling period, and formed well-developed surface and understory canopies by summer. Consequently baby surfperch, which require a cover of understory kelp for protection from piscivores, reappeared for the first time since deforestation after storm I (Ebeling and Laur, 1984). Drift kelp began to accumulate. Hence, the remaining urchins were able to exploit a renewed detrital supply and to reassume their sheltering mode.

Surfperch abundance apparently depended on outputs of the detritus-based food chain. The strong correlation of adult numbers with algal-turf cover indicates that the fish were tracking their food supply of small prey that live in turf (Laur and Ebeling, 1983; Stouder, 1983). Many of these prey, such as amphipods and crabs, are facultative detritivores, ingesting plant litter and other refuse coated with bacterial slime (Mann, 1982). Before urchins had invaded our site, both turf cover and surfperch density varied seasonally, increasing during the spring-summer productivity pulse (Fig. 3). Then both remained at low levels during the extended barren period before storm II. Overlap in microhabitat use between surfperch species increased as fish congregated about reef crest and adjacent slope where urchins were fewer and turf persisted (Stouder, 1983). However, the predictable increase in turf and fish after storm II was not fully realized because our site (Fig. 1, NM) was eventually overrun by surviving urchins (see above).

That severe storms may catalyze regenerative as well as

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degenerative processes may help explain what North (1971) described as 'irregular changes' in southern California kelp forests. In our example, storm I set forth processes disrupting the detritus-based food chain to the extent that the reef community was unable to resume its previous form. This happened despite the facts that (1) winter-storm disturbances generally precede the season of maximum light and productivity (Harger, 1979; North et al., 1982), and (2) loss of the surface canopy of giant kelp allows light for understory growth that would otherwise be suppressed by shading (Foster, 1982; Dayton and Tegner, 1984; Reed and Foster, 1984; Dayton et al., 1984). Storm II reversed the degenerative process by removing sea urchins and aiding kelp recruitment. Hence, our findings suggest that if predators or other agencies control urchin numbers (see introduction), storm effects should be regenerative (Cowen et al., 1982; Foster, 1982). But in mature forests where urchin populations are poorly regulated, severe storms may have degenerative effects because they eliminate the detritus base.

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Table 1. Mean weights (+ S.E.M.) of detatched drift algae at Naples Reef and similar rocky inshore reefs. Means with different letters (in parenthesis) are significantly different by analysis of variance of data values (x) transformed to logs (x + 1) and Duncan's multiple range test ($P < 0.05$).

Locality	Date	Depth (m)	N	Mean wet weight (g)
Inshore reef 1	JA 1980	8 - 12	12	3192 + 432 (A)
Inshore reef 2	"	3 - 10	12	3227 + 606 (A)
Naples Reef	"	7 - 15	14	90 + 27 (C)
"	SO 1983	"	12	482 + 111 (B)
"	JA 1984	"	13	1969 + 184 (A)
Inshore reef 1	"	8 - 12	12	2300 + 159 (A)

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FIGURE CAPTIONS

Fig. 1A-F. Macrocystis pyrifera and Pterygophora californica. Naples Reef with distributions of mature giant kelp M. pyrifera (coarse hatching), mature understory kelp--mostly P. californica (large dots), newly recruited plants (fine hatching or small dots), major sea-urchin fronts (X's), and continuous rocky substrate (shading) before and after storms I and II. Panel D gives scale (30 m), depth contours (7, 11, 15 m), and transect sites (bars marked NE, SE, M, NM).

Fig. 2. 1983 temperature readings from Naples Reef plotted on envelopes delimiting the ranges of monthly means based on semi-weekly observations taken during 1979-1981.

Fig. 3. Strongylocentrotus franciscanus + S. purpuratus, Pterygophora californica, Embiotocidae, and algal turf. Bimonthly means (+ S.E.M.) of pooled sea urchin counts--S. franciscanus + S. purpuratus, percent cover of understory kelp--mostly P. californica, embiotocid surfperch densities, and percent cover of algal turf at monitored transect sites on Naples Reef (Fig. 1D) before and after storms I and II. Numbers by urchin and fish means are sample sizes.

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Fig. 1

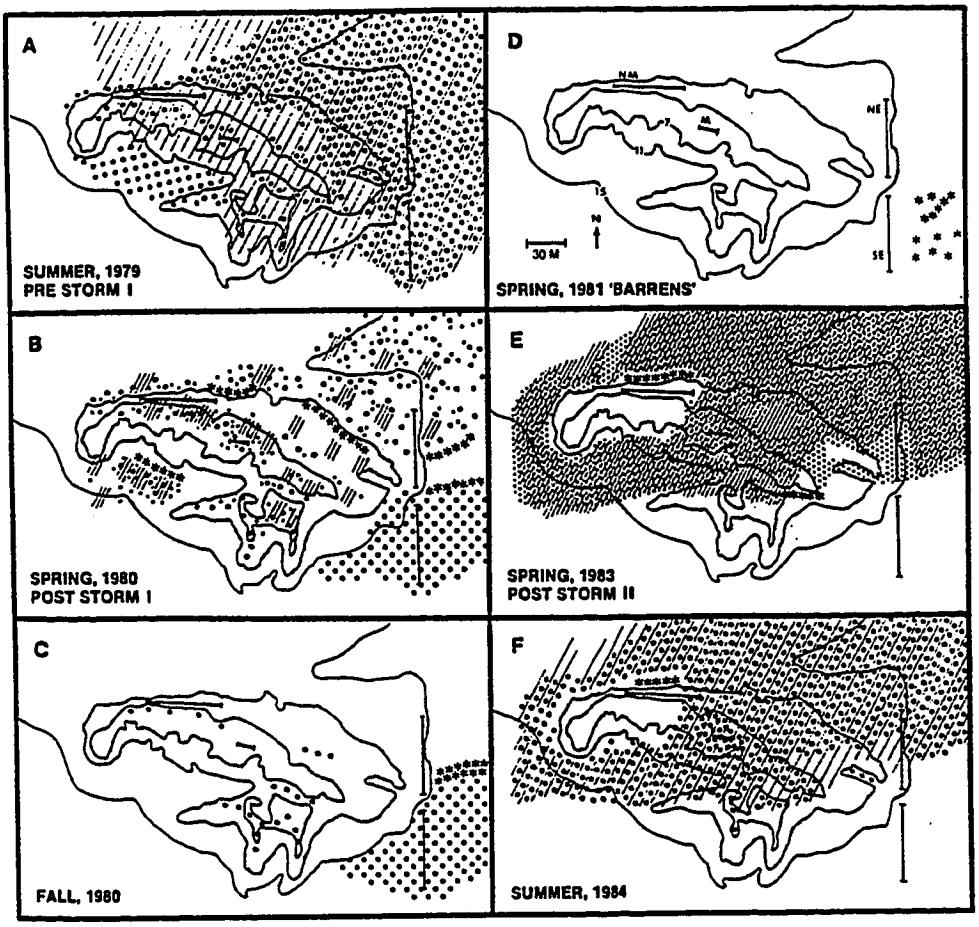

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Fig. 2

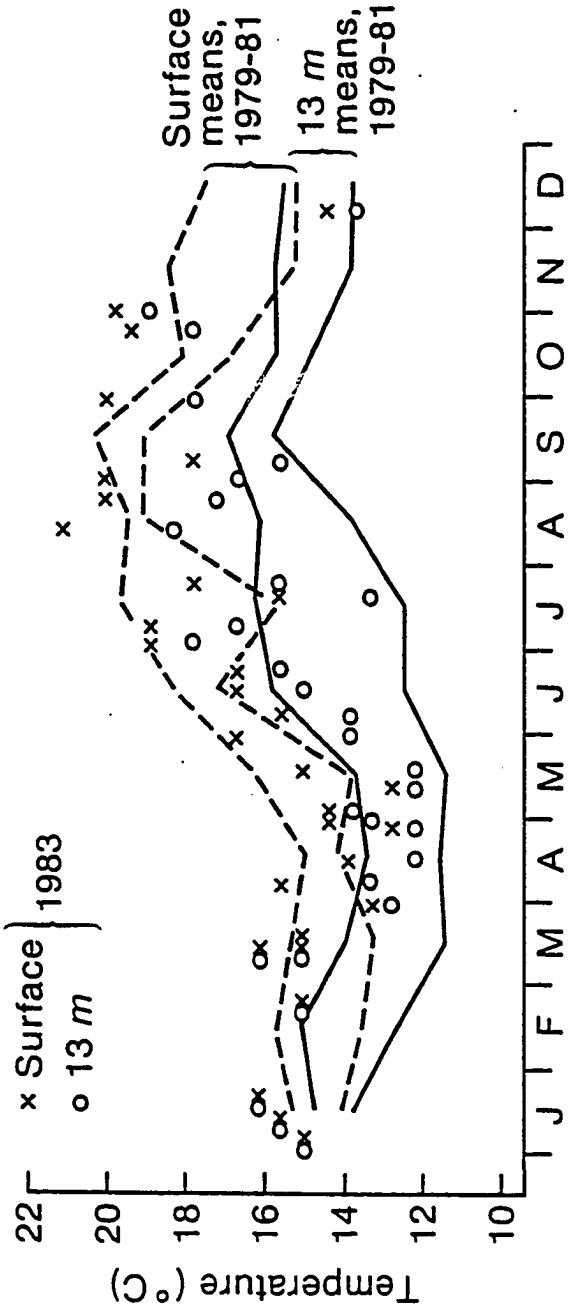

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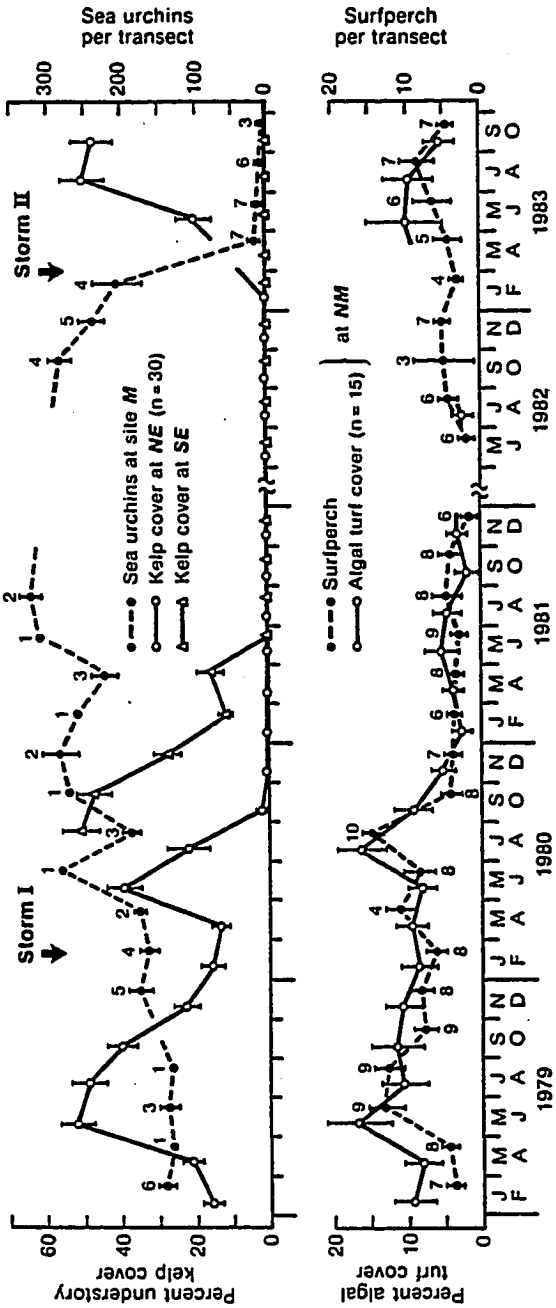
Fig. 3



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CHAPTER 3

PREDATOR-PREY RELATIONSHIPS IN A GUILD OF SURFPERCHES

Introduction

Large epibenthic surfperches are conspicuous members of the bottom assemblages of fishes that inhabit areas of reef and kelp off Santa Barbara, southern California. Surfperches comprise the well-defined family Embiotocidae, whose females bear large, well-developed young (Eigenmann 1894). Eighteen of the 23 species in this North Pacific temperate family inhabit the southern Californian coastal waters (Tarp 1952, Miller & Lea 1972). Many are opportunists and transgress the surrounding sand flats to congregate about piers and enter estuaries (DeMartini 1969). Some are among the first to colonize newly constructed artificial reefs and oil platforms (Carlisle et al. 1964, Turner et al. 1969, Fager 1971).

The Santa Barbara assemblage is unique in that it contains 5 relatively large species living together on the same reefs: black perch Embiotoca jacksoni, striped surfperch E. lateralis, rainbow surfperch Hypsurus caryi, rubberlip surfperch Rhacochilus toxotes, and pile perch Damalichthys vacca (Alevizon 1975a, Ebeling et al. 1980b). Together they comprise more than 20% of the total fish biomass at our study site at Naples Reef. Embiotoca jacksoni has been considered to be the most

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generalized both morphologically (Trap 1952) and ecologically (Limbaugh 1955, DeMartini 1969), although we question this of its feeding mode. It ranges from Baja California, Mexico to north San Francisco (Miller & Lea 1972), but is most common off southern Calfiornia (DeMartini 1969, Ebeling et al. 1980a,b, Hixon 1980). Off Santa Barbara, it is relatively more abundant than its congener E. lateralis (Ebeling et al. 1980a,b, Hixon 1980), which ranges from Baja California to Alaska, though is most common off central California and northward (Haldorson & Moser 1979). Smallest of the 5 species, Hypsurus caryi has about the same total range as E. Jacksoni (Tarp 1952), but prefers cooler water (Terry & Stephens 1978). Unlike the others, it is a summer transient at Naples Reef, arriving during late spring and departing in the fall. Rhacochilus toxotes, the largest and perhaps most specialized of the 5, lives northward to Oregon (Tarp 1952). Damalichthys vacca has the broadest range, from Baja California to Alaska.

During the day, most of these surfperch swim just over the bottom, continually seeking small food items (Limbaugh 1955, Quast 1968, Turner et al. 1969, DeMartini 1969, Alevizon 1975a, Ebeling & Bray 1976, Ellison et al. 1979, Ebeling & Laur, unpub). Thus they form a feeding guild of demersal microcarnivores, and prey on the animal community inhabiting a benthic "turf" of small plants and colonial animals. Chapman (1954) described such turf as a potential food source for fishes of the Azores. Fryer (1959) considered this "Aufwuchs" of fundamental importance to the reef-fish communities of African lakes. Although surfperch also forage in areas of reef sand and cobble in rills and deeper flats, few individuals are

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observed in turf-free areas, such as patches heavily overgrazed by sea urchins. Therefore, the success of a substantial part of the reef-fish community depends on the health of this carpeting food source, about which little is known.

Our objective has been to see how the 5 species share food and space on a semi-isolated offshore reef. Surfperches are well suited for such a study because they are abundant and overt, have a circumscribed and easily sampled forage base, are not easily frightened, and are not sought by fishermen at our study sites. Previous studies have shown that different species may tend to select different items from the array of available prey (Quast 1968, DeMartini 1969, Ellison et al. 1979, Haldorson & Moser 1979) and to segregate somewhat in space (Terry & Stephens 1978, Alevizon 1976a,b, Hixon 1980). Yet these studies did not compare diets quantitatively with the forage base, microhabitat preference, and feeding behavior. In another paper We compare surfperch diets with prey samples from turf and general overlap in microhabitat use (Ebeling and Laur, unpubl.). In the present study, we relate dietary differences to differences in foraging mode and microhabitat use, all relative to resource availabilities.

Methods

Study site

Ebeling et al. (1980a,b) described our study site, an isolated area of reef and kelp located about 1.6 km offshore in the Santa Barbara Channel, 24 km west of Santa Barbara, southern California (lat. 34°25′ N, long.

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119°57′ W). Covering some 2.2 ha, Naples Reef is a mound of shale outcrops and ledges surrounded by extensive flats of sand and cobble, and descending from crests at about 5 m depth to its base at 15 m. The reef supports a canopy of giant kelp (Macrocystis pyrifera) over secondary layers of understory algae and the carpeting turf covering much of the bottom.

Gut-content analysis

Methods of sampling fish, excising guts, partitioning gut sections, sorting contents, and measuring prey volumes are detailed in our companion paper (Ebeling & Laur, unpubl.). Briefly, diets were based on samples of about 30 adults of each species speared from Naples Reef during spring and summer, 1973. After they were removed from the fish, the simple tubular guts were divided into first("foregut") and second quarters and last halves. After fullness of these sections was scored from 0 (empty) to 4 (full), we sorted foregut contents into 14 categories of potential organisms (items) and measured each volumetrically. Since diets did not vary significantly with month of sampling, they were pooled to maximize sample size. Then volumes of items were weighted by fullness score for each fish, totaled among fish for each species, and presented as proportions of total contents.

Benthic sammpling of turf forage base

During about the same times that fish were sampled, we measured availability of food items in aliquots from benthic samples of turf and included patches of sand and cobble. Seven samples were taken from quadrats at

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randomly-selected points where a scuba diver dropped a square of iron bar covering 0.25 m^2. While two divers secured the quadrat and scraped the substrate bare of organisms and debris, a third collected all this in an "air lift" fed by compressed air from his scuba tank. Air bubbles lifted the material through a long plastic tube to be collected in a fine-meshed bag clamped to the top (Chess 1969). Each sample was fixed and stored in 5% buffered formalin. To supplement the original 3 (of 7) samples falling within reef crest and reef slope, 5 more were similarly taken from these microhabitats, where fish concentrated most of their total foraging effort.

Before samples were sorted, organic material was separated from inorganic debris and aliquots were taken. In a solution of zinc chloride adjusted to specific gravity 1.8, nearly all sand, silt and sediment sank to the bottom of a separation jar, leaving most organisms at the surface. Some thick-shelled molluscs had to be retrieved and added to the organic moity. Liquid displacement volumes of organic and inorganic parts were measured before the organic was transferred to a basin and thickened for aliquoting. By repeated testing we found that 150 ml aliquots taken by beaker from a stirred "paste" of turf were more reliable than similar aliquots from liquid suspension. Aliquoting was essential, because the time needed to sort a whole sample was prohibitive. Aliquots were then sorted to potential prey items, whose volumes were measured separately in a syringe. We compared the composition of benthic samples with that of surfperch diets.

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Oral winnows from fish

Some surfperches spit out clouds of material after mouthing bites of turf. Unlike most fishes that do this, however, they do not then pick out "choice" items from the expelled array. This indicated that surfperches can "winnow" preferred prey from rejected items in their mouths before the rejected material ("cast") only is expectorated. To test this, we compared casts with gut contents and benthic samples. When we were not disturbing the area with fish spearing and benthic sampling, we approached fish that had just taken a bite and collected all or most of their cast in a small aquarium net before it could settle to the bottom. Still underwater, the net was then easily reversed into a small bottle, where the cast was later preserved for sorting and identification.

Foraging effort

Within a smaller section of Naples Reef (Fig. 1) we measured foraging activity of the 5 species among 5 different microhabitats and over time by following individual fish selected haphazardly and counting the number of times they bit into the tutf. Using underwater slates supplied with dive watch and ruled into a matrix of rows for individuals and columns for microhabitats, we ticked off bites per fish per microhabitat for 5 min intervals. We found that 5 min was about as long as we could follow a particular fish for any one time. Such observations were made throughout the day for temporal analysis and more intensively during peak foraging periods for spatial analysis by microhabitat. Rates were calculated per bihourly

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interval and relative numbers of bites were tabulated per species per microhabitat.

At the outset of our spring-summer sampling period we delineated and characterized the 5 microhabitats as (Fig. 1): "reef crest," the productive and surgy area along the tops of ridges supporting dense stands of the bushy red alga Gelidium robustum; "reef slope," steep banks below the crests with rich turf but no Gelidium bushes; "reef cobble," narrow areas of cobble, sand, and other debris filling the bottoms of rills below slopes and supporting rich patches of turf; "reef flat," relatively level areas beyond slopes and rills with less dense turf often overgrazed by sea urchins; and "deep cobble, " the flat, evenly cobbled zone at the deep offshore base of the reef with relatively sparse turf. Areas of the different microhabitats in the western observation site (Fig. 1, inset) were estimated from a detailed contour map of Naples Reef compiled from coordinates determined by miniranger and depth recorder on a skiff and two transponders on shore. Initial values were adjusted by estimates of vertical relief made by laying weighted lines across the zones and comparing the length along the substrate with the shorter length of a beeline. We continually certified results by checking the conditions of different parcels: e.g., whether in fact dips supported "reef cobble" or whether rises indeed bore dense stands of bushy algae characteristic of "reef crest." Adjusted areas per microhabitat were used to estimate an "expected" distribution of fish foraging effort.

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Off-reef feeding-tray experiment

Species more generalized in their microhabitat requirements as indicated by their greater dispersion of bites, may be more inclined to wander off the reef to forage, especially if food may be limited locally on the reef itself. To test this, we anchored pairs of m^2 plastic bread trays to deep sandy bottom, one pair at 20 m from the NW base of the reef, the other at 40 m distance on the same line. For each pair, a test tray was loaded with turf-covered rocks from the reef, while a control tray located 10 m from the test was left empty. Once a week, we counted fish inspecting each tray (inspections usually led to feeding at the test trays).

Results

Food availability and diets

Turf appeared to differ more in density (volume) than in composition among microhabitats. Volumes were largest from reef crest, which bore thick stands of lush algae, and smallest from deep cobble, which superficially appeared quite barren (Table 1). Concordance among arrays of ranked abundances of items was high, whether for all 14 items among all 12 samples (Kendall's $W = 0.68$), among 5 groups of samples pooled by microhabitat (0.67), or among the 5 samples from reef slope only (0.74) (all significant at $P < 0.005$). Even discounting the predominating "items of doubtful food value," concordance among arrays of the 10 "items of food value" was high, both among samples (0.59, $P < 0.005$) and among microhabitats (0.53, $P < 0.01$). Therefore, all samples were pooled to estimate the composition of the surfperches' forage base--the availabilities of the

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different items (see Tables 1,2).

Volumetrically, "items of doubtful food value" dominated the benthic samples (Table 1). Although such items occurred frequently in guts of some species, e.g. Embiotoca jacksoni and E. lateralis, they may have been ingested incidentally with selected prey. If so, these items may be passed through the fish's guts essentially unassimilated. For example, E. jacksoni ingested amphipod tube mat (ATM) in relatively large amounts along with amphipods, while Hypsurus caryi ate lots of tubicolous amphipods and expelled most of the mat. Mat is made up of sand and detritus cemented together and is doubtfully nutritious; it probably passes through guts essentially unaltered. Therefore, it is probably not an important item distinguishing diets of E. jacksoni and H. caryi; more likely it shows difference in the species' foraging efficiency.

Such items were identified by having mean forage ratios (proportion in guts/proportion in benthic samples) less than 1.0 (Table 2). Besides amphipod tube mats, they included plants (mostly red algae such as Rhodymenia, Gigartina, and Gelidium), crustose debris (mostly skeletons of the encrusting bryozoans Membranipora, Microporella, Rhynchozoon, mixed with stone coral-tests and other calcarious debris), and branched hydroids and bryozoans (e.g. Plumularia, Abietinaria for hydroids, and Scrupocellaria, Thallamoporelia, Diaperoecia, and bugulids among bryozoans). Nonetheless, occasional individuals of E. lateralis and E. jacksoni may have selected algae encrusted with bryozoans.

We assumed that fish selected "items of food value" (Table 1), whose forage ratios were substantially greater

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than 1.0 (Table 2). As a guild, the surfperches preferred small, motile invertebrates. Forage ratios averaged highest for large (e.g. Erichthonius, Ampelisca) and small (e.g. Lembos, Photis, Gammaropsis) gammarid amphipods, caprellid amphipods (Caprella), shrimps (e.g. Heptacarpus), and small crabs (e.g. Loxorhynchus, young Cancer, xanthiids). Such a generalization from mean forage ratios is somewhat misleading, however, because D. vacca selected only relatively large, hard-shelled items, such as bivalves, shelled gastropods, and brittle stars that were mostly avoided by the others (Table 2): it had a radically different regimen from the others (Ebeling & Laur, unpubl.).

Feeding modes

The five surfperches showed different morphological and behavioral adaptations for selecting prey from the available spectrum. At first glance, these continually searching fish seemed to move more or less indiscriminantly over the bottom, biting at turf covering a variety of surfaces. Yet the fishes' morphology together with our observations of their "oral winnowing" indicated that the different species selected food in fundamentally different ways. Expectedly, the larger species had larger mouths as measured by width of gape, and tended to eat larger food items as measured by the percentages of items of food value in their guts (Table 3). Even so, the correlation between body and gape size ($r = 0.997$, $P < 0.01$) greatly exceeded that between body size and percent "large" items (0.64, NS), indicating that prey size is not a simple correlate of mouth size.

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In fact, the largest species (R. toxotes) ate a singular mix of some of the smallest items (amphipods) along with the largest (crabs). Species whose diets included greater percentages of items of doubtful food value (E. jacksoni, E. lateralis, H. caryi) had significantly longer guts than the others (Table 3).

Species were distinguishable as "oral winnowers" (E. jacksoni, caryi, R. toxotes) or "non-winnowers" (E. lateralis, D. vacca). The winnowers usually expelled casts--material spit out following a bite--whereas non-winnowers almost never did (Fig. 2). The volumes of their casts were substantially greater than nil (Table 3, Fig. 5). Comparison of the composition of the winnowers' gut contents with that of their casts, furthermore, indicated that their bites were indeed winnowed and not merely displayed for reexamination to pick out preferred prey. Fish tended to ignore casts once they were expelled. Also, items of food value were retained preferentially, while items of doubtful food value comprised the greater volumes in casts (Fig. 3). Whereas the compositions of gut contents and cast or of gut and benthic samples were dissimilar or even complementary, those of cast and benthic samples were very similar and positively correlated (Table 4). Casts and benthic samples were dominated by similar rank orders of doubtful food items; gut contents were not. Obviously, fish selectively expelled inorganic debris and the items of doubtful food value in their casts, although a few items of value were lost in the process. This tended to corroborate our initial distinction between items of real and of doubtful food value.

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Among the winnowers, some were more specialized than others. The most adept was R. toxotes. Its casts were largest even when standardized by mouth size, and it swallowed the least amounts of items of doubtful food value (Table 3). It had the greatest complementarity between gut contents and cast and greatest similarity between cast and composition of benthic samples (Fig. 3 Table 4). At the generalized extreme, E. jacksoni may have been unable to reject substantial amounts of doubtful food, especially amphipod tube mat (Table 3). Also it winnowed much less frequently than the other two (Fig. 2). Perhaps E. jacksoni bothers to winnow only those bites with a relatively meagre content of valued food. Its relatively low selectivity may explain why it alone of the winnowers showed a significant rank correlation between the composition of gut + cast, and that of benthic samples (Table 4).

In sum, R. toxotes appeared to be the most specialized or adept winnower, followed in order by H. carvi and E. jacksoni. The average correlation for all pairs of variables--gut contents, casts, benthic samples--would seem to be an inverse measure of such specialization (Table 4).

The non-winnowers, on the other hand, differed markedly in feeding mode from winnowers and from each other. Although both retained all items that they ingested, they selected quite different types of prey in contrasting styles. Embiotoca lateralis is a picker and browser (Hixon 1980, Ebeling & Laur, unpubl.). It frequented the surgy zone of reef crest, where it browsed bryozoans from the bushy stands of Gelidium algae, picked caprellid amphipods abounding in the bush, and picked

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gammarid amphipods and other small prey from tube mats and turf at the base of the taller plants. Gelidium robustum yields a bountiful food supply. A sample of three plants ranging from 400 - 660 ml in volume bore 24.3-31.8% animal prey items by volume, of which 58.1 - 66.6% was caprellid amphipod, 28.6 - 37.4% was encrusting bryozoan, and 3.9 - 6.5% consisted of other items (gammarid amphipods, worms, molluscs, crabs). A single bush of Gelidium harbored an estimated 250,000 caprellids, mostly of the large, red species Caprella californica. In contrast, motile prey comprised less than 2% of the volume of adjacent algae such as Rhodymenia and Gigartina. It was not surprising then that fish on reef crest took some 80% of their feeding bites on Gelidium. Of 12 well-fed fish that were speared after having foraged in and about Gelidium only for some time, 5 contained more than 90% caprellids by volume, 4 had more than 90% algae and encrusting bryozoans, while the rest held mixtures of prey items. Because mid- and hind- guts contained similar prey, individuals carefully inspecting the plants may have concentrated on one prey item to the exclusion of others.

In contrast, D. vacca was a picker and cruncher of relatively hardshelled prey. It ate the small crabs shared with R. toxotes, as well as shelled molluscs and brittle stars, which it often rooted out from under rocks and tore apart before ingesting the pieces. It crushes its prey with strong pharyngeal teeth, which are more massive and pavementlike than those of the other species (DeMartini 1969, Brett 1979).

In sum, the surfperches' basic differences in feeding modes provide them different diets even though

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they may be foraging together in the same place. Embiotoca lateralis and D. vacca selected their food "before the fact" by browsing or picking out their prey after carefully inspecting the source. Rhacochilus toxotes and H. caryi selected their prey "after the fact" by grazing mouthfuls of turf and sand or gravel, then spitting out the rejected items. Having a more generalized diet, E. jacksoni neither inspected the turf as carefully as did the non-winnowers, nor winnowed its food as effectively as the winnowers, Hence its forage ratios had a relatively small variance (Table 2), and it retained relatively more of items of doubtful food value,

Foraging effort by microhabitat

All surfperches showed distributions of feeding bites among microhabitats that differed significantly from that expected from the relative areas (Fig. 5). Although values of chi square based on observed - expected distributions were all highly significant ($P < 0.005$), their varying magnitudes were used to measure degree of microhabitat specialization, Embiotoca jacksoni was least specialized in foraging effort ($X^2 = 54$), while E. lateralis was most specialized (1334) and took almost all bites from reef crest. Like E. jacksoni, A. caryi preferred foraging on reef slope. Rhacochilus toxotes and D. vacca mostly divided their efforts between slope and reef cobble. Therefore, surfperch tended to concentrate their efforts in microhabitats richest in perch food (Fig. 6), Among microhabitats, the correlation between volumes of "items of food value" and total bites pooled among species ($r = 0.98$) was significant ($P < 0.01$), though that between volumes of "items of doubtful

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food value" and total bites (0.84) was not.

Foraging effort by time-of-day

The four species that forage only during the day (of Embiotoca, Hypsurus, and Damalichthys) had peaks of feeding intensity in early morning and afternoon (Table 5). Since the fish's foreguts were mostly full by mid-morning (Ebeling & Bray 1976), the lull before the afternoon peak indicated that the fish were probably satiated and more discriminatory then (cf. Ware 1972). Feeding activity declined from mid-afternoon until dusk when foraging stopped. Damalichthys vacca fed at the slowest and most steady rate throughout the day, It was most opportunistic: usually first on the scene of any disturbance to carefully inspect the site for newly exposed prey.

Rhacochilus toxotes did not show the same pattern of daytime foraging because it fed more consistently at night (Ebeling & Bray 1976), When not actively biting and winnowing along the bottom, it often joined a small school of lethargic individuals drifting about slowly a meter or so off the bottom or even at middepth. Consequently, most foreguts of fish sampled at any daylight time were empty, but were nearly full at night. Even so, fish ate the same kinds of prey at night, except perhaps for relatively more shrimp that are exposed then.

Off-reef forage experiments

As predicted, turf-laden and control trays anchored on sand off the reef attracted microhabitat generalists rather than specialists. Most specialized in

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microhabitat use on the reef (see chi-squares, Fig. 5), E. lateralis and R. toxotes were seen at neither pair of trays, near or far (Table 6), even though the introduced turf thrived and harbored high concentrations of prey throughout the experiment.

Even so, the species with more generalized microhabitat requirements (E. jacksoni, D. vacca, H. caryi) did not differ significantly in their frequency of inspecting trays, either amqng themselves or between near and far trays (Table 6). Hence, counts of inspections differed significantly only between test trays, where sightings usually preceded feeding, and control trays, where but a few wanderers were seen. Apparently the generalists foraged off the reef in numbers independent of their relative abundances on the reef, because ANOVA outcomes were similar whether sightings were weighted by abundance or not.

DISCUSSION

Unlike "switch-feeding carnivores"--large mouthed midwater fishes that can change their feeding habits drastically as the occasion arises (Love & Ebeling 1978)--the five surfperches are more or less restricted to benthic microcarnivory at Naples Reef. They resemble a host of other demersal reef fisher with compressed bodies and small mouths, in that they forage almost continually for small prey hiding in an algal mat or among pebbles and gravel (Hiatt & Strasborg 1960). In foraging strategy, such predators are "searchers" because they spend most of their time seeking out a broad spectrum of small prey instead of ambushing or pursuing larger prey (MacArthur & Levins 1964, Schoener 1969_a).

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They forage widely for abundant small prey to maximize their intake of calories, instead of craftily chasing or subduing large prey to minimize time spent foraging (Griffiths 1980).

The surfperches appear to be obligate exploiters of a common forage base: the many small prey in a turf of algae and colonial animals covering much of the reef bottom (Ebeling & Laur, unpubl.). And generally, their diets are remarkably similar in other places and at other times. Winnowers invariably concentrate on small prey, mainly amphipods, while D. vacca seldom deviates from its principal diet of larger hard-shelled items (Quast 1968, Ellison et al. 1979, Turner et al. 1969, Haldorson & Moser 1979). It feeds at a slower pace than the others because it gets more calories per bite (Ellison et al. 1979). The browser and picker, E. lateralis, has considerable dietary latitude over its geographic range; it eats a broader spectrum of prey, including larger items, where it is more abundant off Santa Cruz Island (Alevizon 1975b) and central California (Haldorson & Moser 1979). Its diet is more restricted to small items at Naples Reef (Haldorson & Moser 1979), where its congener E. jacksoni is generalized in diet and microhabitat use, and so predictably in a fluctuating environment (McNaughton & Wolf 1970, Cody 1974) is the most abundant of the five (see Table 6).

Surfperch diets, therefore, seem to be restricted by specialized adaptations that are probably not subject to further major selection for optimization (Smith 1978). These fixed traits, as distinguished from variable traits (Smith 1978), include fundamental differences in feeding structures and perceptual skills (see Keast & Webb 1966,

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Chao & Musick 1977, Gatz 1979) that distinguish the browser-picker (E. lateralis), cruncher (D. vacca) and winnowers (E. jacksoni, H. caryi, R. toxotes). All have small, simple jaw teeth (DeMartini 1969), which are ill suited for algal scraping and other specialized ventures in herbivory (cf. Fryer 1959, Norris & Prescott 1959). Then, within this constraint common to all five, E. lateralis is most generalized because it is limited in foraging efficiency by neither having D. vacca's ability to crush relatively large, hard items between strong plates of massive pharyngeal teeth (DeMartini 1969, Brett 1979), nor having the winnowers' abilities to sift multitudes of tubicolous amphipods from their homes. Yet D. vacca is constrained by lacking abilities to browse or winnow, so cannot switch to amphipods. And even though generalized in foraging mode, E. lateralis aggressively chases the others from reef crest, where it is particularly adept at quickly spotting and picking abundant prey from among bush algae (Hixon 1980). In turn, the winnowers are most efficient at extracting gammarid amphipods, but are mostly denied the food items of reef crest and cannot very well handle most of the cruncher's prey. But winnowing must confer substantial advantages because it has evolved independently in other fish groups, An Atlantic wrasse, Tautogolabrus adspersus, similarly spits out any excess material ingested along with its prey (Olla et al, 1975); the cichlid Geophagus vigorously chews its mouth contents before ejecting inedible particles (Keenleyside 1979); and various mullets may spit out sand after ingesting mouthfuls of benthos (Ebeling 1957).

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Thick lips, as distinguish R. toxotes, have both a manipulative and winnowing function, which may be preadaptive to nocturnal foraging. Jones (1968) concluded that thick lips in grazing surgeonfishes (Acanthuridae) are (P. 330) "...necessary to provide a seal between the fish and the substratum that allows a suction pressure to build up." This "gasket function" may also apply to thick-lipped cichlid fishes (Barlow & Muncey 1976). Rhacochilus's ability to select food "blindly" may enable it to forage more regularly at night. We have seen fish in pitch dark leave luminescent trails as they scoot along the bottom. They need not see their food so long as they can feel a suitable stand of turf, perhaps probing it with their lips. The rubberlip perch can also lift and move small rocks and pluck crabs. Thus by winnowing and/or plucking it exploits the choice morsels of winnower and cruncher diets: tubicolous amphipods and small crabs.

Within this framework of more or less fixed abilities and proclivities, other traits are variable and may change to optimize energy intake in different environments and circumstances (Ivlev 1961, Werner & Hall 1979). For example, D. vacca easily substitutes within its range of medium-sized hard-shelled food items. About the girders and pillings of an oil platform offshore of Naples Reef, large pile perch substitute small mussels, which abound on the submerged infrastructure, for brittle stars, crabs, and other molluscs that are more available at Naples. Thus fish in the platform population had switched prey, but only within the array of hard-shelled kinds characteristic of the species. They ate no tubicolous amphipods, which also enriched the girders in

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huge numbers, even in the absence of the other four species: they had not expanded their diet in the absence of potential competitors (MacArthur 1972, Werner & Hall 1979), but had selected the most abundant and nutritious item among their set of tractable prey (cf. Ivlev 1961, Schoener 1969b, Emlen 1968).

Use of microhabitat as a place to forage also may vary within the fish's fixed abilities (MacArthur 1972). Manipulations of numbers and food of the two congeners indicate that E. lateralis, which is a habitat specialist, excludes E. jacksoni, a generalist, from reef crest (Hixon 1980). When lateralis was removed from a test site, jacksoni soon expanded its bathymetric distribution to include this rich microhabitat, although lateralis was reluctant to leave the crest when jacksoni was eliminated from another site. Hixon (1980) corroborated this relation by anchoring paired trays, one loaded with reef-crest algae, the other with reef-flat turf, to either reef crest or peripheral microhabitats, Embiotoca lateralis sought out the crest algae, whether set on crest or elsewhere, while jacksoni showed little preference between the choices anchored outside the crest zone.

The surfperches shifted in microhabitat after a major climatic disturbance. Under relatively benign conditions during the present study, the surfperches as a guild foraged most in microhabitats having most perch food. Such microhabitats also had highest plant biomass, and generally faunal density often relates directly to plant density (Gerking 1957). But some 7 years later in February, 1980, unusually high waves effectively defoliated Naples Reef and environs. Thence a chain of

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events culminated in sea urchins (Strongylocentrotus) maintaining the barren state by overgrazing young plant recruits (Laur & Ebeling, unpubl.). Some 9 months later, the surfperch tended to converge their foraging efforts to reef slope and crest (D. Stouder, pers. comm. 1981), bastions against the relentless onslaught of urchins moving up the reef and grazing most turf and understory algae in their wake.

Perhaps the remarkable mechanism of the surfperches' pharyngeal jaws played a dominant role in the evolution of specialized fixed traits of crunching and winnowing, while preserving some flexibility of operation to permit variable traits under changed circumstances. Liem & Greenwood (1981) described "pharyngognathy" in surfperches: Before it is swallowed, food trapped between the lower and upper pharyngeal jaws (p. 93) "...can be crushed, triturated, macerated, compacted, or in other ways prepared depending on the nature of the pharyngeal dentition." They further concluded (p. 95) that it is mechanically possible for the lower jaw to perform a wide range of actions, "...not only a strong bite, but also numerous other finely controlled movements since it is suspended in a muscular sling,... part of which can be kept in continuous and varying tensions." We suggest, therefore, that one line of specialization has realized massive teeth and accouterments for crushing hard-shelled prey in D. vacca, whereas another line has culminated in flexibility of movement for winnowing. We suspect, furthermore, that E. lateralis has the most generalized mechanism of the five, while E. Jacksoni has a less specialized winnowing mechanism than either H. caryi or R. toxotes. Each species, then, is able to shift prey

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within broader or narrower categories (depending on its degree of specialization) and between foraging grounds by varying its overt behavior in conjunction with movements of the sling supporting its lower pharyngeal jaw. Thus, surfperches offer a rich prospect for functional morphological study of feeding mechanisms (K. Liem, pers. comm. 1980).

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Table 1. Volumes of items in 12 benthic samples of turf scraped from 0.25 m^2 quadrats in different microhabitats at Naples Reef. Inorganic debris (sand, rock, shell bits, etc.) was separated out (see text) and not included here. 'Items of food value' for surfperches are: Worms, polychaete worms; Bival., bivalve molluscs; Gastr., shelled gastropod molluscs; Isopod, isopods; LgAmph., 'large' gammarid amphipods 3 mm or more in total length; SmAmph., 'small' gammarid amphipods less than 3 mm; Caprel., caprellid amphipods; Shrimp, decapod shrimps; Crabs, small crabs; Brit., ophiuroid brittle stars. 'Items of doubtful food value' are: Plants, algae; Crust., crustose debris; Branch, branched hydroids and bryozoans; ATM, spongy mats of tubes housing the tubicolous gammarid amphipods, with attached debris.

Micro-habitat	Items of food value											Items of doubtful food value				
	Percentage in aliquot										Est. total samp. vol. (ml)	Percentage in aliquot				Est. total samp. vol. (ml)
	Worms	Bival.	Gastr.	Isopod	LgAmph.	SmAmph.	Caprel.	Shrimp	Crabs	Brit.		Plants	Crust.	Branch	ATM	
Reef crest	17.3	34.6	9.4	2.2	2.9	11.7	15.8	1.7	3.9	0.7	61.0	65.5	19.2	6.0	9.3	616.0
	15.9	27.5	13.6	0.9	4.7	13.1	8.4	0	14.0	1.9	36.9	56.8	29.4	4.9	8.9	565.1
	11.1	13.9	15.0	1.4	1.4	30.5	8.3	0	11.6	6.9	32.2	84.1	11.2	2.1	2.5	660.9
									Means		43.4					614.0
Reef slope	14.3	42.9	2.9	2.9	12.9	4.3	7.1	1.4	5.7	5.7	92.0	22.7	18.8	9.3	49.2	908.0
	16.7	47.0	3.7	0.1	3.0	13.4	1.6	0	9.9	4.5	72.5	30.6	53.9	7.9	7.6	398.5
	11.4	49.4	1.3	1.3	10.1	8.9	3.8	5.1	2.5	6.3	21.8	2.4	7.3	64.2	26.1	228.2
	14.8	55.4	3.0	1.0	6.9	4.0	7.9	0	5.9	1.0	65.3	16.5	25.5	31.4	26.5	657.7
	8.6	38.8	28.0	3.2	8.6	3.7	2.6	0	4.3	2.2	62.7	6.9	33.9	24.5	34.7	496.3
									Means		62.9					537.7
Reef cobble	3.2	0.5	0.6	0.1	1.6	1.3	0.1	0.8	3.8	88.0	38.0	93.7	0.6	0.5	5.2	400.0
Reef flat	8.4	7.5	1.9	0.3	15.5	23.6	6.2	0	34.2	2.5	12.8	94.2	0.1	1.2	4.5	355.2
	10.4	16.6	12.4	2.1	6.2	1.7	2.1	0	41.4	7.2	16.7	21.3	10.1	23.7	43.4	239.3
									Means		14.8					297.2
Deep cobble	11.3	22.6	16.9	5.6	22.6	8.5	0.6	0	11.3	0.6	23.1	35.1	0	0.1	64.8	120.9
Total	12.8	31.8	7.6	1.3	6.0	9.8	6.1	1.0	10.0	13.8	508.4	51.7	18.0	13.0	17.2	5724.6

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Table 2. Availability and forage ratios of items in 12 benthic samples of turf (excluding inorganic debris) from Naples Reef. Items of food value and of doubtful food value are identified in Table 1.

Food items	Availability (Vol. % in pooled benthic samples	Forage ratio (vol. % in guts per in benthic samples)					
		E. jacksoni	*E. lateralis*	*H. caryi*	*R. toxotes*	*D. vacca*	Mean
Items of food value							
Worms	1.05	8.81	1.13	2.86	0.87	0.27	2.79
Bival.	2.60	2.17	0.47	0.65	0.14	7.22	2.13
Gastr.	0.62	0.63	0.66	0.82	0.60	18.48	4.24
Isopod	0.11	9.45	19.00	30.36	9.00	2.55	14.07
LgAmph.	0.49	29.76	32.24	55.49	63.76	3.04	36.86
SmAmph.	0.79	9.46	10.24	43.40	10.75	2.10	15.19
Caprel.	0.50	21.98	58.62	7.44	4.60	0.40	18.61
Shrimp	0.08	3.88	203.75	37.50	130.25	8.12	76.70
Crabs	0.81	2.43	1.21	5.74	49.44	29.64	17.69
Brit.	1.12	0.72	0.04	3.81	0.69	33.44	7.74
Items of doubtful food value							
Plants	45.64	0.25	0.28	0.03	0.01	0.03	0.12
Crust.	16.01	0.23	0.05	0.02	0.02	0.04	0.07
Branch.	10.98	0.20	0.10	0.08	0.08	0.08	0.11
ATM	19.21	1.58	0.52	0.62	0.12	0.05	0.58

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Table 3. Characteristics distinguishing the five surfperches relating to their feeding modes at Naples Reef. Volumes of ingested matter rejected by oral winnowing (Casts) are standardized by the fishes' average mouth size (Gape width). Proportionate similarity (PSI) between arrays of items in guts and arrays in the organic components of benthic samples is $\sum_{j=1}^{14} \min(a_j, p_{ij})$, where a_j is the proportion of item j ($j = 1, \ldots, 14$) in the pooled benthic array, and p_{ij} is that for the ith of 5 species.

	N	Standard length (SL) (cm) $\bar{X} \pm SE$	Gut length/ SL $\bar{X} \pm SE$	Gape width (cm) $\bar{X} \pm SE$	N	Cast/ Gape width (ml/cm) $\bar{X} \pm SE$	PSI	Items of doubtful food value in guts (%)	Amphipod tube mat (ATM) in guts (%)	Items of food value longer than 3 mm in guts (%)
E. lateralis	40	20.0 ± .65	1.23 ± .033	1.39 ± .045	24	negl.	0.30	24.5	10.0	87.2
D. vacca	62	21.0 ± .44	0.94 ± .032	1.48 ± .031	25	negl.	0.11	3.8	1.0	98.7
E. jacksoni	100	19.6 ± .34	1.24 ± .025	1.37 ± .024	28	0.06 ± .010	0.55	47.6	30.4	84.5
H. caryi	58	16.4 ± .45	1.18 ± .036	1.00 ± .027	25	0.14 ± .017	0.22	14.3	11.8	56.2
R. toxotes	77	27.9 ± .36	0.90 ± .024	2.23 ± .029	17	0.40 ± .050	0.09	4.1	2.4	91.8

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Table 4. Relations between arrays of gut contents (Gut), casts, and benthic samples for the winnowing species of surfperches. *Tau*, Kendall's coefficient of rank correlation; *PSI*, proportionate similarity $(\sum_{i=1}^{15} \min(p_{ij}, p_{ik})$ for $i = 1, \ldots, 15$ items, between arrays j and k).

Species	Pairs of arrays compared									
	Gut and Cast		Gut and Benthic sample		Gut + Cast and Benthic sample		Cast and Benthic sample		Means	
	Tau	PSI	Tau	PSI	Tau	PSI	Tau	PSI	Tau	PSI
Embiotoca jacksoni	0.02	0.35	0.17	0.34	0.43*	0.59	0.59*	0.73	0.30	0.50
Hypsurus caryi	−0.01	0.33	−0.21	0.22	0.22	0.44	0.52*	0.58	0.24	0.39
Rhacochilus toxotes	−0.44*	0.17	−0.35*	0.10	0.16	0.49	0.48*	0.74	−0.04	0.38
Means	−0.14	0.28	−0.13	0.22	0.27	0.51	0.53	0.68		

* Significantly different from zero at $P \leq 0.05$.

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Table 5. Bihourly variation in feeding rates (bites per min) for the surfperches at Naples Reef. Numbers of fish observed are in parenthesis.

Species	Dawn–0700 h	0700–0900 h	0900–1100 h	1100–1300 h	1300–1500 h	1500–1700 h	1700–1900 h	Dusk–Dark	Weighted means (pre- 1700 h)
E. jacksoni	2.19 (5)	0.91 (11)	0.57 (25)	0.08 (6)	1.50 (7)	0.86 (15)	0.41 (3)	0 (4)	0.83
E. lateralis	2.88 (5)	1.35 (11)	1.50 (7)	3.0 (1)	2.33 (3)	1.80 (6)	0.62 (4)	0 (3)	1.71
H. caryi	0.90 (7)	0.92 (8)	0 (3)	2.06 (4)	2.54 (7)	0.80 (1)	—	—	1.34
*R. toxotes**	0 (2)	0.79 (8)	0.59 (12)	2.80 (2)	—	1.20 (11)	0.80 (3)	1.40 (2)	0.91
D. vacca	0.65 (4)	1.19 (8)	0.70 (17)	0.49 (12)	0.80 (2)	0.60 (1)	0 (2)	0 (2)	0.69
Unweighted means (excluding *R. toxotes*)	1.66	1.09	0.69	1.41	1.79	1.02	0.34	0	

* Solitary individuals only (during the day, most individuals assemble as non-feeding schools above the bottom).

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Table 6. Inspections by surfperches of feeding-tray pairs anchored at 20 m (Near) and 40 m (Far) from Naples Reef, compared to their densities on the reef from Ebeling et al. (1980a). Each pair consisted of a turf-laden food tray and an empty control. Counts of fish sightings at trays, which usually preceded feeding, were transformed to their square-roots + 0.5 to equalize variances. Means ± standard errors (SE) are given for the transformed variates, each based on N = 6 sightings or N = 4 density estimates; three-way analyses of variance (test vs. control, distance, species) are limited to counts of the only three species to inspect trays; outcomes were similar whether counts were transformed by square roots or weighted by relative densities of the species. All interactions were non-significant (P> 0.05).

Species	Est. no. of fish per ha of reef (square root)	Turf-laden tray (Test)		Empty tray (Control)	
		Near (20 m)	Far (40 m)	Near (20 m)	Far (40 m)
E. lateralis	7.3 ± 1.70	0	0	0	0
R. toxotes	5.5 ± 1.17	0	0	0	0
E. jacksoni	19.2 ± 1.35	1.5 ± .36	1.1 ± .24	0.8 ± .27	0.8 ± .19
H. caryi	9.2 ± 2.12	1.0 ± .25	2.1 ± .42	0.6 ± .12	0.6 ± .12
D. vacca	9.1 ± 0.72	1.5 ± .25	1.5 ± .35	1.0 ± .32	0.7 ± .18

Three-way anovas of counts of sightings: F values	Counts unweighted, but transformed to $\sqrt{X + 0.5}$	Counts weighted by relative density of reef fish
Test vs. control	6.0 (P = 0.02)	5.0 (P = 0.03)
Near vs. Far	< 1 (NS)	< 1 (NS)
Among 3 species	1.3 (NS)	2.2 (NS)

Figure Captions.

Fig. 1. Section of Naples Reef (A - A' on inset map) in the area (hatched) where surfperch feeding bites were counted. Microhabits are: DC, deep cobble; RCo, reef cobble (at bottom of rills); RCr, reef crest (with bushes of Gelidium algae); RF, reef flat; and RS, reef slope (with carpeting turf). Fig. 2. Comparison of winnowing frequency and cast size among surfperches that either do (winnowers) or do not (non-winnowers) winnow doubtful items from valued food in their mouth. Guts, no. of foreguts examined; Casts, no. of casts collected.

Fig. 3. Comparison of relative volumes between valued food and doubtful items in diet, benthic samples (resource), and expectorated casts for surf perches that winnow out the doubtful iitems in their mouth. Items (identified in Table 1) with similar relations are grouped as one. N's for diet, benthic samples, and casts are as in Tables 1 & 2 and Fig. 2.

Fig. 4. Comparison of relative volumes between valued food and doubtful items in diet and in benthic samples (resource) for surfperches that do not winnow out the doubtful items in their mouth (see Fig. 3).

Fig. 5. Distributions of foraging efforts as feeding bites by surfperches in Naples Reef microhabitats compared with that expected from relative microhabitat areas. Insets give total fish observed, total bites counted, and the chi-square deviation from expected. Microhabitats are: DC, deep cobble; RCo, reef cobble; RCr, reef crest; RF reef flat; and RS, reef slope.

Fig. 6. Relation between total foraging effort of surfperches (Y axis) and richness of microhabitat (X) measured by either the valued or doubtfulfood components of benthic samples from Naples Reef (Table 1).

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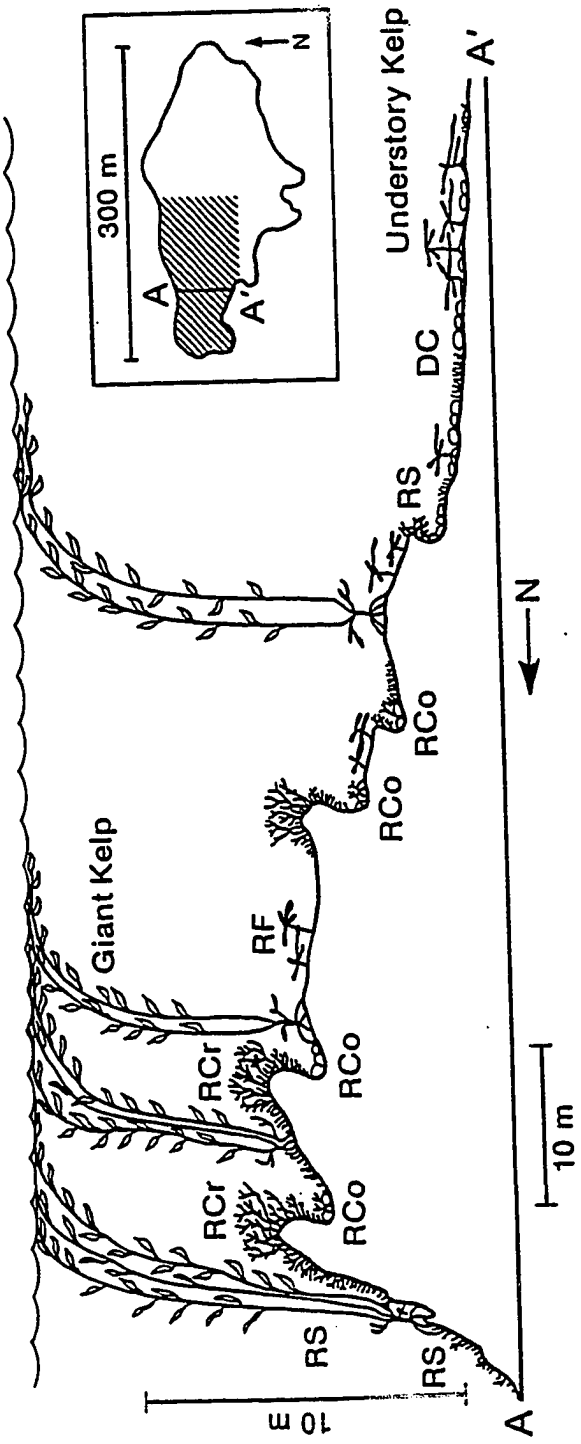
Fig. 1



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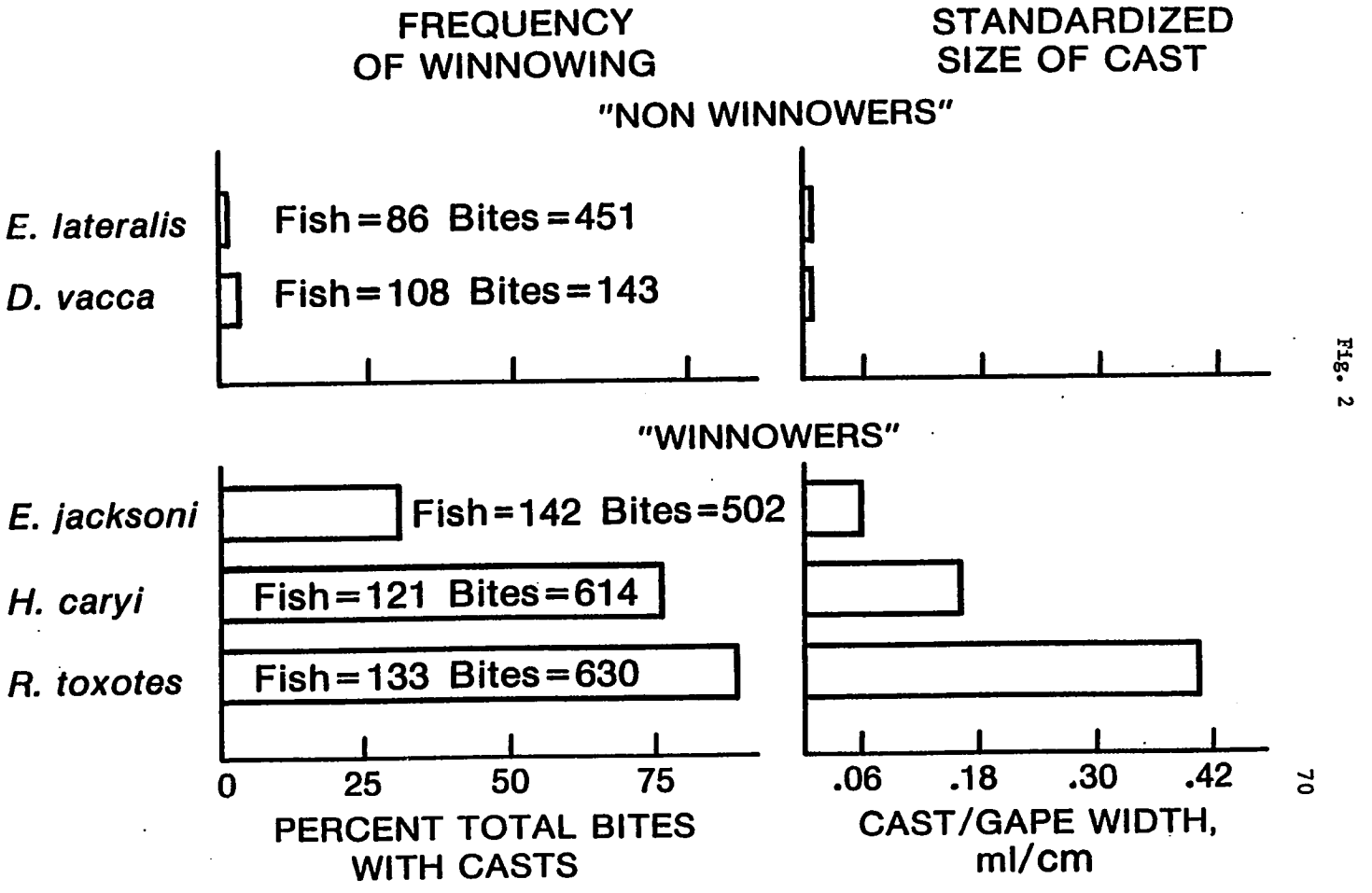
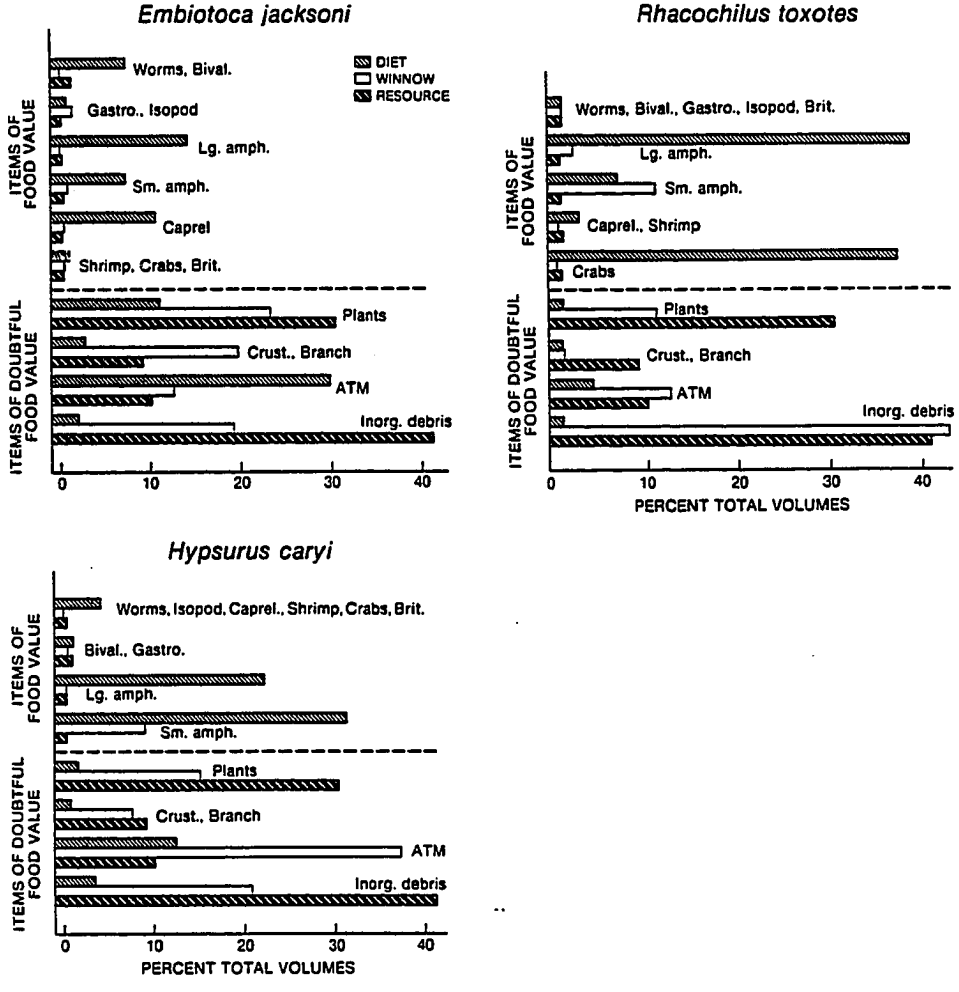


Fig. 2



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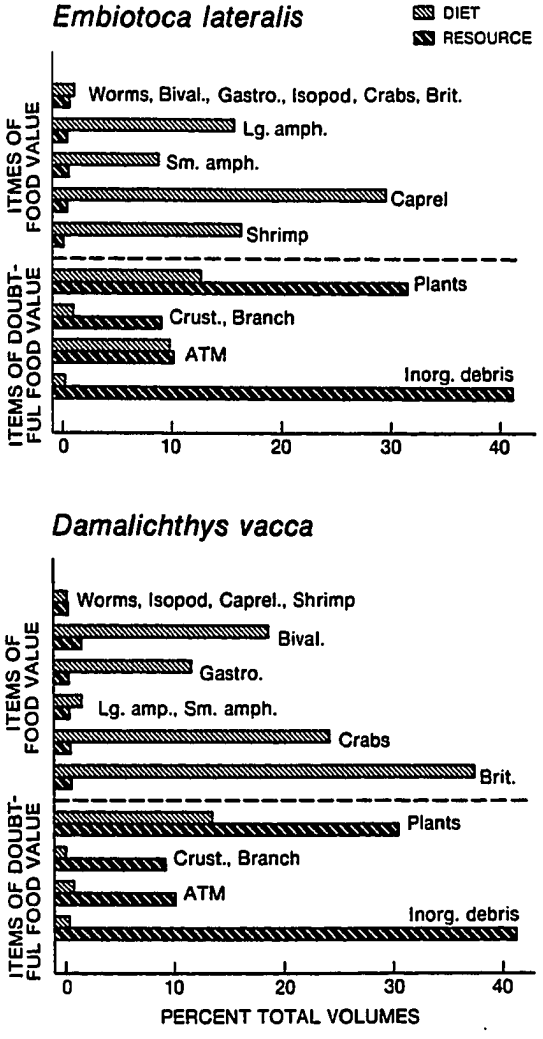

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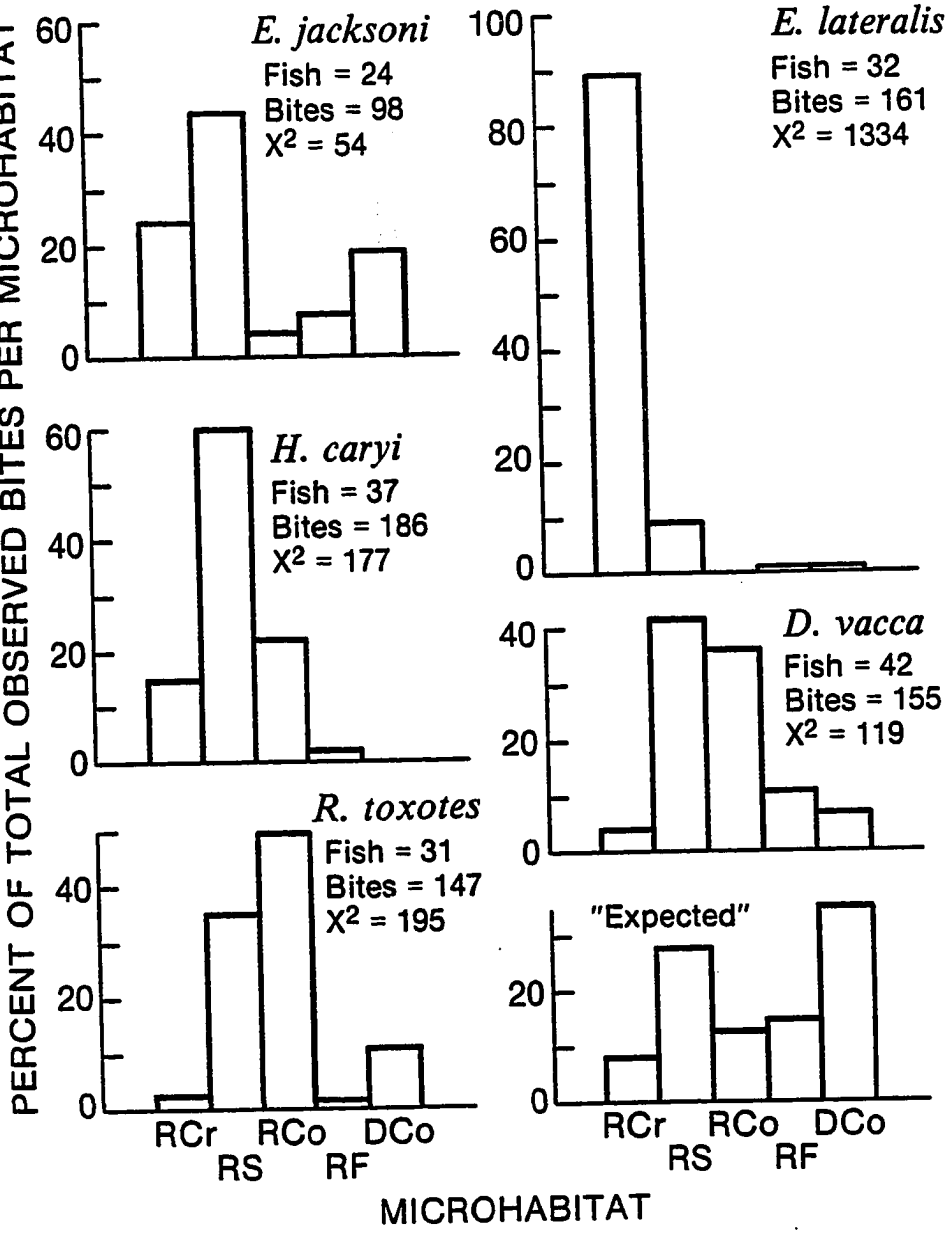

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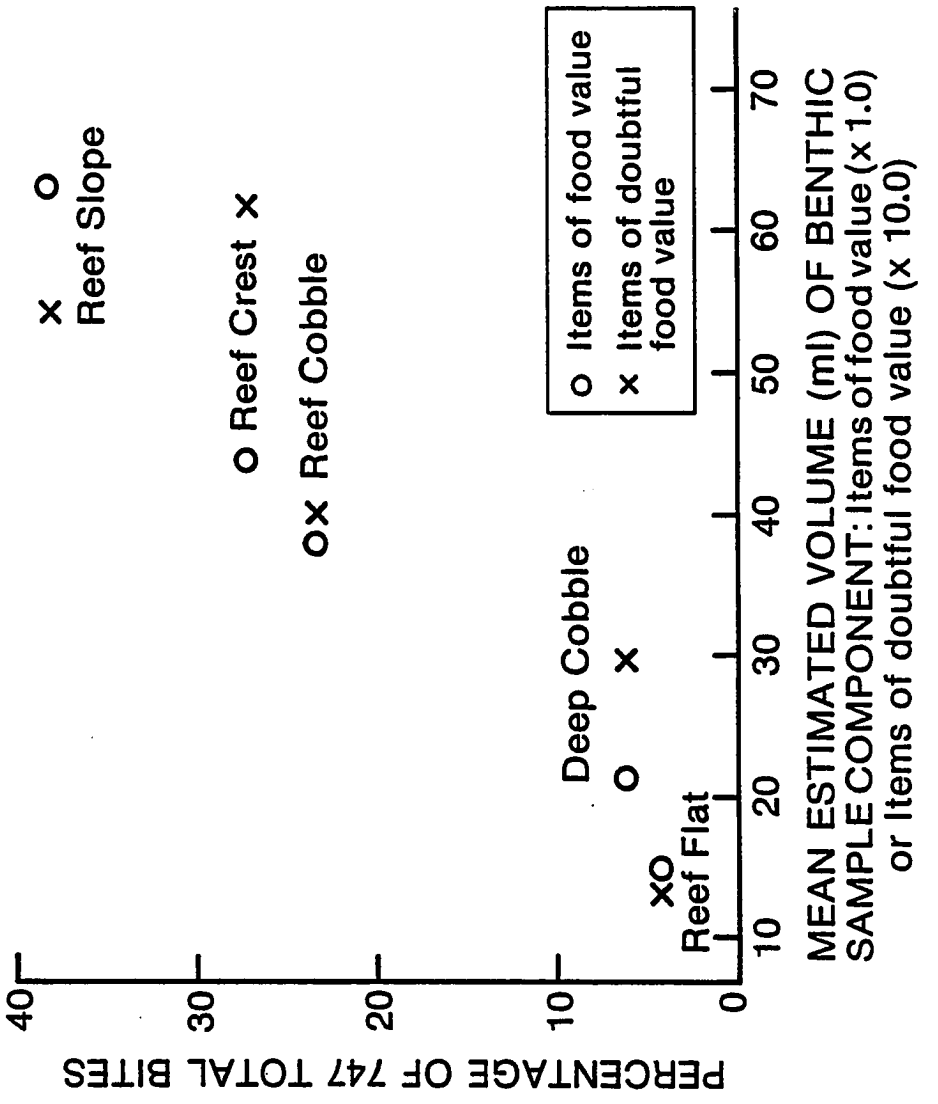
Fig. 6



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CHAPTER 4

EXPERIMENTAL EVALUATIONS OF SUBSTRATE TYPES AS BARRIERS TO SEA URCHIN (STRONGYLOCENTROTUS SPP.) MOVEMENT

INTRODUCTION

Sea urchin grazing interacts with environmental factors to alter spatial patterns of laminarian kelp in many temperate marine reef communities (reviews in Dayton, 1985; Schiel and Foster, 1986). For example, severe-storm waves may either reduce kelp biomass enough to cause urchins to overgraze previously forested areas or, conversely, decrease urchin numbers sufficiently to allow kelp recruitment and survival in the urchin-dominated barrens (Ebeling et al., 1985). Alternatively, environmental conditions that favor kelp recruitment may stimulate reforestation of the barrens even without a decrease in urchins (Harrold and Reed, 1985). In the absence of storms or effective predators, however, urchin numbers may increase, with individuals forming broad moving fronts that eliminate entire kelp stands (Leighton, 1971; Breen and Mann, 1976; Bernstein et al., 1981; Dean et al., 1984; Mann et al., 1984).

Previous observations suggest that physical obstacles may discourage the formation of such fronts. For example, some individuals may not be able to cross stretches of sand and other soft substrates,

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as dislocation by water movement, abrasion by shifting sand, or physiological stress by heavy sediment loads impede their progress (Miller, 1985). Also, urchins may have difficulty surmounting ledges or moving about in shallow high-relief areas of turbulence and heavy surge (Breen and Mann, 1976; Schroeter, 1978; Lissner, 1980; Chapman, 1981; Miller, 1985). Vertical slopes and undercut ledges may constitute obstacles because they bear dense colonies of stinging anemones (Foster and Schiel, 1985) or provide poor traction for the urchin's tube feet (personal observations). Thus, the tops of submarine pinnacles and ridges provide refuges for kelp on continuous rocky surfaces while the deep low-relief flats are prone to overgrazing (Estes et al., 1978; Laur et al., submitted).

Ebeling et al. (1985) have presented the descriptive evidence that sandy substrates and rocky ledges inhibit progress of moving urchin fronts on a subtidal reef (Naples Reef) off Santa Barbara, southern California: Red (Strongylocentrotus franciscanus) and purple (S. purpuratus) sea urchins consumed all understory kelp (Pterygophora californica) on continuous flat rock after a severe storm in winter 1980 eliminated the overstory canopy of giant kelp (Macrocystis pyrifera). Although the urchins' advance was temporarily halted at a ledge decending to sand and scattered cobble, urchins gradually worked their way down the cliff to accumulate at the sand's edge. Later, red, but not purple urchins finally moved out across the sand to consume a large stand of Pterygophora. These red urchins remained on the sand

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through summer and fall 1981, sitting singly or in clumps on isolated cobbles or directly on the soft sand and eating diatoms and filamentous brown algae (see also Duggins, 1981). Finally, all such exposed urchins disappeared after the next winter's storms.

This paper presents our experimental evidence, both from laboratory and field, that soft substrates and steep slopes impede the urchins' movement.

METHODS

Laboratory tests of sand effect

We collected experimental animals from urchin-dominated barrens (barrens) where all macroalgae had been grazed away or from nearby forested areas (forest) where algal food was plentiful. Initial dissections of individuals from the two habitats confirmed previous reports (Pearse, 1980; Dean et al., 1984; Harrold and Reed, 1985) that red or purple sea urchins living in barrens have emaciated gonads while most from the forest have well-developed gonads filling much of their body cavity. In addition, the relative size of urchin gonads has been shown to be a reliable index of the animals' nutritional well-being (Bennett and Giese, 1955; Fuji, 1967; Pearse, 1969; Pearse et al., 1970). On this basis, we provided the two essential experimental categories of urchins: "starved" (poorly nourished) animals from

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barrens and "well-fed" (well-nourished) individuals from forest. These urchins were transported in coolers ashore, where they were maintained in running sea water aquaria at 11.5 - 14.5°C under a 12 h:12 h light:dark (day:night) cycle for at least 10 days before testing. Starved urchins remained unfed; the others were provided an excess of giant kelp blades (Macrocystis pyrifera), their preferred food (Leighton, 1966, 1971; Tegner and Levin, 1982).

To examine the effect of sand on urchin movement, we observed the progress of starved red or purple urchins toward food on sandy or hard surfaces in large fiberglass tanks at the University of California at Santa Barbara. Approximately 5 cm of sand was spread over the bottoms of two circular tanks, each 2 m in diameter. At opposite ends of each tank, a single flat rock measuring about 20 x 50 cm was placed flush with the sand surface before seawater was added to a depth of 20 cm. For each trial, one starved red or purple urchin was introduced to the middle of the rock, about 75 cm from 300 grams of detached giant kelp blade. Urchins were also introduced to the rock in a sand-free tank with the kelp to measure their performance on a hard bottom. For each of the 10-11 trials per experimental treatment, we recorded the length of time the urchin took to leave the rock and move onto sand as well as the distance the animal traveled, first on rock and then on sand (or bare tank bottom). We discontinued all input of water or air during the experiments because initial trials indicated that constant water flow disrupted the system. Trials were run during daylight and lasted three

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hours or until the urchin reached the kelp. No urchin was used more than once and each tank was drained and refilled between trials. After each trial, we measured water temperature and sacrificed the urchin to measure its test diameter and gonad index (wet weight gonad/ wet weight urchin). Results were analyzed by a two-way ANOVA of the effects of substrate and species after variates were transformed to their logarithms to equalize variances (as indicated by F_{max} test--see Sokal and Rohlf, 1981).

Since the urchins used their tube feet to move on hard surfaces but their spines to walk over sand, we assumed that oral (bottom) spine length relative to body size may relate to ambulatory ability on sand. Given two individuals with equal test sizes (inertias), the one with the longer spines should progress the more rapidly per angle of spine rotation because the tips of its spines will subtend the greater arc. Thus, we estimated the potential ambulatory abilities of the two species by measuring relative spine lengths of individuals with similar test diameters. The average length to nearest mm of the ten longest oral spines was calculated for each of nine red urchins ranging from 42-60 mm in test diameter, and for each of eleven purple urchins ranging from 40-58 mm in size. Relative spine length, the average per individual divided by its test diameter, was averaged over individuals of each species for comparison of species means by t-test.

Using the same experimental set-up, we also examined the influence of other factors on the tendency of red sea urchins to cross the sand.

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Treatments on sand bottoms were varied by: (1) replacing the kelp with an artificial blade of beaded silicon stripping to observe any consequences of removing food from the environment, (2) by running trials at night to test for differences in diel behavior, (3) using well-fed instead of starved urchins to test for behavioral differences due to nutritional condition, and (4) by placing urchins directly onto kelp laid out on the rock to see if contact with food suppresses locomotory movements. Results were analyzed by t-test of the difference between treatment means.

Field tests of sand and rocky slope effects

Observations were made at Naples Reef, a shale outcrop located 1.6 km offshore, 23 km west of Santa Barbara, southern California ($34^{o}25'$ N, $119^{o}57'$ W). The reef covers 2.2 ha and ranges in depth from 5 m at crest to 15 m at base. Ebeling et al. (1985) has contour maps showing the study area of rocky and sandy substrates at reef base, and chronicles events leading to the eventual destruction of kelp to transform the area into a barrens.

The first experiment was designed to test the influence of sand on the foraging efficiency of red sea urchins in our study area. Presumably starved adults from a nearby barrens were transplanted to both sandy and rocky plots in continuous stands of understory kelp (Pterygophora californica) in October 1980. The kelp growing in sand usually had holdfasts anchored to a rock substrate about 5-15 cm below

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the soft surface layer. Plots measuring 12.6 m^2 (2 m radius) in area were located 5-10 m apart. Fifteen large urchins were placed in the center of each of six plots, three located in the sand and three in rocky habitats. A seventh plot in the rocky habitat without urchins served to control for any changes in kelp biomass unrelated to urchin grazing.

Periodic observations within plots included counts of remaining urchins, of attached kelp blades longer than 30 cm, and of blades being held down and eaten. Immigration of urchins into the study site was nil and natural densities of urchins in the area were negligible during the experiment.

Feeding rates $urchin^{-1}$ day^{-1} were estimated in two of the rocky plots. We did this indirectly by converting blade loss into wet weight of kelp based on the mean weight of 54 blades sampled haphazardly from the surrounding area. Rates were then calculated as the number of blades (including parts of blades) lost, times the mean weight, divided by the number of urchins (15) and number of days between observations.

In a second experiment to see if rock walls discourage urchin movement toward food, we installed a ramp from a urchin dominated barrens patch up to a forested ledge before Naples Reef was defoliated. The ramp ascended over a 2.5 m high vertical wall to the partially undercut ledge, which measured approximately 4 by 11 m and was isolated by cliffs and rocky overhangs. About 30% of the wall was covered with dense colonies of the coral-like anemone Corynactis californica, which

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has large stinging nematocysts. The ledge supported a lush stand of kelp (Pterygophora californica and Macrocystis pyrifera) and mat of algal turf, but few urchins. The ramp was made of 1.3 cm Vexar plastic mesh stretched between parallel pipes of PVC plastic secured at their ends by bolts in the barrens and ledge substrates, and at their middles by nylon lines tied to eye-bolts in the barrens substrate. Measuring 1 x 5 m, the ramp presented the urchins with a 50% grade of passage over the vertical slope. After the ramp was installed, the few urchins on the ledge were removed in June 1980. Periodic observations included counts of urchins and kelp plants on the ledge.

RESULTS

Laboratory tests of sand effect

Red and purple sea urchins differed in their tendency to leave rock and travel over sand (Table 1A). The significant substrate x species ANOVA interaction coupled with strong main effects indicated that the sandy substrate inhibited purple urchins much more than red urchins. Purple urchins took almost six times longer to leave the rock for sand than for hard substrate and only one individual reached the kelp during the 3 h trials. Purple urchins appeared hesitant to leave the rock for sand, as they often moved cautiously along the rock-sand interface, holding onto the rock with a few tube feet. Substrate type had no significant effect on the tendency of red urchins to move out from the

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rock; in both treatments most individuals quickly left the rock and reached kelp during the three hour trial.

The presence of sand inhibited the movements of red and purple urchins differentially. While their total distances traveled were similar, both species moved significantly less in tanks with a sand bottom (Table 1B). Yet as indicated by the significant ANOVA interaction, the species differed in partitioning their travel between rock and sand (Table 1C). Purple urchins traveled only proportionately half as far (40% vs. 83% of total distance traveled) on a sand substrate as on the hard tank bottom, while red urchins showed no apparent difference in this regard. Red urchins moved significantly faster [1.7±0.7(SD) cm min^{-1}] on sand than purple urchins (0.9±0.4, $\underline{t}$ = 3.14, $P<0.02$) and both species traveled equally faster over the hard surface (5.5, 5.1) than sand. All urchins used their tube feet to move over the hard bottom, but used their spines, which left characteristic tracks, to walk on the sand.

Comparison of red and purple urchins indicates that species differences in tendency to cross sand were not due to urchin size (test diameter) per se. Red urchins averaging 45±10 (SD) mm test diameter consistently moved onto sand in less time ($\underline{t}$ = -4.09, $P<<0.001$), and traveled a greater proportion of the total distance on sand ($\underline{t}$ = 2.89, $P<0.01$) than did similar sized purple urchins (44±4.4) mm (Table 1A). Red urchins have relatively longer oral spines: the mean ratio of the average length of ten longest spines to test diameter (0.68±0.05) for

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nine red urchins (51±5 mm test diameter) significantly exceeded that (0.29±0.05) for eleven purple urchins of similar size (48±7 mm) (t = 13.3, P<<0.001). This difference may provide red urchins with better leverage for moving across unconsolidated surfaces.

Table 2 summarizes responses of red sea urchins to additional experimental treatments that may influence their performance on sand. During 3 h trials, red urchins showed no significant responses to the replacement of kelp by a silicon facsimile, or to the changeover from day to night (Table 2: treatments 2 or 3 vs. 1). Otherwise, well-fed urchins (gonad indices = 0.10-0.17) traveled proportionately less on sand at a significantly slower speed (1.05±0.5 cm min^{-1} vs. 1.7±0.7, t=2.4, P=0.05) and reached the kelp less frequently than did starved ones (gonad indices = 0.01-0.05) (treatments 4 vs. 1). Starved urchins reacted immediately to contact with food as they sharply reduced their total distance traveled when placed directly on kelp (treatments 5 vs. 1). Seven individuals remained on the kelp during their entire trial, as all ten fed at a mean rate of 0.7 grams (wet weight) $urchin^{-1}$ $trial^{-1}$. Likewise in the other treatments, urchins invariably stopped traveling and began feeding upon reaching kelp.

Field test of sand effect

The transplanted red sea urchins soon disappeared from sandy plots, but persisted in rocky plots. They were gone from the three sandy plots

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within a week (Fig. 1A), even though they initially held and ate kelp blades just as in rocky plots (Fig. 1B). The lost individuals may have left sand to seek shelter. We found nine individuals in a crevice about 2 m outside the only sandy plot with nearby rock, but none during extended searches in the surrounding sand-based kelp stands. There was no evidence that lost urchins succumbed to predation or water turbulence, as no broken test fragments were found during the entire experimental period. In contrast, numbers of individuals in rocky plots were nearly constant over the 21 day experimental period (Fig. 1A). Four days after translocation, all urchins had moved to sheltered crevices from where they continued to hold attached blades (Fig. 1B).

The feeding rate of transplanted urchins decreased periodically as a function of blade loss in the two rocky plots where it was monitored (Fig. 2). Rates were initially high in both plots, then fluctuated concordantly during the 21 day experimental period, and remained low during 19 more days of post-experimental monitoring as individuals became well-fed. In the 40 days total, the average number of whole unforaged blades fell from 71±18 (SD) to 36±10 in the two plots, compared to almost no change (88 to 85) in the control plot without urchins. Thereafter, the rate again rose in the single plot monitored, as the original individuals were joined by new invaders from the adjacent barrens.

Field test of rocky slope effect

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From the barrens below, red and purple urchins breached the 2.5 m cliff with patches of stinging anemones by ascending the artificial ramp to attain the foliated ledge above. Newly arrived urchins of both species were observed holding and eating attached kelps. As the number of urchins on the ledge steadily increased the number of kelp plants decreased (Fig. 3). Red and purple urchins tagged in situ below the ledge were observed on or above the ramp 1-2 weeks later (R. Rowley, personal communication).

Similar nearby ledges lacking the artificial access showed much less change in urchin and kelp abundance during the six month experimental period. Urchins had crawled up some walls, but appeared hesitant to cross dense colonies of noxious anemones, Corynactis californica. Individuals seemed to have trouble finding suitable purchase for their tube feet (especially at the edges of undercut walls) and were often broken loose by heavy surge. When urchins surmounted walls, they usually did so through lower gaps and clefts or at corners where they could find greater contact.

DISCUSSION AND CONCLUSIONS

Field observations and laboratory experiments indicated that sand does not provide a complete refuge for kelp from grazing sea urchins. In the field, only red urchins invaded a sand-based kelp bed. In the laboratory, purple as well as red urchins negotiated sand in quiet

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standing water, though less efficiently than hard substrate where both species moved faster by using their tube feet. Although both species moved through sand using their oral spines and leaving characteristic tracks, the red urchins' relatively longer spines may provide greater traction or leverage. We have noticed that, unlike even small red urchins, purple urchins occasionally bear small pebbles (as do the smaller white urchins, Lytechinus anamesus), perhaps for added weight or camouflage. In both field and laboratory, red urchins appeared less hesitant than similar-sized purple urchins to move from rocks out onto sand.

The patterns of urchin movements seemed haphazard or random. When placed away from food in the laboratory, most urchins traveled for long distances before contacting kelp and eating; many did not even reach the kelp during the 3 h trials. As indicated by their meandering tracks, individuals showed no directed movement toward food and their total distances traveled (200-300 cm) were always much greater than the initial distance to the kelp (75 cm). Individuals that were given kelp stopped and ate almost immediately upon touching it. Thus chemosensory cues (see Leighton, 1966; Mann et al., 1984) were probably weak or lacking at any distance from the kelp in quiet water.

We believe that these experimental results were due primarily to treatment effects rather than artificial constraints and disturbance to urchins. All individuals were handled as gently as possible in the same way for each laboratory experiment. Since all animals were alone and

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topographic discontinuities such as intakes and drainpipes were withdrawn from the circular tanks, the animals' movements were uninterrupted by other urchins or artifacts (see Vadas et al., 1986); the smooth circular tank wall had little effect other than limiting their sphere of activity. Yet, we realize that disappearances of transplanted sea urchins in the field (Breen and Mann, 1976; S. Schroeter, personal communication) may result primarily from handling effects. In our study, however, starved red urchins transplanted to either rock or sand plots responded favorably to the manipulation at first. All were holding and eating kelp within two hours. Then only the urchins in sand plots disappeared, some moving to nearby rock crevices.

We suggest that the disappearance of red urchins from sand plots was mostly due to the unsuitability of the substrate. Perhaps a small group of urchins cannot immobilize and consume large blades of kelp because scattered individuals are easily dislodged as the plant is whipped about in the surge (Breen and Mann, 1976; Breen, 1980; Schiel, 1982). Thus, destructive grazing usually occurs only in protected sites or in areas where urchins reach densities high enough to counter surge and hold their food.

Alternatively, small groups of urchins may remain in place within stands of kelp if individuals can find adequate shelter. Besides avoiding predators, urchins can resist strong water motion by wedging themselves in cracks and crevices (Lissner, 1980; Ebeling et al., 1985). We showed that small numbers of transplanted starved red urchins

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stayed at least a month in an open rocky plot having crevices and other shelter holes. Here they held and eventually ate all kelp blades within a few square meters. Urchins were initially starved and no algal drift was seen in the area. Hence, their perception of shelter, rather than a feeling of satiation, may have quieted them at first.

The progress of large feeding aggregations of urchins (sensu Vadas et al., 1986) as moving fronts (sensu Dean et al., 1984) may be affected by several factors: (1) satiation of the larger individuals at the leading edge (Dean et al., 1984); (2) seasonal and temperature effects (Tegner and Levin, 1982; Mann et al., 1984); (3) topological barriers (Estes et al., 1978); (4) wave action (Himmelman et al., 1983; Dean et al.); and substrate type (Breen and Mann, 1976; Miller, 1985). But even though general factors such as satiation and seasonal change may contribute to the intermittant progress of a front, they do not explain its stopping at a ledge as we observed.

We presented experimental evidence that rock ledges and walls impede urchin dispersal. Both red and purple urchins readily take advantage of any opportunity to circumvent such obstacles, as indicated by the relatively short time it took groups of hungry individuals to locate and use an artificial ramp to reach a ledge harboring a kelp stand. Urchins seem to have more difficulty gaining purchase with their tube feed on walls and edges than in gaps, crevices, or on flat surfaces. Also, vertical slopes often support dense colonies of stinging animals such as Corynactis anemones that tend to deter large

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mobile invertebrates (Foster and Schiel, 1985; personal observation). Thus, rock walls and ledges as well as sandy stretches may be the last refuges for kelp in a progressive barrens.

Urchins may be most likely to invade such refuges during periods of calm water (see Lissner, 1980). Himmelman et al. (1983) suggested that green urchin numbers decrease during periods of strong water motion, as individuals are swept away by waving algal fronds. Dean et al. (1984) believe that surge may temporarily halt the grazing activity of white sea urchins (Lytechinus anamesus). At Naples Reef, red urchins breached a ledge and moved out over sand as wave action subsided. Previously, we saw large numbers of broken test fragments, especially of purple urchins, after storms and heavy surge in January 1981. Then red urchins invaded the sand-based kelp bed only after the waters had calmed, and remained there only until waves again increased during the next winter (see Introduction). More recently following three weeks of unusually light surge, we observed a tripling of red and purple urchin densities and intensified destructive grazing about an area of ledges and reef crest where there was insufficient drift kelp to eat. Even purple urchins had ventured onto small ($<0.25\ m^2$) patches of sand and cobble among the rock.

In conclusion, soft substrates and rock walls, especially those covered with stinging anemones, impede the progress of grazing red and purple sea urchins, as individuals of both species move best over flat hard surfaces. Yet in the absence of effective predator control,

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urchins surmount most such barriers when water motion subsides. Thus, even red urchins exploit sand-based plants only during periods of calm. Both species can move over hard surfaces more rapidly using their tube feet. Hence, the ability to coordinate spine movements to walk on soft substrates may be an adaptation to invade kelp refuges during quiet periods when detached drift food is unavailable.

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Table 1. *Strongylocentrotus purpuratus* (purple sea urchin) and *S. franciscanus* (red sea urchin). Performance of starved individuals placed singly on a flat rock 75 cm away from a small pile of kelp in a cylindrical tank with a sandy or hard (no sand) substrate during 3 h trials.

(A) Time (min) to move from a flat rock to the tank-bottom substrate

Untransformed means + SD (mm test diameter, fraction reaching kelp)

Substrate	Purple sea urchins	Red sea urchins
Sand	44+33 (44, 1/11)	10+5.2 (45, 7/11)
No sand	7.4+4.0 (51, 6/10)	6.3+8.2 (64, 9/10)

Two-way ANOVA of log-transformed variates

Source of variation	d. f.	MS	F	Significance
Substrate	1	2.668	26.2	P<<0.001
Species	1	1.489	14.6	P<<0.001
Substrate x Species	1	0.430	4.2	P=0.05
Error	38	0.102		

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(B) Total distance (cm) traveled on rock and tank-bottom substrate

Untransformed means + standard deviation

Substrate	Purple sea urchins	Red sea urchins
Sand	258+124	180+80
No sand	339+254	380+203

Two-way ANOVA of log-transformed variates

Source of variation	d. f.	MS	F	Significance
Substrate	1	0.400	6.7	P=0.01
Species	1	0.007	0.1	P>0.5 (NS)
Substrate x Species	1	0.154	2.6	P=0.1 (NS)
Error	38	0.060		

(C) Percent of the total distance traveled on tank-bottom substrate

Two-way ANOVA of log-transformed variates

Untransformed means + standard deviation

Substrate	Purple sea urchins	Red sea urchins
Sand	40+32	82+17
No sand	83+16	91+5.4

Source of variation	d. f.	MS	F	Significance
Substrate	1	2.154	26.6	P<<0.001
Species	1	1.215	15.0	P<<0.001
Substrate x Species	1	0.423	5.2	P=0.03
Error	38	0.081		

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Table 2. Strongylocentrotus franciscanus (red sea urchin). Influences of food, darkness (night), and satiation on the performance of individuals in a cylindrical tank with a sandy substrate during 3 h trials. "Treatment" is any variation from initial placement of a starved urchin on a bare flat rock 75 cm away from kelp during daylight hours. Starred values are significantly different from treatment 1 means by t-test using log-transformed variates: *, $t = 2.5$, $P=0.02$; **, $t = 3.4$, $P<0.01$.

			Response			
		Test diameter (mm)	Time for moving off of flat rock to sand (min)	Total distance traveled on rock and sand (cm)	% of total distance traveled on sand	Number reaching kelp or facsimile
Treatment	N	x + SD	x + SD	x + SD	x + SD	(of N)
1. (None)	11	45+10	10+5.2	180+80	82+17	7
2. Kelp replaced by silicon facsimile	10	45+8.8	13+4.4	224+95	74+29	5
3. During the night	11	59+8.3	6.7+3.6	215+112	80+14	7
4. With well-fed urchin	10	72+10	14+11	262+104	61+20*	3
5. Placed directly on kelp reward	10	59+10	(long)	72+109**	(negl.)	10

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FIGURE CAPTIONS

Fig. 1. Strongylocentrotus franciscanus. Periodic mean counts (+SD) of (A) transplanted sea urchins and (B) the kelp blades that they were holding onto and eating in n=3 replicated rocky or sandy plots in a bed of understory kelp (Pterygophora californica) at the base of Naples Reef.

Fig. 2. Strongylocentrotus franciscanus. Periodic feeding rates of transplanted sea urchins eating blades of understory kelp in two rocky plots.

Fig. 3. Strongylocentrotus franciscanus and S. purpuratus. Periodic counts of sea urchins after they had ascended an artificial ramp to reach a ledge where they consumed and thereby decreased numbers of two species of kelp plants (Pterygophora californica and Macrocystis pyrifera).

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Fig. 1

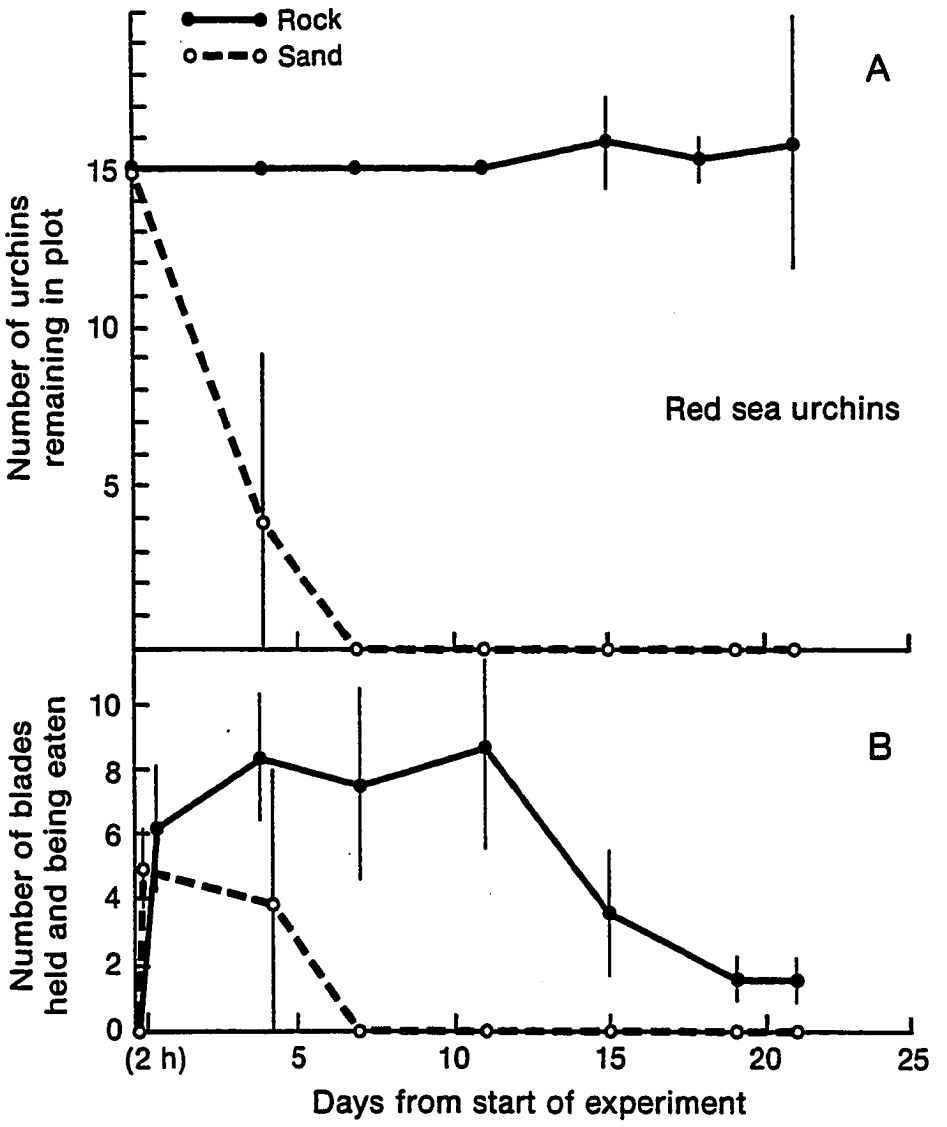

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Fig. 2

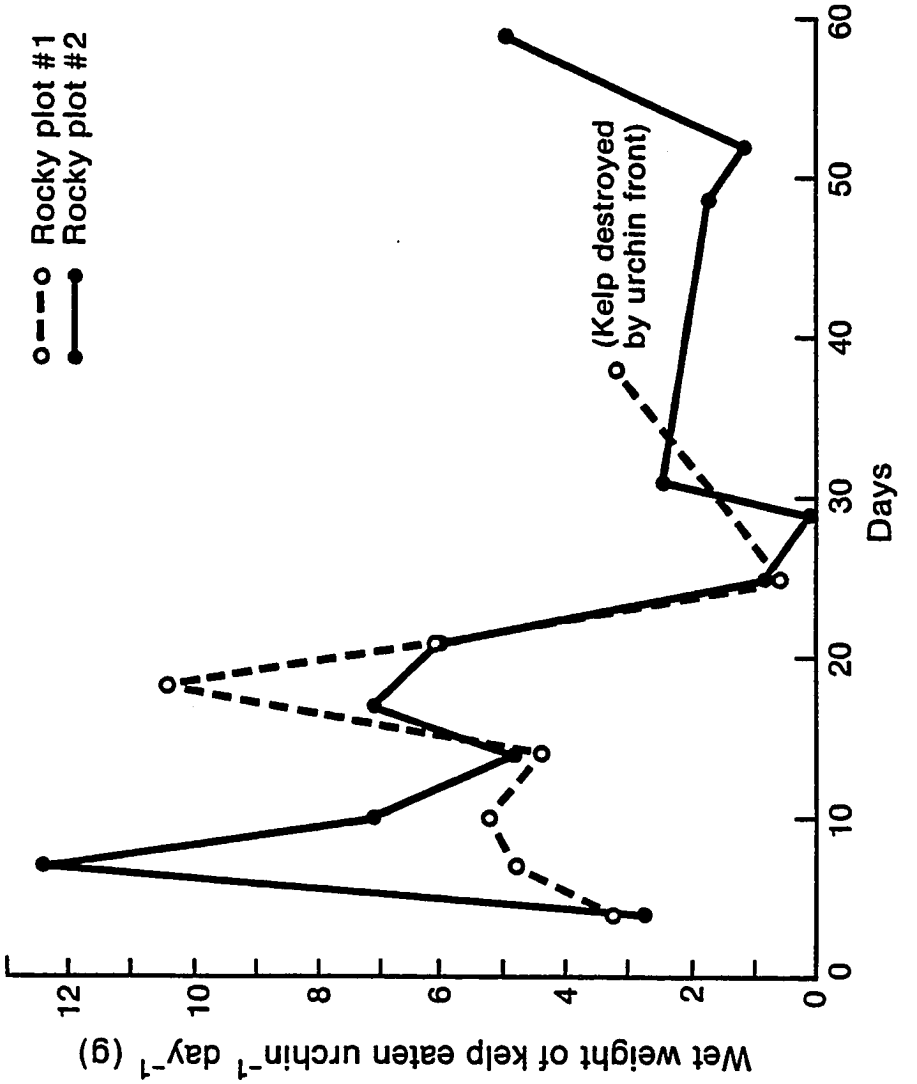

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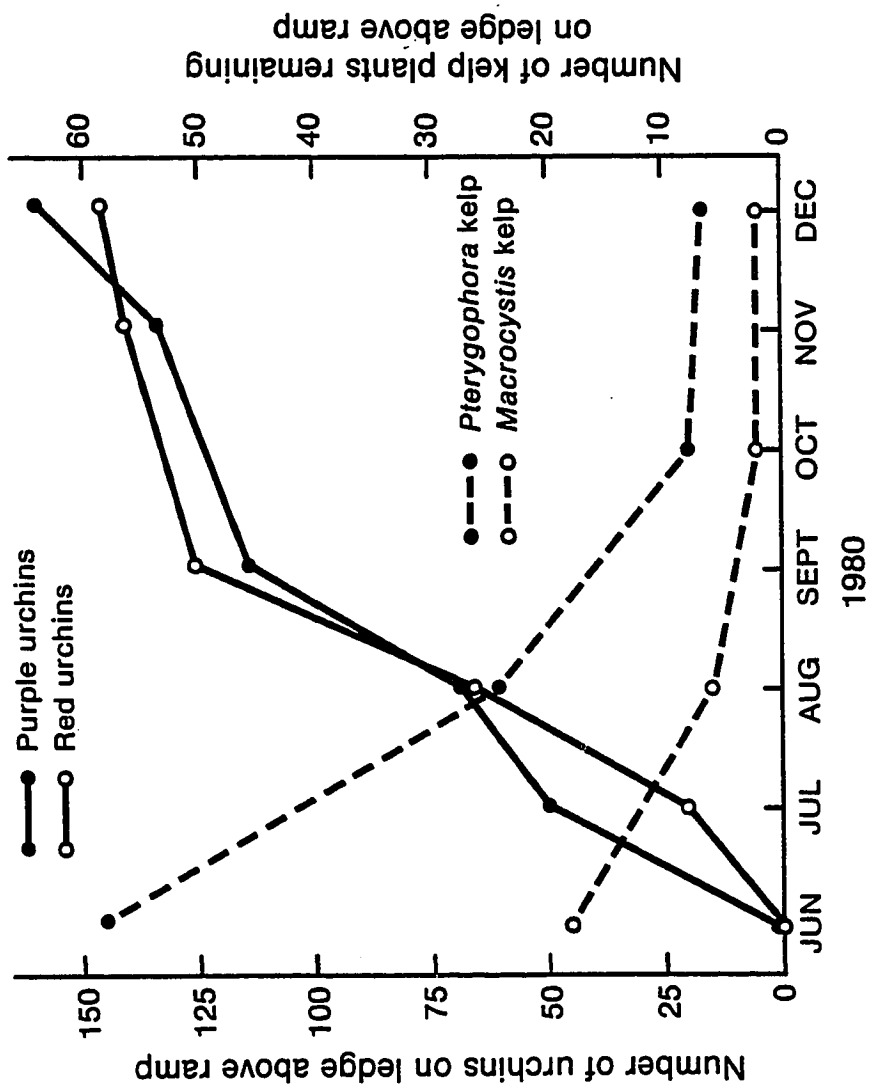
Fig. 3



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CHAPTER 5

EFFECTS OF SEA OTTER FORAGING ON SUBTIDAL REEF COMMUNITIES OFF CENTRAL CALIFORNIA

INTRODUCTION

As a major predator of sea urchins, the sea otter (Enhydra lutris) plays a determining role in structuring many subtidal kelp-forest communities in the North Pacific (reviewed in Estes and Harrold; Riedman and Estes; 1987). In the absence of otters, patches of kelp and other erect algae survive only on shallow pinnacles, crests, and other high-relief zones of turbulence (Estes et al. 1978; VanBlaricom 1984), which are unstable platforms for sea urchins (Dayton 1985a; Laur et al. 1986). Thus, after otters return to reef habitats previously overgrazed by exposed urchins (Strongylocentrotus spp.), large stands of kelp reappear as the remaining urchins become restricted to cracks and crevices (Estes and Palmisano 1974; Dayton 1975; Estes et al. 1978; Duggins 1980; Breen et al. 1982). As otters remove the destructive grazers, furthermore, enhanced productivity creates an environment favorable for greater numbers of finfish (Simenstad et al. 1978; Estes et al. 1981, 1982; VanBlaricom 1984; Estes and VanBlaricom 1985).

The indirect relationship between sea otters and kelp beds in central California may require further clarification, however (see Estes and Harrold; Foster and Schiel; 1987). For instance, North (1965)

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attributed enhancement of canopies of the giant kelp Macrocystis pyrifera to the otters' presence, but Miller and Geibel (1973) pointed out that kelp also regrew during the same period off southern California outside the otters' range. Cowen et al. (1982) suggested that winter-storm disturbances may be more important than otter-grazer interactions in structuring nearshore kelp communities. On the other hand, VanBlaricom (1984) compiled historical evidence that the reduction of urchin numbers when otters enter overgrazed habitats initiates a predictable succession of kelps: a sequence beginning with stands of the annual canopy kelp Nereocystis luetkeana and various understory kelps eventually culminates in a forest of perennial Macrocystis pyrifera, which is apparently the more favorable habitat for fish production (Bodkin 1986).

Yet, the initial direct effects of sea otter foraging are indisputable. Soon after moving into new areas, otters drastically reduce exposed populations of their preferred prey--sea urchins, abalone, and rock crabs (e.g. Ostfeld 1982), leaving the cast shells as evidence of their activity (Hines and Pearse 1982).

The main purpose of the present study was to measure both the direct and indirect effects of sea otters as they exploited new reef environments in central California. Until 1976 when their populations may have begun to stabilize, peripheral groups of otters were moving southward into previously unforaged habitats (e.g. Estes et al. 1981). Thus, we took advantage of a natural manipulation by observing two

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different reef communities just before and after otter foraging. We compared the effects of otters immigrating to a small high-relief reef, which had not been badly overgrazed by urchins but may have never supported a persistent surface canopy of kelp, with effects on a large, mostly low-relief reef, which had been grazed nearly bare of erect algae except for a remnant of kelp canopy surviving on reef crest (i.e., was mostly an urchin-dominated barren ground (sensu Lawrence 1975). Hence, the central Californian sites provided two important contrasts: (1) between pre-otter and post-otter communities, and (2) between responses of communities inhabiting different reef types (sensu Foster and Schiel 1987).

A secondary objective was to simulate effects of sea otters, on a reduced scale, by excluding urchins from small plots in a barren ground on a reef off southern California, beyond the otters' range. This was done to provide some experimental verification of the descriptive results.

Events beyond our control severely compromised our sampling schedule off central California. Due to delays in obtaining research support, adequate baseline observations of the pre-otter condition could not be completed before otters arrived at our sites. Thus, only brief surveys, including movies, still photos, and macroinvertebrate counts, could be made in October 1976 before winter's rough weather made further scuba operations impossible. Improving weather conditions finally allowed a resumption of work in July 1977, about five months

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after otters were first seen in the area during February (S. Benech, Benech Biological & Assoc., Ventura, Ca., pers. comm.). In addition, much of the post-otter monitoring suffered from design by hindsight: We had concentrated most of our time and effort at the high-relief reef before we realized that the major response was occurring at the larger, deeper, and flatter site. To meet deadlines and budgetary limits, therefore, we often sampled reduced quadrat sizes as quickly as possible with minimum replication.

Nonetheless, our study was successful to the extent that most post-otter changes were large enough to be detectable by these methods. Results were consistent with the previous predictions of direct and indirect effects: (1) foraging otters virtually eliminated all exposed sea urchins and abalone; (2) a surface canopy of annual Nereocystis kelp reappeared at the deeper, low-relief reef; (3) subsurface canopies of algal turf and understory kelp returned; (4) the high-relief reef, subject to stronger water motion, was inherently less vulnerable to urchin grazing and did not sustain a surface canopy of kelp; and (5) young fish recruited to kelp canopies, where greater numbers of adult fish were observed as well.

STUDY SITES

In 1976 at the outset, the southern periphery of the sea otter's range was between Pt. Buchon and Avila, San Luis Obispo County in central California (Estes et al. 1981; S. Benech, Benech Biological & Assoc.,

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Ventura, Ca., pers. comm.). Hence, we explored several possible areas downcoast. Two remote sites, Lone Black Reef and Santa Rosa Reef, were chosen because they were located directly in the path of the otters' southward advance and appeared to be suitable for supporting diverse communities (Fig. 7.1). The experiment to simulate otter effects in southern California was conducted at Naples Reef, Santa Barbara County, a site that had been previously monitored for several years (see Ebeling and Laur 1987).

Lone Black Reef (LBR) was selected first because it is circumscribed and easily surveyable. Located 475 m offshore and 2.0 km west of the Avila Breakwater, LBR is a rectangular monolith of rock measuring about 20 by 60 m, with its long axis extending east and west. Its reef crest, which is 4.25 - 6.0 m deep and shoals to 3 m at one end, is influenced by heavy wave surge. It bore stands of algal turf and patches of understory kelp, but no surface canopy. The reef drops off steeply to its 10-12 m deep base, which is surrounded by patches of coarse sand, cobble, boulders, and high-relief rock.

Santa Rosa Reef (SRR) is located 1500 m farther offshore from LBR. Measuring about 100 by 500 m, it is an irregular expanse of flat rock, sand channels, and boulders, with its long axis extending east and west. Most of its high-relief crest and slope is 7.5-9.0 m deep, shoaling to less than 5 m at one end. The crest retained patches of the understory kelp Laminaria dentigera together with bushy stands of Gelidium robustum and other leafy red algae. The reef apparently had

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had no surface canopy for at least ten years before the sea otters came (R. Burge, Dep. of Fish and Game, pers. comm.). Its rocky flats are crossed by sand channels, average 14.5 m in depth, and are about 20 times greater in area than the combined crest and slope. Initially, sea urchins dominated the flats, which, having been grazed nearly bare of erect algae, were paved with crustose coralline species.

Naples Reef (NR) is located 1.6 km offshore in the Santa Barbara Channel west of Santa Barbara (Fig. 1). It is an irregular offshore mound of shale outcrops and ledges measuring 75 by 300 m and descending from 5 m depth at reef crest to 15 m at its base (Ebeling et al. 1980). In 1979 a much smaller area of urchin-dominated barren ground was limited to the reef's west end. The extensive surface canopy of Macrocystis was destroyed by a severe storm in 1980, after which exposed urchins consumed the remaining large stands of understory kelp, Pterygophora california (Ebeling et al. 1985; Ebeling and Laur 1987).

METHODS

Sampling Schedule

The central Californian sites (LBR, SRR) were sampled during a total of 10 dive-days by four scuba observers in yearly sets from 1976 through 1980. The pre-otter baseline was limited to an initial reconnaissance, as winter's rough weather prevented further diving before otters

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arrived at the sites sooner than expected. Hence, pre-otter sampling in 1976 was limited to a total of only two days spent either counting macroinvertebrates along permanent transects installed previously at LBR, or completing a photographic survey of SRR. In addition, almost all effort budgeted for site surveying and transect construction was expended at LBR, which was to have been the only site monitored. Consequently, post-otter sampling (macroinvertebrates, algae, benthic cover) was performed as originally designed at LBR only, covering four days in July-August 1977 and two days in July 1978. By then it was obvious that LBR could show few indirect effects of otter foraging, and that our remaining limited resources could be better spent elsewhere. Therefore, post-otter monitoring of SRR was begun much later on an ad hoc basis, as effort was necessarily confined to rapid photographic surveys and selective counts during single days in December 1979 and October 1980.

At the southern Californian site (NR), urchin exclusion experiments and macroinvertebrate densities were monitored quarterly for three years. Observations were begun in 1979, when treatments were installed in a barrens patch at the reef's west end, and were continued through 1981, after all remaining kelp was lost following a severe storm in 1980 (see Ebeling et al. 1985).

Macroinvertebrate Sampling

For all three sites, yearly samples of sea urchin, sea star, and

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abalone densities were compiled from counts usually made firsthand in band transects. At LBR, exposed individuals were counted in six 1 x 37 m permanent transects (sampling units), each positioned along the crest, slope, or base on either side of the reef. Animals in holes and crevices were counted separately. At SRR, however, band-transect or photoquadrat sampling units were positioned about midreef at points determined from a random-number table as compass direction and number of swimming kicks. In 1979 and 1980, counts were made directly from 1 x 13 m band transects extended from each of four points. In 1976, however, they were made later from 36 photoquadrats, each taken by a Nikonos camera with a 28 mm lense held at the length of a slender rod above a different point, such that about one square meter of surface was covered. To measure the temporal consistency of macroinvertebrate densisties in the persistent urchin barrens at NR, 27-31 counts per year were made in a single 1 x 13 m band located near the experimental plots.

Algae and Sessile Invertebrates

Central Californian Sites

Benthic cover was sampled yearly by photoquadrat. At LBR, 36-54 0.25 m^2 quadrats were positioned at random intervals along the transect line on reef slope. Coverage of each quadrat was from six 35 mm color slides

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taken by the Nikonos camera and 0.042 m^2 close-up framer. Sampling by photoquadrat was reliable to the extent that the species dominating the percent cover as estimated from photographs also dominated the algal biomass as measured from four destructive air-lift collections made at reef crest and base during 1977. Photographic sampling of SRR was carried out in a similar way, except that the sampling units were 24-63 individual slides (0.042 m^2) taken at random positions along the transect lines.

To measure percent cover of different taxa, slides were analyzed collectively in groups of six (LBR) or singly (SRR) by projecting them, one at a time, onto a screen under a grid of 24 crossed lines and counting the number of point intercepts falling on each taxon. Taxa were pooled into four functional categories: fleshy red algae (leafy and filamentous species), crustose coralline algae (pavement-like species), sessile invertebrates (hydroids, tunicates, sponges, worms, and bryozoans), and tubicolous amphipods (species used as an index of food available for fishes). Percent cover of each category was estimated as the category's proportion of the total intercepts (144 per group of six, or 24 per single-slide sampling unit).

At SRR, we measured understory kelp density on reef flat and reef crest in 1976 and 1980 by counting all stipes, mostly of Laminaria dentigera, in 18-35 1.0 m^2 bar quadrats positioned randomly along transects through the respective habitats. Percent cover of kelp blades was estimated roughly by eye before stipes were counted in each

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quadrat.

Urchin Exclusion Experiment

At NR off southern California, treatments either excluding or not excluding sea urchins and other macroinvertebrates were randomly assigned to 0.25 m^2 plots of flat overgrazed substrate. In addition, macroinvertebrate densities were monitored yearly outside the plots as explained above. Over the plots, pyrimidal cages of 1.25 cm Vexar plastic mesh supported by 2.5 cm diameter PVC plastic pipe were secured to the bottom by PVC strips bolted to the rock through lips of mesh extending out from the 1.0 m^2 base of the pipe frame. The three caged treatments consisted of topless cages for macroinvertebrate exclusion, bottomless cages for fish exclusion, and complete cages for total exclusion (Fig. 2). The uncaged controls included two free plots, and two plots with mesh fitted only on the south and east sides as shade controls. Since urchin grazing overwhelmed the other factors and partial caging made little or no difference, all results were classified simply as either exclusion (macroinvertebrate plus total exclusion treatments) or non-exclusion (all other treatments and controls) for the present analysis. Percent cover of the four categories of organisms was compared between exclusion and non-exclusion groups, represented by samples of 23 and 32 photoquadrats taken within the plots and pooled among years (see above).

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Fish Sampling

Reef fish assemblages were sampled at LBR and SRR in cinetransects: 2.5-min, super-8, high-speed color movie films taken by divers swimming unidirectionally (Ebeling et al. 1980b). The course for each film (sampling unit) was begun in a direction selected at random, but was occasionally altered to stay within the same deep or shallow habitat. It was covered at a constant rate at a depth about 1-2 m over the bottom or in midwater under the kelp canopy (7 of 19 films at SRR 1980) and was never reversed so as not to record fish that tend to follow. The camera housing was directed forward or slightly downward, and panned as steadily as possible in a 10 degree arc, though occasionally stopped to film all fish sighted in a school. Coverage averaged some 211 m^2 of projected area (see Ebeling et al. 1980b). Transects per sample ranged from 4-19, as time permitted.

Data Analysis

This opportunistic sampling of very heterogeneous reef systems presented unavoidable problems for proper statistical analysis. In the restricted space of LBR, large sampling units could not be randomly placed. Macroinvertebrate transects, for example, had to be stratified to cover different microhabitats (reef base, crest, etc.), but confined to fields large enough to accommodate transect tracks; any randomization of both position and direction of tracks would have

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underrepresented microhabitats or extended surveys into open water and across sand. Hence, positions along tracks could be randomized for small-scale sampling of sessile benthos, but not the tracks themselves for large-scale sampling of sea urchins, etc. For repeated sampling, as of fish, that likely covers the same limited number of tracks, however, the mobile animals will eventually randomize themselves over the sampling units, such that sampling conforms to a "restricted systematic design" (Venrick 1978). Fish may accomplish this to a certain extent between cinetransects.

The varying sizes of sampling units presented further problems in statistical comparison, especially between sites. For example, sampling units for macroinvertebrates were either 37 m^2 (LBR) and 13 m^2 (SRR, NR) transect bands or 1 m^2 photoquadrats (SRR). For comparison, therefore, all individual observations had to be standardized to number m^{-2}, such that those from transects are rates and those from quadrats are discrete counts. Cross comparisons of percent cover by sessile benthos is also subject to the bias of different unit sizes: 0.25 m^2 (LBR) vs. 0.042 m^2 (SRR). It is doubtful that the two units sample the same scale of patchiness. Nonetheless, the more important comparisons--between years within sites--are more reliable because sampling units were usually of the same size within sites.

To facilitate comparisons despite these problems of bias and scale, samples were simply contrasted in a gross way by graphing all statistics in the same format: means and their 95% confidence intervals

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based on transformed values converted back to their geometric or percentage equivalents. [Because their statistical distributions were strongly skewed, most counts (x) were transformed to $\log(x+1)$ for calculation of parametric statistics; analogously, values of percent cover of sessile organisms were arcsine transformed (Sokal and Rohlf 1981).] These are more realistic measures of central tendency than arithmetic means because they approximate medians (with asymmetric intervals), the better descriptors of skewed distributions (Sokal and Rohlf 1981). Furthermore, they may be contrasted informally by rule of thumb: If the interval of one mean covers the value of another, the two means probably do not differ significantly by t-test; if the two intervals themselves do not overlap or barely overlap, the difference is highly significant (Simpson et al. 1960).

RESULTS

Macroinvertebrates

In April 1977, evidence of sea otter foraging--scattered broken red abalone (*Haliotis rufescens*) shells and red sea urchin (*Strongylocentrotus franciscanus*) tests--was found about the base of LBR (pers. observ.). In addition, a raft of 58-97 otters had been sighted near LBR and SRR in February, 1977, and six animals were seen foraging over LBR in June (S. Benech, Benech Biological Assoc., Ventura CA., pers. commun.).

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Subsequent results indicated that the otters continued harvesting abalones and urchins from LBR during the entire 15-month study period. Total exposed red abalones (Haliotis rufescens) counted in all six transects declined from 26 in 1976 before otters arrived, to 4 in 1977 three months after, and zero a year later in 1978 when all 11 seen were deep in cracks and crevices. The density of red sea urchins (Strongylocentrotus franciscanus) decreased significantly after otters came, while purple sea urchins (S. purpuratus) were rare at the outset (Fig. 3). Like abalones, the surviving red urchins found refuges, with covert numbers increasing from zero in 1976 to 27 in 1977 and 37 a year later. Similarly at reefs near Monterey, broken shells and tests littered the bottom before abalones and urchins were restricted to crevices after otters returned in the 1960s (Lowry and Pearse 1973; Cooper et al. 1977; Hines and Pearse 1982).

Apparently, however, otters had not depleted abalones and urchins to the point of eating sea stars. Annual fluctuations in densities of Patiria miniata and Pisaster spp. (mostly Pisaster ochraceus and P. giganteus) were unrelated to otter presence at LBR or SRR (Fig. 3). Although otters may eat sea stars on occasion (Woodhouse 1982; D. Reed, pers. commun.), they presumably do so only as urchins, abalones, and crabs become unavailable (Ebert 1968; Ostfeld 1982).

Even before otter foraging, LBR supported a much lower density of urchins than the larger sites (Fig. 3). This may be typical of small high-relief reefs where strong wave action (Lissner 1980) and steep

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vertical walls with patches of the stinging anemone Corynactis californica restrict urchin positioning and movement (Foster and Schiel 1985; Laur et al. 1986). In contrast, SRR had high densities of exposed red urchins before otter foraging. But within a year after otters arrived at SRR, densities had dropped from more than six m^{-2} to zero as urchins virtually disappeared along with the abalones.

At the southern Californian site NR, densities of all exposed macroinvertebrates remained high throughout the barrens period in an environment without otters. Even large abalones remained scattered about. Many individuals appeared to be wasting from starvation, in that their muscular foot had regressed noticeably in size and they could be easily dislodged from rocks by hand. Although both urchins and abalone prefer to feed on drift kelp when available, abalones are both morphologically and physiologically less able to exploit alternative limited food sources when drift is absent (Tegner and Levin 1982).

Algae and Sessile Invertebrates

The flora of LBR was typical of a small rugged reef of the open coast without a permanent kelp canopy (see Foster and Schiel 1987). Although we saw scattered signs of Nereocystis luetkeana in the area throughout the study, no obvious canopy formed near the reef even after the sea otters came. Thus most of the dense algae consisted of low bushy forms and turf (Fig. 4). Dominant species of fleshy red algae included

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Gelidium robustum, Gigartina exasperata, Callophyllis pinnata, Rhodymenia pacifica, and Botryoglossum farlowianum growing with articulated coralline algae such as Calliarthron cheilosporoides. Species common at reef crest--of Gelidium, Calliarthron, Gigartina, Callophyllis, and the understory kelp Laminaria dentigera--flourish in zones of good water circulation and high light levels (Burge and Schultz 1973; Foster and Schiel 1985).

At LBR, benthic cover showed little because invertebrates had not overgrazed the pre-otter reef. Percent cover of exposed crustose corallines, which otherwise would decrease wherever relaxed grazing pressure allows the upright species to regenerate, actually increased slightly along with fleshy red algae and tubicolous amphipods (Fig. 7.4). However, the small increases in upright cover may have occurred independently of the otter effect as species filled space vacated by barnacles. An initial dense cover of barnacles (Balanus crenatus) on parts of the reef in 1977 had declined to nil by 1978; this was also noted by M. Foster (pers. commun.) in other areas both with and without sea otters along the central California coast. In addition, J. Estes and G. VanBlaricom (pers. commun.) "...observed an extraordinary settlement of B. crenatus at Pt. Piedras Blancas (about 80 km N of our sites) in fall 1977."

In contrast, SRR showed a dramatic post-otter increase in cover (Fig. 5). A carpet of fleshy red algae and sessile invertebrates harboring greater abundances of tubicolous amphipods overgrew the

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nearly continuous pavement of exposed crustose corallines (Fig. 4). A thick canopy of Nereocystis measuring some 80 x 100 m had reached the surface within two years time. Previously restricted to shallow areas of high relief and strong water motion, stands of understory kelp (Laminaria dentigera) had spread over all deeper areas of reef flat within three years (Fig. 6).

This post-otter effect was simulated experimentally on a smaller scale at NR. All three categories of upright cover increased significantly in caged plots as the exposed crust was overgrown (Fig. 3). Even small kelp plants (Macrocystis pyrifera and Pterygophora californica) appeared in the cages and were eventually grazed by fish in the topless treatments. Continually grazed by urchins, the uncaged plots retained a significantly larger cover of coralline pavement.

Fish

The large drop in total fish abundance at LBR reflected the virtual disappearance of young rockfish (Sebastes mystinus and S. serranoides) from the small reef between 1977 and 1978 (Fig. 7). Such crashes in rockfish recruitment are not unusual along California and may result from climatic shifts and variations in larval abundance as well as loss of cover structure (reviewed in Ebeling and Laur 1987). The young fish had aggregated near the low cover that draped the reef even before otters came. However, the significant increase in surfperch coincided with a vigorous growth of fleshy red algae, especially Gelidium

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robustum, on reef crest. Striped surfperch (Embiotoca lateralis) concentrate about the crest where they pick amphipods from the algal surfaces (Laur and Ebeling 1983).

At SRR, a large maximum in fish abundance was recorded between 1977-1979 on the post-otter reef (Fig. 7). Although this may have been a reproductive response to a favorable climatic shift of which we were unaware, it is tempting to attribute this initial rise to the otter effect. First, a canopy assemblage of fishes (sensu Ebeling et al. 1980a) had begun to form: increasing numbers of senorita (Oxyjulis californica) and blue rockfish (Sebastes mystinus) had moved higher in the water column; kelp surfperch (Brachyistius frenatus), which are obligate canopy dwellers (Bray and Ebeling 1975), were seen for the first time. Second, the increases included young rockfish (Sebastes) and surfperch (Embiotoca, Damalichthys), which use kelp for refuge, as well as adult surfperch, which respond to greater prey (tubicolous amphipod) availability as kelp litter refuels the detrital food chain (Ebeling and Laur 1987). The 1979 abundance of Embiotoca lateralis included many young and subadult recruits probably born on the reef. But this provides no good explanation for the observed decrease in 1980. Perhaps fish were generally less visible then: D. Laur (pers. observ.) noted many fish in the kelp understory and in large schools outside the scope of our cinetransects.

DISCUSSION AND CONCLUSIONS

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Sea otter foraging brought about changes in the Santa Rosa Reef (SRR) community like changes observed elsewhere off central California. After otters returned to the Monterey area during the 1940s and 1950s, for example, large gaps in kelp beds were filled in by both canopy and understory species (McLean 1962). Surviving urchins were driven to deep crevices and other refuges, where they fed on accumulating drift kelp instead of living plants (Lowry and Pearse 1973). Likewise at SRR, exposed abalones and sea urchins--the otters' preferred food--disappeared, as turf, kelp, and sessile animals filled the space once dominated by urchins and paved with crustose coralline algae. Abalones and urchins became restricted to crevices: algal turf overgrew the corallines; a canopy of Nereocystis luetkeana formed at the water surface; and an understory of Laminaria dentigera spread over the reef bottom. Similar changes occurred on a much smaller scale in our urchin-exclusion plots in a persistent urchin-dominated barren ground at Naples Reef off southern California, where there are no otters: Rich algal turfs and small kelp plants soon covered the coralline pavements wherever urchins were excluded.

The indirect effects of sea otter foraging that we observed at SRR resembled previously described early stages in a lengthy successional process of kelp-forest development. North (1965) suggested that since perennial Macrocystis is competitively dominant over annual Nereocystis, a return of sea otters should herald the ultimate

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reestablishment of Macrocystis canopies on barren grounds off central California. Using historical data collected from the area, VanBlaricom (1984) composed a qualitative model of the process: The surface-canopy kelp Nereocystis is among the first colonizers because it persists on marginal substrates; during the initial few years, an understory of perennial kelps, including Laminaria, develops; finally, the maturing system is invaded by Macrocystis, which forms another surface canopy, has the potential of rapid vegetative regrowth, and may persist indefinitely. Hence at SRR, the Nereocystis canopy, which formed within two years after exposed urchins were eliminated, may be eventually replaced by Macrocystis invading rifts in the Laminaria understory.

Thus, the establishment of a persistent Macrocystis canopy may not occur for a decade or more after the exposed sea urchins are removed (VanBlaricom 1984). Similarly, Dayton and Tegner (1984a) concluded that seral replacement in understory patches requires a minimum of ten years in the Pt. Loma kelp off southern California, and major changes in Macrocystis cover occur on even larger time scales.

Physical disturbance may disrupt the long-term process, however. Although the taller "climax" canopy of perennials dominates the competition for light, it is more vulnerable to wave stress, so that the dominance hierarchy may be reversed in areas exposed to storm action (Cowen et al. 1982; Dayton and Tegner 1984b; Dayton et al. 1984; VanBlaricom 1984). The canopies surviving in areas of greater wave stress often release their gametes into stronger currents and thereby

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may have the greater dispersal and colonizing potentials (Neushul 1972). Thus, annual Nereocystis and perennial understory canopies are typical of shallower cobbly or more exposed central Californian localities subject to frequent wave disturbance, while Macrocystis dominates deeper, more protected sites with hard, stable substrata (Dayton et al. 1984; Reed and Foster 1984).

In addition to demonstrating marked post-otter changes within the reef community, our study supports Foster and Schiel's (1987) contention that reef "type" should be considered in predicting the indirect effects of sea otters on the community. Whereas the larger, deeper, and more low-relief type at SRR showed a dramatic post-otter changeover, the smaller, rugged type at LBR was less affected. Perhaps the LBR system is controlled mostly by physical disturbance. Thus, LBR may have never supported a permanent kelp canopy or large urchin population.

Perhaps small protruding reefs like LBR present exposed and unstable platforms for conspicuous and sedentary organisms with large hydrodynamic drag because such reefs are relatively isolated and create strong water motion. Carter et al. (1985) concluded that small modular piles of boulders making up Pendleton Artificial Reef (PAR) off southern California harbored few urchins because the structures generated turbulence and were surrounded by barriers of sand; also, transplanted kelp was either torn off by the surge or eroded away by grazing fishes attracted to the conspicuous foliage. Previously, North

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(1971) and Dayton and Tegner (1984a) had suggested that small isolated patches of kelp may attract high densities of encrusting organisms and browsing fishes, thereby setting a lower size threshold to the establishment of a stable kelp forest.

A likely reef type for Macrocystis establishment may be indicated by the aspect ratio (depth of surrounding water/modal reef height). The optimal aspect ratio for producing a favorable lee wave in a moderate current is 10 (Nakamura 1985), comparable to that of the SRR flats. However, the aspect ratios of the LBR and above-mentioned PAR prominences are all less than three. With steep sides buffeted by a heavy swell, therefore, the latter reefs will tend to maximize hydrodynamic pressures and turbulence to the point where plants and animals with large drag, such as surface kelp and exposed sea urchins, are likely to be torn loose or pulled off the bottom (see Foster and Schiel 1985).

The post-otter regrowth of the SRR kelp forest may have enhanced some fish populations. By the end of the second year (1979), a canopy group of fishes (sensu Ebeling et al. 1980a), including an obligate canopy species (Brachyistius frenatus), had assembled, together with large schools of young rockfish and surfperch, in and about the kelp stands (although, perhaps due mostly to sampling error, the resulting increase in fish abundance was not documented by transects made during the single day's sampling for 1980). As also observed in other central Californian localities (Miller and Geibel 1973; Bodkin et al. 1986;

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Bodkin 1986), blue rockfish (Sebastes mystinus) were by far the most abundant species in the new SRR kelp forest.

Future standing stocks of fish may be larger if Macrocystis eventually replaces the Nereocystis canopy. Bodkin (1986) estimated that Macrocystis beds near Pt. Piedras Blancas (about 80 km N of our sites) supported more than twice the fish biomass as occurred in equivalent Nereocystis beds, due largely to greater abundances of blue rockfish. This difference was attributed to the perennial Macrocystis forest's greater persistence, foliage biomass, and structurally diverse habitat (VanBlaricom 1984; Botkin 1986).

Nonetheless, changes in fish abundance due to revegetation may be confounded with changes due to spawning or recruitment success associated with large-scale shifts in ocean-current and temperature patterns (Stephens et al. 1984; Cowen 1985; Bodkin et al. 1986; Ebeling and Laur 1987). Adult fishes that tap the detritus-based food chain or young fishes that recruit to the shelter of the algal canopies are more likely to respond to revegetation (Quast 1968; Miller and Geibel 1973; Burge and Schultz 1973; Estes et al. 1978; Simenstad et al. 1978; Ebeling and Laur 1987). Some are species like surfperches that seek cover in the canopies as young and eat tiny prey living on bushy algae and in the carpeting turf as adults (Stouder 1983; Ebeling and Laur 1986). For instance, overall abundance of Embiotoca lateralis increased at SRR as young found refuge in the understory kelp (see Ebeling and Laur 1985) and adults may have encountered greater food supplies

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related to the increasing algal abundance (see Hixon 1980; Laur and Ebeling 1983; Schmitt and Holbrook 1984). The large fluctuations in abundances of young rockfish may have reflected widespread recruitment failures associated with northerly ocean currents or increasing water temperature, as well as changes in cover (reviewed in Ebeling and Laur 1987). Yet to our knowledge, no large shifts in weather pattern, such as El Nino episodes, occurred during the period of study (see Seymour et al. 1984; Ebeling an Laur 1987, Fig. 2).

The potential for kelp-related enhancement of reef-fish assemblages may be greater in central than southern California, so long as a complex rocky substratum is provided (review in Ebeling and Laur 1987). During a three-year cycle of loss and regeneration of a southern Californian kelp forest at Naples Reef, for example, total fish density varied by only about 20% because losses in some species were offset by gains in others (Ebeling and Laur 1987). In fact, abundances of some species that do not always rely on the kelp forest for food and cover actually increased (see also Quast 1968). These planktivores (Chromis punctipinnis) and "switch-feeders" (Girella nigricans, Medialuna californiensis, Paralabrax clathratus) were southern species, rare in central California waters north of Point Conception: Although rank orders of fish species abundance for LBR and SRR correlated significantly (tau = 0.40, P=0.05), those for either northern site and Naples did not (0.03-0.15, NS). Hence, this kind of species replacement may not occur in waters to the north (see also Burge and Schultz 1973;

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Bodkin 1986).

In perspective, Californian kelp forests vary in response to a number of factors--storm disturbance, water temperature, light levels, kelp harvesting, and local pollution--besides overgrazing by herbivores (recent reviews in VanBlaricom 1984; Dayton 1985b; Foster and Schiel 1985 1987; Estes and Harrold 1987; Schiel and Foster 1987). For example, Cowen et al. (1982, p. 200) concluded of a central Californian kelp forest: "Once the urchins are removed, the maintenance of community structures will be a function of physical disturbance and variations in algal recruitment." The obverse is also true: in the midst of grazing urchins, new growth may not survive even in a favorable disturbance regime with sufficient supplies of potential recruits (Ebeling et al. 1985). Thus, "(b)y removing sea urchins as important grazers, ...sea otters eliminate a major source of kelp forest variability and may strengthen the resilience of the kelp community to extrinsic disturbance" (VanBlaricom 1984, p 23). Doubtless the extent of the otter effect will vary among areas with different disturbance regimes and susceptibilities to overgrazing (Estes and Harrold 1987; Foster and Schiel 1987).

Future Research

A wealth of descriptive and experimental evidence has proven that kelp and other algae regrow where the high densities of exposed sea urchins are removed from a barren ground. Hence, further experiments in which

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urchins are excluded from small barren plots are no longer needed to demonstrate this outcome (Foster and Schiel 1987). There is also adequate evidence that otters are most capable of eliminating exposed urchins, and so can bring about the regeneration or preservation of kelp forests on a local scale (Estes and Harrold 1987). Nonetheless, it should be emphasized that the successional development of a kelp forest into its most productive form may be a lengthy process, requiring a decade or more of observation to confirm (Dayton and Tegner 1984a; VanBlaricom 1984).

What remains to be done from our perspective is to predict the vulnerability of a reef to urchin domination and to clarify indirect effects of overgrazing on higher trophic groups such as fishes. Thus, more research is needed on how best to classify reefs by environmental "type," as some types will be more vulnerable to overgrazing than others (Foster and Schiel 1987). What physical settings present barriers to urchin settlement, recruitment, and immigration? (see Laur et al. in press). Perhaps a reef's aspect ratio (depth of surrounding water/modal reef height), average vertical slope (inclination from the horizontal), and percent unconsolidated substrate (cobble and sand) could be measured for a beginning. Once different sites are identified by these characteristics, urchins could be transplanted at high density to plots and their survival compared with natural controls. But this can be done only after major problems in stabilizing the transplanted animals are solved (see Laur et al. 1986). Ultimately, the

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comprehensive effect of otters moving into a new area may be predictable from the distribution of reef types.

As recommended by Duggins (1987), the contribution of the kelp detritus-based food chain to fish production should be determined by tracing energy sources and transplanting secondary producers. Experiments manipulating kelp canopies and measuring fish-recruitment responses should be supported as well (M. Carr, Univ. California Santa Barbara, pers. commun.). Determining the role of the canopy's "edge effect" in enhancing fish populations is equally important (Dayton and Tegner 1984a; Dayton 1985b). Experiments could be designed to test the idea that kelp forests with open spaces (barren patches) support larger and more diverse fish assemblages because their canopies have more "edge" (M. Carr, Univ. California Santa Barbara, pers. commun.). If this is so, otters eliminating urchins that maintain such patches (see Harrold and Reed 1985) might occasionally cause a modest decline in fish abundance by bringing about the ultimate restoration of a continuous thick canopy.

SUMMARY

Annual transect and photographic surveys of two subtidal reef communities in San Luis Obispo County, central California were made, often opportunistically, from 1976-1980, before and after sea otters arrived in winter, 1977. Results generally confirmed previous models of

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the effect of otter foraging on kelp-forest communities overgrazed by sea urchins. As indicated by the litter of broken shells and tests as well as the survey counts, otters directly eliminated most exposed abalones and sea urchins, which were eventually confined to crevices. Indirectly, the resulting relaxation from urchin grazing pressure brought about a marked change in community structure at the larger, deeper, and flatter reef: Within two years, canopies of algal turf, understory kelp (Laminaria dentigera), and surface kelp (Nereocystis luetkeana) overgrew pavements of crustose coralline algae in an urchin-dominated "barren ground." This "otter effect" was simulated on a smaller scale in urchin-exclusion plots on an equivalent barren ground at a reef near Santa Barbara, southern California, where there are no otters. Yet, other investigators have pointed out that an effect such as we observed may only include the early stages in a lengthy successional process lasting a decade or more.

The magnitude of the otter effect depended on the physical setting. At the shallower, high-relief reef, vertical walls and strong water motion probably provided refuges from urchin grazing, but created unsuitable substrata for development of a surface kelp canopy. Thus, the indirect consequences of otter foraging were minor because subsurface algal stands had not been overgrazed before otters arrived and the reef may have never supported a persistent surface canopy of kelp.

Observed numerical responses of fish to the new canopy refuge and

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to a resurgence of the detrital food chain may have been confounded by widespread recruitment fluctuations. Nonetheless, the reef-fish assemblage may be more vulnerable to defoliation in central than in southern California, where a large indigenous array of southern species includes abundant planktivores and switch-feeders not requiring products of an intact kelp forest.

Thus as emphasized by other symposium contributors, local conditions must be considered in predicting otter effects. In particular, we recommend that physical properties of reefs should be measured as indicators of supportable plant cover and vulnerability to grazing. For example, reef depth and shape affect water motion and, therefore, the stability of platforms for sessile organisms with large hydrodynamic drag like kelp plants and sea urchins. Future work should also include experiments to test the importance of kelp canopies to reef-fish recruitment and survival.

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FIGURE CAPTIONS

Fig. 1.--Location of study reefs (upper arrow) where the effects of sea otters on reef communities were observed in central California north of Pt. Conception and where (lower arrow) the effects were simulated by macroinvertebrate exclusion cages in an urchin-dominated barren ground in southern California near Santa Barbara.

Fig. 2.--Structure of caged treatments for the urchin exclusion experiment at Naples Reef in southern California. A, macroinvertebrate exclusion; B, fish exclusion; C, total exclusion.

Fig. 3.--Yearly densities of macroinvertebrates at the three study sites. Species are, from left to right: S.p., purple sea urchin *S. purpuratus*; S.f., red sea urchin *Strongylocentrotus franciscanus*; P.m., bat star *Patiria miniata*; Pisaster, *Pisaster* sea stars pooled. Bars measure geometric mean numbers m^{-2} with 95% confidence intervals: Lone Black Reef, clear for 1976 before sea otters arrived (N=6 transects), stippled for 1977 (N=6), and hatched for 1978 (N=6); Santa Rosa Reef, clear for 1976 before otters (N=36 1.0 m^2 photoquadrats), stippled for 1979 (N=4 transects), and hatched for 1980 (N=4); Naples Reef, clear for 1979 (N=31 transects), stippled for 1980 (N=27), and hatched for 1981 (N=29).

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Fig. 4.--Yearly percent cover of four categories of benthic organisms at the three study sites. Bars measure back-converted mean percentages with 95% confidence intervals: Lone Black Reef, clear for 1977 (N=54 six-slide photoquadrats) and stippled for 1978 N=36); Santa Rosa Reef, clear for 1976 before sea otters (N=24 single-slide photoquadrats), stippled for 1979 (N=34), and hatched for 1980 (N=63); Naples Reef, clear for the non-exclusion that allowed urchins to enter (N=32 six-slide photoquadrats, pooled among years) and stippled for the urchin-exclusion plots (N=192).

Fig. 5.--Photographs showing expansion of erect benthic cover on Santa Rosa Reef flats after sea otters arrived in winter, 1977. A, exposed pavement of crustose coralline algae before otters; B, fleshy red algae and amphipod tube mats overgrowing the pavement after otters; C, stipes of the understory kelp Laminaria dentigera after otters. A and B include 0.042 m^{-2} of area.

Fig. 6.--Density of understory kelp (Laminaria dentigera) on Santa Rosa Reef before (1976, N=35 1.0 m^2 quadrats) and after (1980, N=18) sea otters arrived in 1977. Percent cover is the back-converted mean with 95% confidence interval.

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Fig. 7.--Yearly densities of fishes at the three study sites. Species are, from left to right: O.j., senorita Oxyjulis californica; S.m. yoy, blue rockfish Sebastes mystinus young; S.m, blue rockfish adults; S.s. yoy, yellow rockfish S. serranoides young; E.l., striped surfperch Embiotoca lateralis; D.v., pile perch Damalichthys vacca. Bars measure geometric mean numbers per cinetransect with 95% confidence intervals: Lone Black Reef, clear for 1977 (N=20 cinetransects) and stippled for 1978 (N=12); Santa Rosa Reef, clear for 1976 before sea otters (N=4), stippled for 1979 (N=4), and hatched for 1980 (N=19). Total fish includes other species as well.

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Fig. 1

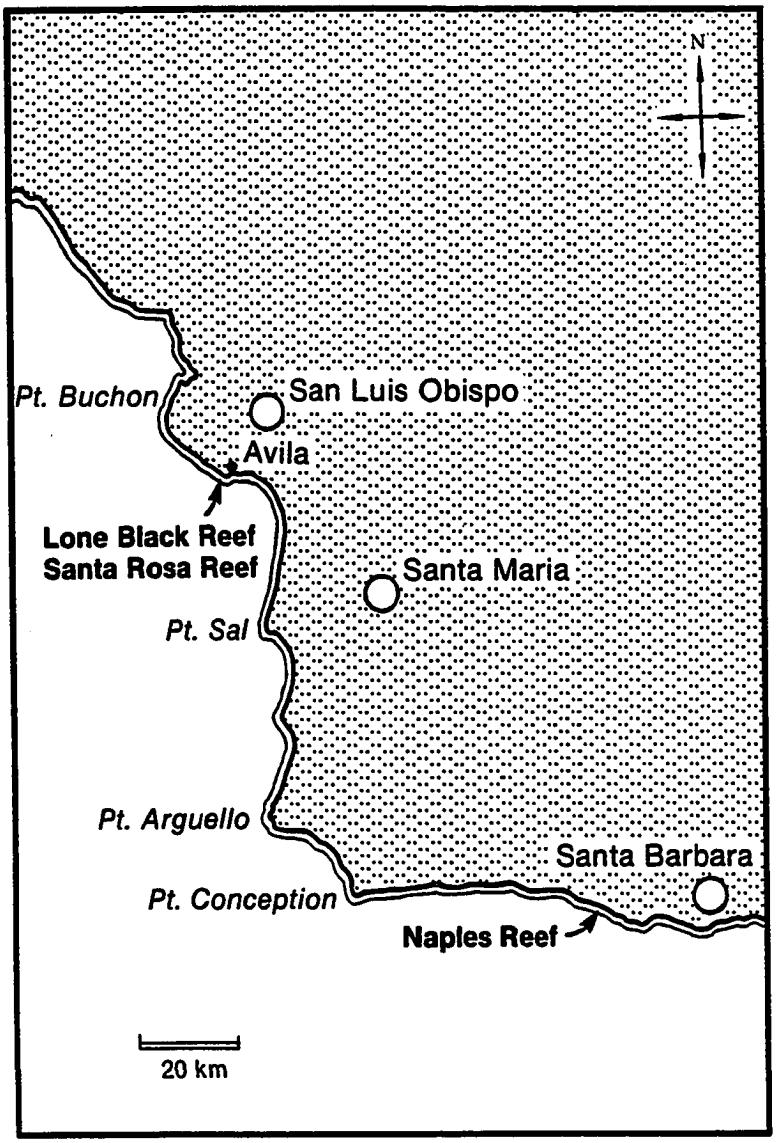

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Fig. 2

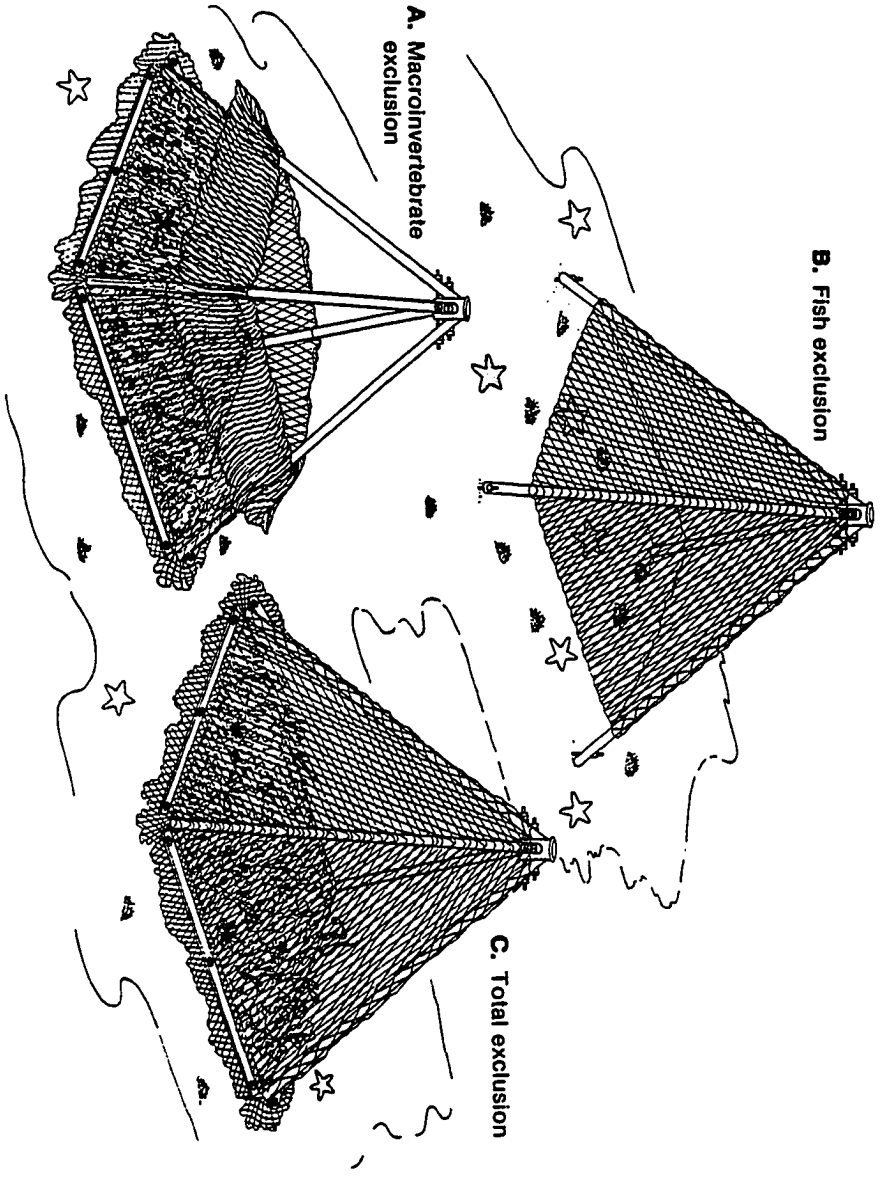

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Fig. 3

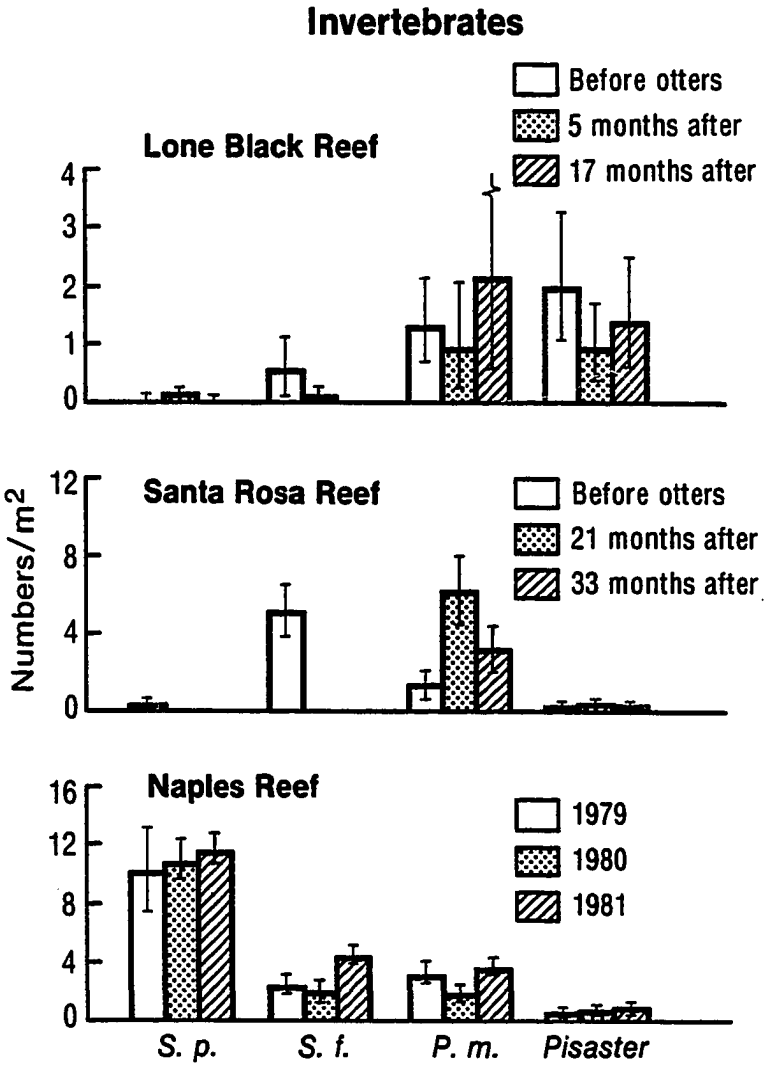

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Fig. 4

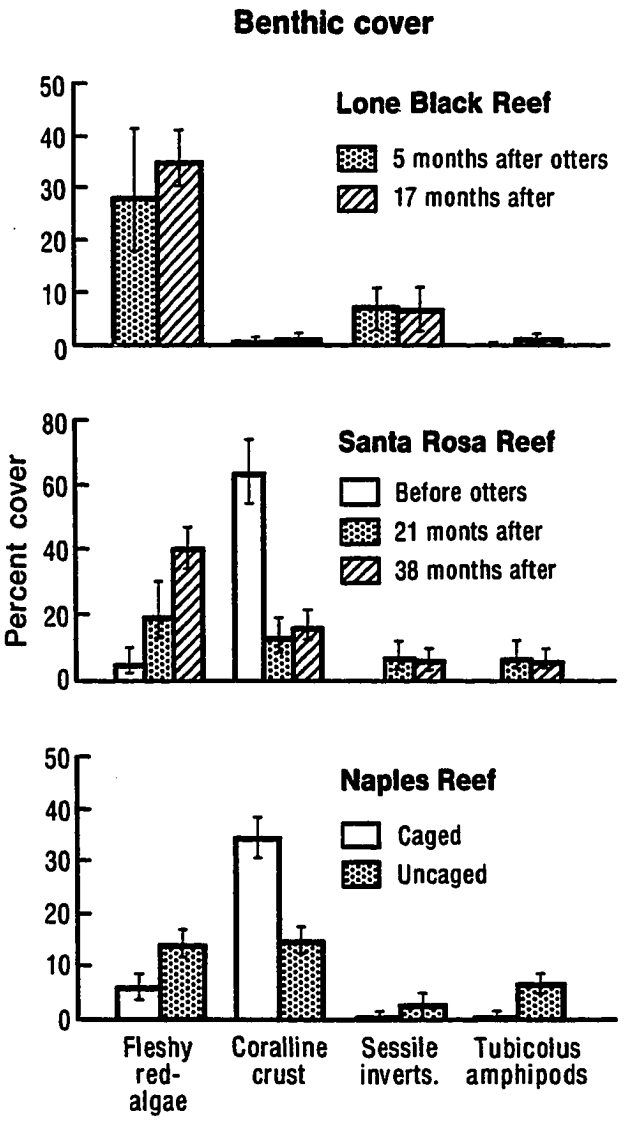

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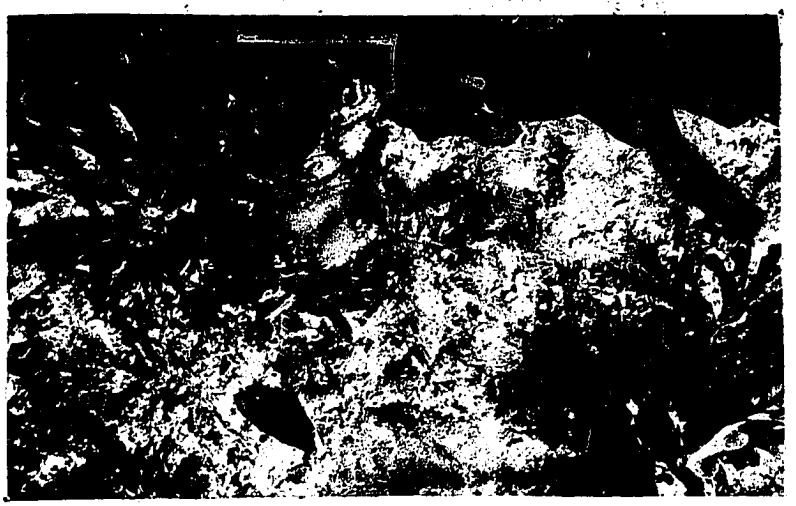
Fig. 5

A

B



C

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Fig. 6

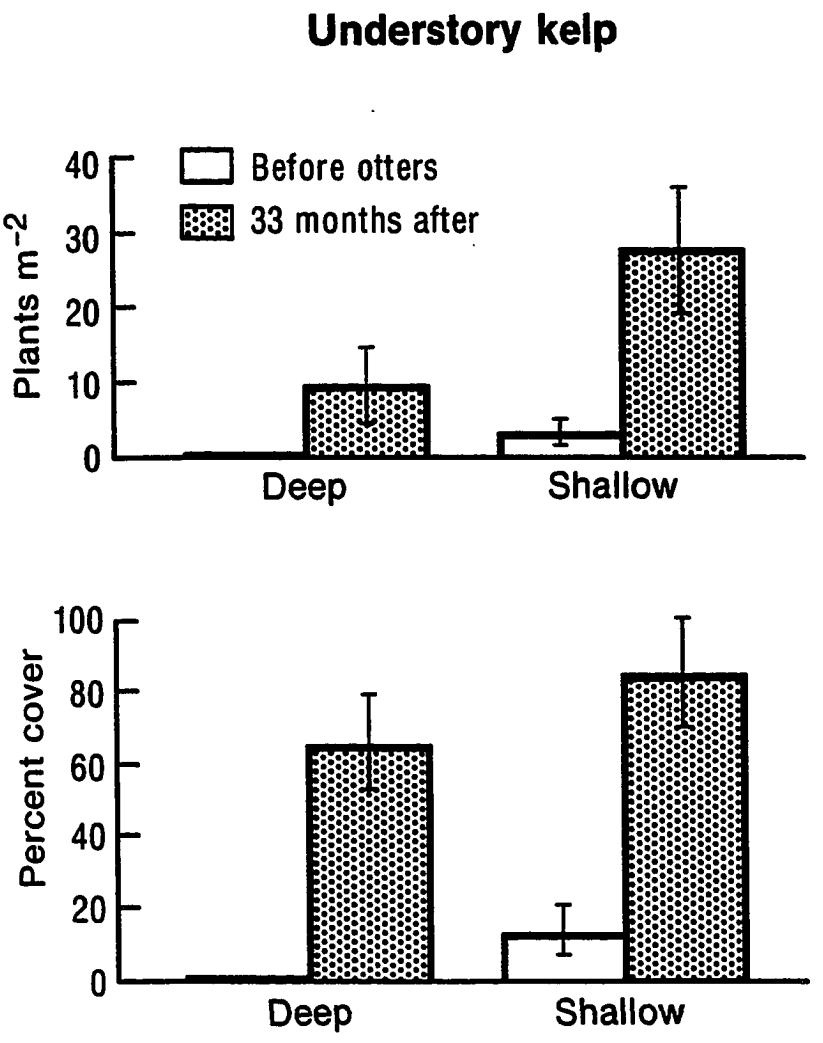

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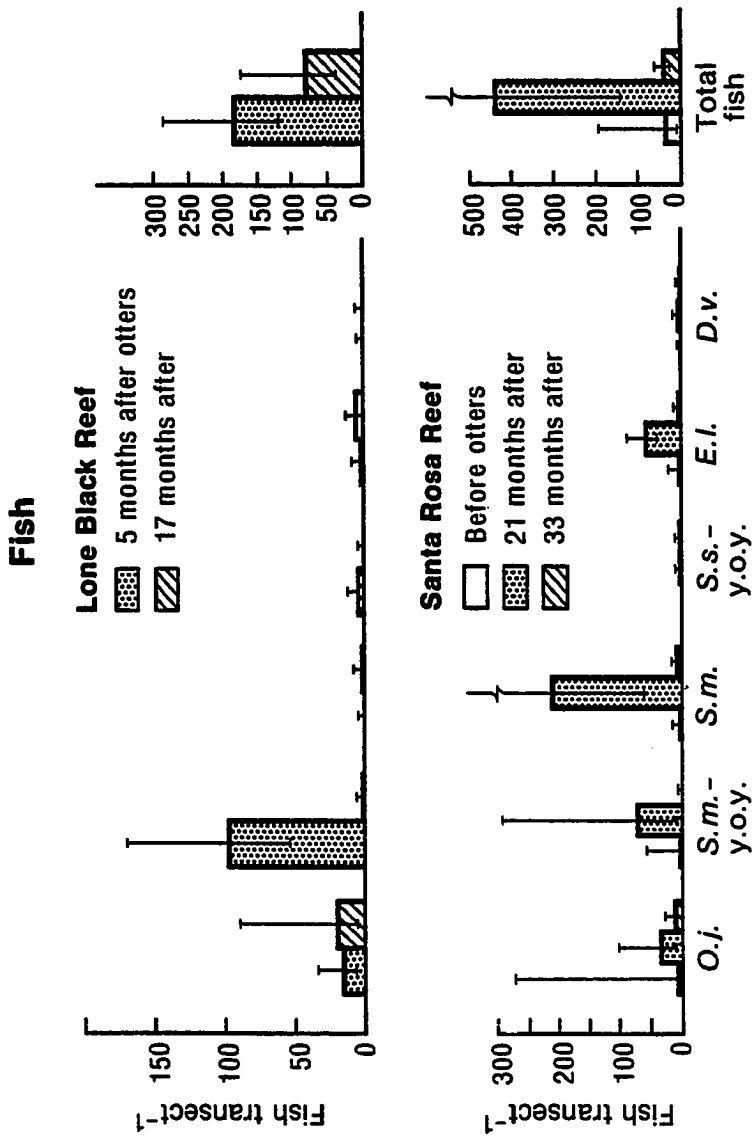
Fig. 7



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CHAPTER 6

INFLUENCES OF MACROINVERTEBRATE AND FISH GRAZING ON A DISTURBANCE-REGULATED BENTHIC COMMUNITY OFF SOUTHERN CALIFORNIA

INTRODUCTION

Biological and physical disturbances interact to shape the structure of temperate subtidal reef communities (Dayton & Tegner, 1984; Dayton et al., 1984; review in Dayton, 1985). Moderate levels of biological disturbance--grazing and predation by macroinvertebrates and fishes--may maintain locally high diversities of algal turf and associated prey organisms (Ayling, 1981) by providing free space for colonizers and preventing domination by superior space competitors (e.g., Dayton, 1971; Paine, 1974; Levin & Paine, 1974; Connell, 1978; Lubchenco, 1978; Menge, et al., 1985; review in Sousa, 1984). Thus, at low grazing levels, diversity may decrease as competitive superiors dominate the space, while at high levels diversity is maintained only if spatial refuges exist (Hixon & Brostoff, 1983, 1985; review in Hixon, 1986). However, major physical disturbances--dislodging and scour by powerful wave action--may perturb community structure to the extent that biological disturbance intensifies. For example, destruction of the kelp forest and loss of detached plant litter can elicit chronic overgrazing by sea urchins (Ebeling et al., 1985; Harrold & Reed,

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1985).

The kelp-forest community on Naples Reef, our study site off Santa Barbara, southern California, has provided the opportunity to observe this kind of modification of biological disturbance by physical disturbance. During most of the 1970s the system was fairly stable, with no evidence of markedly altered disturbance regimes. Winters were relatively benign, predictable seasonal change increased productivity in spring and summer, and the kelp forest persisted through regular cycles of partial dieback during fall and winter and regeneration in spring and summer (Ebeling & Laur, 1987). In winter 1978, however, storm surge dislodged most kelp from the reef's west end, transforming the area into an urchin-dominated barren ground (sensu Lawrence, 1975), contrasting sharply with the continuous kelp forest with a carpet of algal turf remaining over most of the reef. Obviously, the wave damage had created a new local condition wherein newly exposed urchins with less detached kelp to eat were grazing back surviving turf and new plant recruits (see Dean et al., 1984; Ebeling et al., 1985; Harrold & Reed, 1985). Then in 1980, an even greater storm swell destroyed the remaining large surface kelp canopy, and exposed urchins consumed most remaining foliage and prevented successful recruitment (Breitburg, 1985; Ebeling et al., 1985; Ebeling & Laur, 1987).

Thus, the dramatic changes supported the prevailing consensus that macroinvertebrates, especially sea urchins, are the main exploiters of temperate-reef turf communities, while fish browsing may play a lesser

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role (Leighton, 1971; Ayling, 1981; reviewed by Choat, 1982). Hence it may be difficult to separate subtle effects of fishes from major effects of sea urchins (Ogden & Lobel, 1978). Nonetheless, some studies indicate that several fish species browse large quantities of algae harboring epiphytic or refuging animal prey (Quast, 1968; Bray & Ebeling, 1975; Bernstein & Jung, 1979). Rosenthal et al. (1974) concluded that fish grazing was a major factor accounting for death of young kelp plants at a reef near San Diego.

Therefore, the aims of our study were twofold: (1) to see if biological disturbance is greatly intensified in a large patch of reef bereft of kelp and partly scoured of turf during a storm; and (2) evaluate the relative contributions of macroinvertebrates and fishes. Dayton et al. (1984) distinguish local determinants of patch dynamics as being biological, whereas on a more global scale differences between areas are more likely due to physical disturbances (but see Schiel & Foster, in press). However, we demonstrate the interplay of biological and physical disturbance within one study area, our Naples Reef study site. To do this, sets of predator exclusion cages placed about benthic communities monitored by photoquadrat were constructed in the defoliated patch and in a patch where the kelp forest remained intact. At the same time, predator densities were monitored in both sites, and suction samples of benthos were made periodically to supplement the photographic sampling. Fish diets and feeding rates were analyzed in previous studies (Bray & Ebeling, 1975; Love & Ebeling, 1978; Laur &

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Ebeling, 1983; Ebeling & Laur, 1986).

METHODS

Study Site

Located 1.6 km offshore, 23 km upcoast from Santa Barbara, southern California, Naples Reef (lat. 34°25'N, long. 119°57'W) has been described in a number of publications (e.g., Ebeling et al., 1980). Briefly, it is an irregular mound of exposed shale covering 2.2 ha, averaging 8-12 m in depth, though some crests project to within 5 m of the surface. Before 1980, the reef was surrounded by flat sand or cobble bottom with occasional rock outcrops, but much of the sand was swept clear by storm waves, leaving pavement rock in their wake. Above the reef a surface canopy of giant kelp Macrocystis pyrifera and subsurface canopy of Pterygophora californica usually proliferated during spring and summer (April-September), but thinned during fall and winter (October-March). The sea urchin-dominated barrens patch (barrens) covered about 1500 m^2 at the reef's west end.

Much of the reef bottom was carpeted by a rich benthic community of algal turf, colonial animals, and small mobile animals using the turf as a refuge. This turf and its animal community is sustained by photosynthetic, detrital, and planktonic inputs, and it is foraged by macroinvertebrates and microcarnivorous or omnivorous fishes (Laur & Ebeling, 1983; Ebeling et al., 1985; Ebeling & Laur, 1987; Stouder,

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1983).

At Naples Reef predator densities and predator exclusion experiments were monitored for three years. Observations were begun in spring, 1978, when the first experimental units were constructed in the forested mid-reef site. They were continued through 1979, when the array of cages and controls was duplicated in an urchin-dominated, overgrazed patch ("barrens") at the reef's west end, and 1980, when cages were lost but replaced in the barrens only, and the kelp forest was destroyed as a result of a severe winter storm (see Ebeling et al., 1985). Measurements of physical variables (surface and bottom temperature, wave height, nutrient levels) during the experimental period are provided in Ebeling & Laur (1987).

Predator Densities

To measure densities of macroinvertebrate predators in the west end barrens site, periodic counts were made in 1 x 13 m bands marked alongside the experimental plots in the rills at midreef and in the midst of the scatter of cages at west end. Nylon lines were stretched between nails driven into the substrate at the beginning and end, so an observer could count animals between ends of a meter bar pushed forward to the right of the line. Mean densities of total sea urchins and two species of sea stars were computed per seasonal period from January-March, 1978 to October-December, 1980.

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Fishes were counted along transects through mid-reef (forested) and west-end (barrens) sites throughout the experimental period. Transects were extended beyond the immediate area of plots as required to sample the large, mobile predators. At the west end site, two ropes, 60 m long and secured 10-20 m apart, marked more or less parallel paths, one running by the deeper margin of the scatter of cages and beyond, the other along the shallower margin on the slope. At the midreef site, large nails marked an equally long path in and out of three rills, two of which contained the experimental plots. All adult and subadult fish were counted in an imaginary 3 m wide band centered on the lines, upward to about 3 m into the water column.

Densities of 11 common fish species known to forage in algal turf or browse on larger plants were pooled into four guilds (see Ebeling & Laur, 1987) to compute the collective means among seasonal periods. The five species of "demersal microcarnivores," surfperches (Embiotocidae) that glean small prey from turf (Laur & Ebeling, 1983; Ebeling & Laur, 1986), were, in order of abundance: Embiotoca jacksoni, Damalichthys vacca, Rhacochilus toxotes, Hypsurus caryi, and Embiotoca lateralis. "Picker-type microcarnivores" that nip small pieces from algal blades to obtain prey (Bray & Ebeling, 1975) were mostly the wrasse (Labridae) Oxyjulis californica with fewer of the surfperch Phanerodon furcatus. "Switch-feeding predators" taking pieces of kelp and other plants along with larger animal prey (Love & Ebeling, 1978) were almost all of the kelp bass Paralabrax clathratus, along with a few of the blue rockfish

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Sebastes mystinus. Finally, "plant-cropping omnivores," which ate mostly macroalgae including young kelp plants (personal observations), were more evenly divided between two kyphosid species, Medialuna californiensis and Girella nigricans.

Predator Exclusion Experiments

Caged treatments (X) and adjacent uncaged controls (C), marked by bolts driven into the bottom at four corners, were randomly assigned to paired 0.25 m^2 plots of more or less even substrate in reef-slope microhabitat. Surrounding the X plots, pyramidal cages of 1.25 cm Vexar plastic mesh supported by 2.5 cm diameter PVC plastic pipe were secured to the bottom by PVC strips bolted to the rock through lips of mesh extending out from the 1.0 m^2 base of the pipe frame. Thus the smaller plots were surrounded by much larger cage bases to minimize edge effects where the mesh met the rocky substrate (see e.g., Foster, 1975; Dayton & Oliver, 1980; Summerson & Peterson, 1984). The three caged treatments consisted of bottomless cages for exclusion of browsing suprabenthic fishes with deep bodies but allowing in sea urchins and other macroinvertebrates (Fig. 1: FX, fish exclusion), topless cages for exclusion of sea urchins and other macroinvertebrate grazers about the bottom but allowing free access to fishes from above (IX, macroinvertebrate exclusion), and complete cages for exclusion of both browsing fishes and macroinvertebrates (TX, total exclusion). Thus, plot pairs consisted of a treatment designated FX, IX, or TX, and

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adjacent control designated FC, IC, or TC. In addition, two plots with mesh fitted only on the south and east sides were sampled as shade controls.

Benthic cover was sampled quarterly by 0.25 m^2 photoquadrat. Coverage of each quadrat was from six 35 mm color slides taken by the Nikonos camera and 0.042 m^2 close-up framer (cages were large enough for the photographer's entry). Sampling by photoquadrat was reliable to the extent that the species dominating the percent cover as estimated from photographs also dominated the algal biomass as measured from four destructive air-lift collections made at the conclusion of the experiment. To measure percent cover of different taxa, slides were analyzed collectively in groups of six by projecting them, one at a time, onto a screen under a grid of 24 crossed lines and counting the number of point intercepts falling on each of 99 categories either of living edible taxa (single or small groups of "species" such as different leafy algae, hydroids, worms, and tubicolous amphipods) generally inedible taxa (crustose coralline algae, anthozoans, etc.) and non-living substrate (bare rock, sand, shell bits, etc). Density of each category was estimated as the number of intercepts covering it. For anova comparison of treatments, however, only percent cover of all edible species pooled was estimated as the number of intercepts covering all such species divided by the total intercepts (144 per group of six slides). Other dependent variables were number of edible "species," diversity (H') and evenness (V' as defined in Pielou, 1977).

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For general monitoring, categories were also pooled into four functional groups: fleshy red algae (leafy and filamentous species), crustose coralline algae (pavement-like species), sessile invertebrates (hydroids, tunicates, sponges, worms, and bryozoans), and tubicolous amphipods (species used as an index of food available for fishes).

The experiment was begun in the forested mid-reef site to also test the differential effects of fish browsing and macroinvertebrate grazing on well-developed turf during different seasons. Since suitable space for installing cages was limited and considerable effort was spent per cage installing and cleaning the mesh of fouling organisms, the number of cages was kept minimal at the outset. At mid-reef, suitable surfaces were limited to the sides of two rills, at about 8-10 m depth, which ran along the long axis of the reef for 10-15 m. Therefore, the two replicate treatments had to be constructed in somewhat different environments (rills). Each rill was assigned 8 plots, a pair for each treatment (FX, IX, TX) and adjacent control (FC, IC, or TC), and two extra for additional replicate pairs as fail safe or light control. It was soon evident that the experiment as designed was insensitive to any major seasonal change because of the limited replication and the lack of any obvious response of the initially heavy mid-reef turf to caging.

Hence, most subsequent effort was focused on repeating the experiment at the west-end barrens site. Here plots were randomly assigned in a more haphazard pattern, as the terrain was more even on

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reef-slope microhabitat at depths between 8-12 m. Only one series of X-C pairs was functioning during 1979. Since a severe storm in winter of 1980 destroyed the cages at both sites, therefore, all available effort went to completing the west-end experiment, replacing the original series and adding a second on new plots. During 1980 mid-reef plots thus remained uncaged while the caged-uncaged experiment was run at the west end only. Consequently, the outcomes at the two sites could not be compared statistically during the same year, 1979 or 1980. At the end of the whole experiment in winter 1980-81, all remaining cages were removed. Several exposed plots of turf at mid-reef and caged and control plots at west end were selected for air-lift biomass sampling and analysis (method described in Laur & Ebeling, 1983).

Because treatments could not be assigned randomly among all forested vs. barrens patches on all reefs, site could not be properly replicated (see Hurlbert, 1984). Therefore, each site (mid-reef forest or west-end barrens) was analyzed separately. Since each site was variable in terrain and other conditions, furthermore, each treatment was compared with its control in a separate anova to eliminate any bias due to placement of the treatment-control pairs.

The anova design was repeated measures (Freund & Littell, 1981) to remove the effects of sampling the same plots through time. In this model, a replicate (series or block) random factor is nested within the treatment factor to create the denominator mean square in the F test for the effect of treatment (X versus C). The model not only eliminates

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the effect of time by averaging over the four seasonal periods, but also removes the effect of differences between the locations of the two replicate arrays of experimental units (similar example in Hairston, 1986). Thus the test is conservative because this denominator mean square carries only two (2 treatments x 2-1 blocks) degrees of freedom. Of the response variables, percent cover of edible species was log-transformed to eliminate the correlation of variance and mean; species number, diversity, and evenness measures were untransformed because F_{max} tests of sample variance ratios were non-significant (Sokal & Rohlf, 1981).

RESULTS

Predator Densities

Abundances of macroinvertebrate grazers were actually greater about experimental plots under the mid-reef forest than in the west-end barrens. Total densities of sea urchins (Strongylocentrotus franciscanus plus S. purpuratus), the most destructive of the lot, averaged more than twice those about the barrens plots during our three-year study (Fig. 2). About equal between sites at first, densities of the omnivorous bat star Patiria miniata fell during late 1979, then returned briefly to former levels at the west-end only. In contrast, numbers of the commonest carnivorous sea star Pisaster

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giganteus were almost constant at both sites during the study period.

Fishes making up guilds of demersal microcarnivores (surfperches) and picker-type microcarnivores (mostly Oxyjulis californica) were much more abundant in the forest than in the barrens (Fig. 3). Only the switch-feeding predators, mostly large kelp bass Paralabrax clathratus, were equally abundant between the two sites. Densities of the plant-cropping omnivores Medialuna californiensis and Girella nigricans increased at mid-reef during 1979-80, and, surprisingly, at both sites in 1980 after the kelp canopy was destroyed by a severe winter storm.

Predator Exclusion Experiments

Responses to the experimental treatments differed dramatically between the two sites (Table 1, Figs. 4-6). Although the caged treatments remained essentially the same as the freely accessible controls in the forested mid-reef site, those excluding macroinvertebrates (TX, IX) rose significantly in percent cover of edible turf organisms as well as in species richness and diversity in the barren west-end site (Table 1, Figs. 4,5). The west-end treatments that excluded macroinvertebrates, principally sea urchins, produced the greatest effect whether allowing in just fish (IX) or prohibiting all large grazers and browsers (TX). Thus the fish effect was weak; responses under cages admitting macroinvertebrates but not fishes (FX) were not much greater than those under controls (FC) and were only marginally significant (Table 1, Fig. 6).

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Whereas allowing in macroinvertebrates (TC, IC, FX-C) to barrens cages drastically reduced percent cover of all turf groups across-the-board, admitting just fishes (IX) caused only modest decreases selectively. Nonetheless, the leafy red algal and hydroid groups averaged only half as much under just fish predation in IX (4.6±3.5(SD)% and 2.5±1.7%, respectively) versus no predation in TX (9.0±5.9% and 5.4±4.0%); the difference in cover of colonial anemones (Corynactis californica) was even greater (0.8±0.5% IX versus 5.5±4.1% TX). Cover of amphipod tube mat was surprisingly similar between the two treatments (11.1±8.6% IX versus 14.4±9.1% TX). Filamentous red algal cover was noticeably higher under selective fish predation (28.9±18.2% IX versus 8.1±7.0 TX), as though these ephemeral species filled space browsed bare of more preferred species. Excluding fish but not macroinvertebrates (FX) produced similar trends in fish effect, even though the benthic community was severely grazed by macroinvertebrates. Covers of leafy red algae and colonial anemones were about twice as high in the FX treatments as in adjacent controls (2.1±1.7% versus 0.9±0.7% and 0.7±0.7% versus <0.1%, respectively), while amphipods showed little difference (1.9±1.7% FX versus 1.8±1.7% FC) and hydroids were negligible in both (<0.3%).

All other edible groups, such as kelps and other leafy brown algae, sponges, worms, non-tubicolous crustaceans, mollusks, and colonial tunicates, covered too little space for meaningful analysis. Bryozoans were also rare under point contact, except for one instance

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of the domination of a plot by a single species as described below.

Percent cover of edible turf (64-67%) under macroinvertebrate exclusion cages (TX,IX) set on initially barren plots at west-end never reached levels (74-83%) of the turfed plots at mid-reef (Table 1). Having regenerated from scratch, west-end cover seemed to stabilize at lower levels (Figs. 4,5). Under TX, a rise in cover accompanied by a drop in diversity during late 1980 was due to preemption of space by a dense and pervasive colony of the upright bryozoan Thalamoporella californica. At mid-reef, the large ranges of values during 1980 after cages were lost and not replaced reflected the differential disturbance to plots, some of which were scoured almost bare while others remained intact or were grazed heavily by sea urchins. Ephemeral and opportunistic species became more abundant then; average cover of filamentous red algae (Pterosiphonia spp.) increased from 2±1.5% - 13±10% among the various treatments and controls before the storm, to 21±17% - 26±14% afterward; early colonizing filamentous browns (Ectocarpus spp., Giffordia spp.) rose in cover from nil to 6±9% - 8±9%.

Thus, trends reflected the basic structural difference between forested and barren sites. At mid-reef, pooled mean percent cover in exposed controls equalled that under caged treatments. All plots had a cover of red-algal turf plus amphipod mat exceeding 50%, compared to less than 10% bare rock plus crustose coralline algae (e.g. Lithothamnium spp.) with patches of stone corals (Fig. 7). At west-end,

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however, cover differed markedly between treatments and controls, which included large patches of coralline pavement.

Trends of cover of each component group were more episodic than seasonal. Pooled among all treatment and control plots, mean percent cover of leafy red algae (e.g. Gigartina spp., Callophyllis flabellulata, Nienburgia andersoniana, Polyneura latissima, Rhodymenia spp.) decreased at mid-reef during 1978-1979 as cover of amphipod tube mat (e.g. of Ericthonius brasiliensis, Ampelisca lobata, Lembos concavus, Photis spp., Melita spp.) increased (Fig. 8). Then both groups plunged to low levels as the forested site was devastated by the winter storm of 1980. In the barrens these two groups also varied inversely under caged plots during 1980, although both rose slightly during April-Sept. 1979 when production was high reefwide. The modest cover (< 10%) of hydroids (e.g. Obelia spp., Plumularia spp., Abietinaria spp., Sertularia sp., Eudendrium spp., Tubularia crocea, Aglaophenia sp.) also peaked in 1979, as did the colonial anemone Corynactis californica.

Destructive sampling following the experiment provided direct comparisons of the biomass of small mobile invertebrates between caged plots protected from heavy grazing and uncaged plots open to urchins and other macroinvertebrates (Table 2). Although at mid-reef liquid displacement volumes of bivalves, amphipods, crabs, and brittle stars were similar in caged and uncaged plots, they decreased substantially after the 1980 storm destroyed cages and patches of algal turf. At the

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west-end site, however, volumes of all categories, including polychaetes and shrimp, increased markedly under macroinvertebrate exclusion cages (IX,TX). The greatest divergence occurred between members of the first installed TX-TC pair, which had been in place twice as long as most others and whose caged member (TX) provided the most extensive refuge composed of algal turf and upright bryozoans (Thalamoporella californica).

DISCUSSION

An acute storm disturbance set the stage for chronic biological disturbances by grazers at Naples Reef. Although in 1978 strong waves tore macroalgae from an area covering only 7.5% of the reef surface, sea urchins (Strongylocentrotus spp.) and other grazers reduced the patch to a coralline algal encrusted barrens after it could no longer sustain the urchins' detrital food resource, mostly from the kelps Macrocystis pyrifera and Pterygophora californica. Hungry urchins destroyed much of the remaining macroalgae and most new recruits; browsing fishes were attracted to solitary plants or copses (pers. observ.). Vertical walls and turbulent crests, which deter urchin movements, helped maintain the integrity of this barrens (see Laur et al., 1986,1987). Generally, furthermore, urchins at the barrens' edge tend to remain stationary as they trap and eat peripheral drift from the kelp forest (Mattison et al., 1977). Thus, the patch persisted

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until 1980 when more widespread urchin grazing created a continuous barrens lasting three more years after another storm tore away most remaining kelp canopies (Ebeling et al. 1985).

Harrold and Reed (1985) found that storm impacts initiate similar transformations at San Nicholas Island beyond the Santa Barbara Channel. They concluded that subsequent episodes of high kelp recruitment and drift accumulation may reverse the process as barrens are filled in with new plant recruits. If the biological disturbance is mitigated by predators or some other factor, community structure is determined mainly by physical disturbance, algal recruitment, and competitive interactions (Cowen et al., 1982). Hence, Schiel & Foster (in press) suggested that a reef community has a characteristic "dynamic range" of different structures, depending on its physical setting, response to natural disturbances, and many other factors.

Provided a sufficient source of detritus, large numbers of grazers can be accommodated without widespread destruction of living plants (Pearse & Hines, 1979; Dean et al., 1984; Ebeling et al., 1985; Harrold & Reed, 1985). Pringle (1986) reviewed worldwide evidence that production of drift kelp can satisfy sea urchins in rich and turbulent waters. Through much of the climatically benign 1970's at Naples Reef, detrital production thus met the requirements of consumers, especially sea urchins. At times supply exceeded demand as detached kelp and other decomposing algae filled the bottoms of rills (Ebeling & Laur, 1987). Consequently, predator density was not an accurate measure of predation

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intensity (see also Choat, 1982; Hixon, 1986). Even though others have observed far fewer urchins in forested than in contiguous barrens patches (Mattison et al., 1977; Andrew & Choat, 1985; Miller, 1985; but see Rosenthal et al., 1974), we found that rich turf cover survived in the forested site alongside grazer densities that were more than twice those in the barrens.

Uncontrolled by predators or other external agencies, however, populations of urchins, which are long-lived and resist starvation (Ebert, 1967; Lang & Mann, 1976; Estes et al., 1978), would gradually build to the point of outstripping their favored detrital food supply (Dean et al., 1984). Under these circumstances overgrazing may be mitigated only by limitations to sea urchin recruitment or low juvenile survivorship in algal turf (Andrew & Choat, 1982, 1985; Choat & Ayling, in press; R. Rowley, unpubl. data). At Naples Reef, for instance, ratios of small/large urchins were only about 1:20 during 1977-1982 when highest total densities of purple (Strongylocentrotus purpuratus) plus red (S. franciscanus) averaged no more than 14.2 m^{-2} and purple outnumbered red urchins by 3:1 (unpubl. data; Ebeling et al., 1985). Then after the present study was completed, the 1982/1984 El Nino event, whose severe storms decimated the adult urchin population and thus began the regeneration of Naples Reef kelp (Ebeling et al. 1985), also heralded an enormous recruitment of purple sea urchins (R. Rowley, unpubl. data). By 1985, ratios of small:large individuals had reached 1:1.5, individuals averaged as much as 60 m^{-2}, and purple outnumbered

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red urchins by 6.5:1. Consequently by 1987, most of the reef surface had once again been overgrazed to barrens (unpubl. data), despite a 1984 accumulation of algal drift to pre-1980 levels (Ebeling et al. 1985).

Grazing effects of fishes as well as macroinvertebrates were observable only in the barrens. In the forested site, species diversity and percent cover of forage organisms remained virtually identical between caged treatments and freely accessible controls even in the midst of abundant grazers. This was also true of component groups, such as leafy and filamentous red algae, tubicolous amphipods, and hydroids. In the barrens, diversity and cover were much greater in treatments excluding sea urchins and other macroinvertebrates, as Breitburg (1985) observed on settlement plates set in the same general area. The effect of browsing fishes was more subtle and only marginally significant, just as others have found when partitioning the fish effect from a much larger effect due to urchins (Carpenter, 1986; Foster, 1987).

Most caging designs have been criticized as altering the environment to the extent that responses may be misinterpreted (Neushul et al., 1976; Young et al., 1976; Dayton & Oliver, 1980; Choat, 1982; Edwards et al., 1982; Kennelly, 1983; Summerson and Peterson, 1984). Within the accuracy of our observations, however, there was essentially no difference between the caged and open plots in the forested site. In addition, we detected no differential impact from small grazers such as little fish and tiny crustaceans that are attracted by the added

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structure and enter through the mesh (see Young et al., 1976; Choat, 1982); also, mesh size was too large to trap recruits growing during the course of the experiment (see Arntz, 1977) or form a refuge for them (see Hay, 1981; Kennelly, 1983; Dayton et al., 1984). At best, therefore, any effect of small herbivores was probably much less than that of sea urchins or large browsing fishes and would be mostly restricted to refuges inaccessible to the large grazers (Dayton et al., 1984; Carpenter, 1986).

Evidence that fish select from the array of edible organisms was unclear. In the barrens, covers of fleshy red algae and hydroids were greater under cages from which all large predators were excluded than under cages excluding only fish. Thus, these observations are more like those of Foster (1975) and of Neushul et al. (1976) who observed greater cover of some fleshy algae where fish were excluded, than those of Young et al. (1976) or Kennelly (1983) who found that algal cover may be less under fish exclusion because numbers of small invertebrate grazers increase. However, cover of amphipod tube mat was similar between treatments, even though gammarid amphipods are top-ranked prey of microcarnivorous fishes in southern Californian kelp beds (Quast, 1968) and should show local effects of harvesting (see Holbrook & Schmitt, 1984). Likewise, Choat and Kingett (1982) found no significant effect of fish exclusion on the small invertebrate prey, mainly gammarid amphipods, that are a major part of fish diets in New Zealand. Either our methods were insensitive to changes in amphipod abundance or

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turnover of these tiny prey is very rapid.

Hixon (1986) provided predictions of the effects of predation on the structure of prey assemblages that show competitive hierarchies. Decreases in species richness, evenness, and diversity should occur when competitively subordinate prey are disproportionately reduced in areas of scant refuge where local and regional species pools are similar. We observed such decreases in barrens plots open to grazers. The flat substrate of our plots offered few refuges and the species pool is probably widespread. Yet there is no evidence that competitively subordinate species were selected by the principal grazers: barrens-inhabiting sea urchins, which tend to have indiscriminate foraging habits (e.g., Leighton, 1971). Perhaps intense grazing pressure if casually applied can in itself account for uneven losses of species (Lubchenco, 1978; Himmelman et al., 1983).

Thus, our results support the widespread idea that sea urchins are the main exploiters of macroalgae in temperate-reef communities (e.g., Bakus, 1969; Ogden and Lobel, 1978; reviewed in Choat, 1982), and in some tropical Caribbean areas as well (Carpenter, 1986; Foster, 1987). Browsing fishes played a much smaller role at Naples Reef. Where grazing effects were detectable, only plots open to macroinvertebrates showed significant decreases in prey abundance and diversity. Moreover, macroinvertebrates other than urchins seemed to have little added effect. For example, a severe reefwide drop in numbers of bat stars (Patiria miniata), the only other potentially destructive

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macroinvertebrate grazer in high abundance, had no discernible effect on turf cover at either site; this, despite the fact that bat stars are highly opportunistic omnivores that can evert their stomach to digest small patches of turf (L. G. Harris, pers. commun.), spread out in barrens or even associate with urchins to intercept pieces of drift algae, and move about quickly to appear almost instantaneously at sampled quadrats (pers. observ.). Red abalone (Haliotis rufescens), which compete successfully with urchins for detrital resources (Tegner & Levin, 1982), have been overfished at Naples, and so lack the potential impact of urchins. In addition, abalones are less resistant to starvation than urchins (Tegner & Levin 1982) and may appear emaciated and severely weakened in persistent urchin barrens (Leighton, 1968; Laur et al., 1987). Grazing by herbivorous turban snails (Tegula spp.) was negligible at Naples Reef, and is of minor importance even where they are abundant (Foster, 1982). Whelks (Kelletia kelletii) and cone snails (Conus californicus) were patchily distributed. These gastropods are scavengers at Naples Reef and often aggregate in crevices, although such concentrations had little or no observable impact on ambient turf cover (pers. observ.).

Yet the potential effects of fishes may be greater under special circumstances. For example, picker types such as senorita (Oxyjulis californica) may mitigate outbreaks of grazing isopods or amphipods in the kelp canopy (Bernstein & Jung 1979; P. K. Dayton & M. J. Tegner, pers. commun.). In large numbers, however, the same picker types erode

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kelp blades as they take bryozoans and other substrate-oriented prey (Bray & Ebeling, 1975; Bernstein & Jung 1979). Rosenthal et al. (1974) concluded that black surfperch (Embiotoca jacksoni) were the primary predators of young kelp plants near San Diego. As grazers and browsers of plants, fish are very mobile and can exploit wider areas into microhabitats of reef crest and surge that would otherwise serve as refuges for plants from sea urchins (John & Pople, 1973; Ogden & Lobel, 1978; Hay, 1984; Carpenter, 1986; Foster, 1987). Nonetheless, macroalgae often survive in such microhabitats even where herbivorous or omnivorous fishes are common (Foster & Schiel, 1985; Laur et al., 1986, 1987).

Fish browsing may be most severe on small salient patches of kelp and other macroalgae. Such patches include isolated stands or "oases" on small reefs or in barrens. For instance, fish have destroyed kelp transplanted to small artificial reefs (Carter et al., 1985). Exposed patches of kelp tend to attract high densities of encrusting organisms and browsing fishes, perhaps due to a large patch-edge/patch-volume ratio (Bernstein & Jung, 1979). However, because such fishes are more evenly distributed throughout a large kelp forest (Ebeling & Laur, 1987), their effects are probably diluted by a huge biomass of canopy.

In conclusion, barrens with exposed crusts of coralline algae are formed in temperate kelp forests whenever there is insufficient detritus to feed the resident urchin population. Thus, for example, a storm may eliminate the major biomass of kelp supplying most of the

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detrital drift; this greatly intensifies the biological dis urbance to the extent that much of the remaining cover of macroalgae a d other benthic forage is grazed away, new "turf" organisms cannot · nmigrate successfully, and species diversity falls. In addition, any salient patches of plants that escape urchin grazing may attract he bivorous or omnivorous fishes for intense bouts of browsing. Usually, h wever, macroinvertebrates--primarily sea urchins--contribute far m re to the chronic biological disturbance than do the opportunistic fi hes.

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TABLE I

Cover and diversity of edible "turf" organisms on caged treatment versus adjacent uncaged control plots at kelp-dominated forested and urchin-dominated barrens sites at Naples Reef. The F values are for a repeated measures anova design, using replicate blocks nested within treatments as the denominator mean square.

Response variable	Exclusion cage design	Means		Anova	
		Treatment	Control	$F_{1,2}$	P
A. Forested mid-reef site (during 1979)					
Percent cover	Total	82.7	77.2	0.66	.50
	Invertebrate	80.8	81.6	0.16	.73
	Fish	73.6	79.7	0.28	.70
Species no.	Total	18.8	17.8	0.96	.43
	Invertebrate	19.8	15.2	12.00	.07*
	Fish	18.5	18.3	0.16	.73
Diversity (H')	Total	2.16	2.03	0.79	.47
	Invertebrate	2.33	1.96	3.65	.20
	Fish	2.28	2.30	3.08	.28
Evenness (V')	Total	0.74	0.70	0.63	.51
	Invertebrate	0.78	0.72	1.20	.39
	Fish	0.78	0.79	0.50	.61

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B. Barren west-end site (during 1980)

Percent cover	Total	67.2	14.6	28.83	.03**
	Invertebrate	63.9	8.3	34.86	.03**
	Fish	24.4	9.7	8.26	.10*
Species no.	Total	15.5	7.1	26.96	.04**
	Invertebrate	13.0	5.8	31.22	.03**
	Fish	11.8	6.2	9.80	.09*
Diversity (H')	Total	1.85	1.03	25.20	.04**
	Invertebrate	1.45	0.74	65.42	.02**
	Fish	1.41	0.78	22.18	.04**
Evenness (V')	Total	0.66	0.52	9.02	.09*
	Invertebrate	0.57	0.43	38.20	.03**
	Fish	0.57	0.44	34.12	.03**

*Marginally significant at P <= 0.10; Significant at P < 0.05.

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TABLE II

Liquid displacement volumes (ml 0.25 m^{-2}) of small mobile invertebrate prey sampled by airlift following the caging experiment.

	Mid-reef plots		West-end plots						
			Sampled after 3 years		Sampled after 1.5 years				
Taxon	Caged+ uncaged before storm*	Open plots after storm	TX	TC	IX	IC	IX	IC	FX
Polychaetes	4.4+3.7	5.7+4.9	10.5	3.9	4.4	0.4	7.5	0.8	2.2
Bivalves	13.3+7.3	1.0+1.2	3.0	2.9	14.7	4.0	6.0	0.4	3.0
Amphipods	7.0+4.3	2.1+2.0	27.0	1.5	4.4	1.1	2.0	1.5	1.5
Small crabs	2.6+0.7	1.2+1.1	22.5	0.7	2.2	0.9	1.5	1.5	2.5
Brittle stars	0.9+0.4	0.5+0.4	12.0	1.5	0.7	0.0	3.0	1.5	0.7
Shrimp	0.3+0.1	0.2+0.2	4.5	2.2	0.1	0.6	0.0	0.1	0.0
Total	28.5+8.7	10.9+5.3	79.5	12.7	26.5	7.0	20.0	5.8	9.9

*N=12

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FIGURE CAPTIONS

Fig. 1. Design of cages used as treatments in the predator exclusion experiment at Naples Reef. **TX**, total exclusion of all large predators; **IX**, invertebrate exclusion only; **FX**, fish exclusion only.

Fig. 2. Trimonthly densities of macroinvertebrates at the forested mid-reef and barren west-end experimental sites.

Fig. 3. Trimonthly densities of fish guilds at the forested mid-reef and barren west-end experimental sites.

Fig. 4. Trimonthly percent cover and diversity of all edible "turf" organisms in total exclusion (TX) and in adjacent uncaged control plots (TC) in the forested mid-reef and barren west-end sites.

Fig. 5. Trimonthly percent cover and diversity of all edible "turf" organisms in macroinvertebrate exclusion (IX) and in adjacent uncaged control plots (IC) in the forested mid-reef and barren west-end sites.

Fig. 6. Trimonthly percent cover and diversity of edible "turf" organisms in fish exclusion (FX) and in adjacent uncaged control plots (FC) in the forested mid-reef and barren west-end sites.

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Fig. 7. Summer percent cover of leafy red algae + amphipod tube mat compared to coralline pavement in all plots excluding macroinvertebrates (TX+IX) and in adjacent uncaged controls (TC+IC) in the forested mid-reef and barren west-end sites.

Fig. 8. Semiannual percent cover of leafy red algae and of tubicolous amphipods in all plots at the forested mid-reef site.

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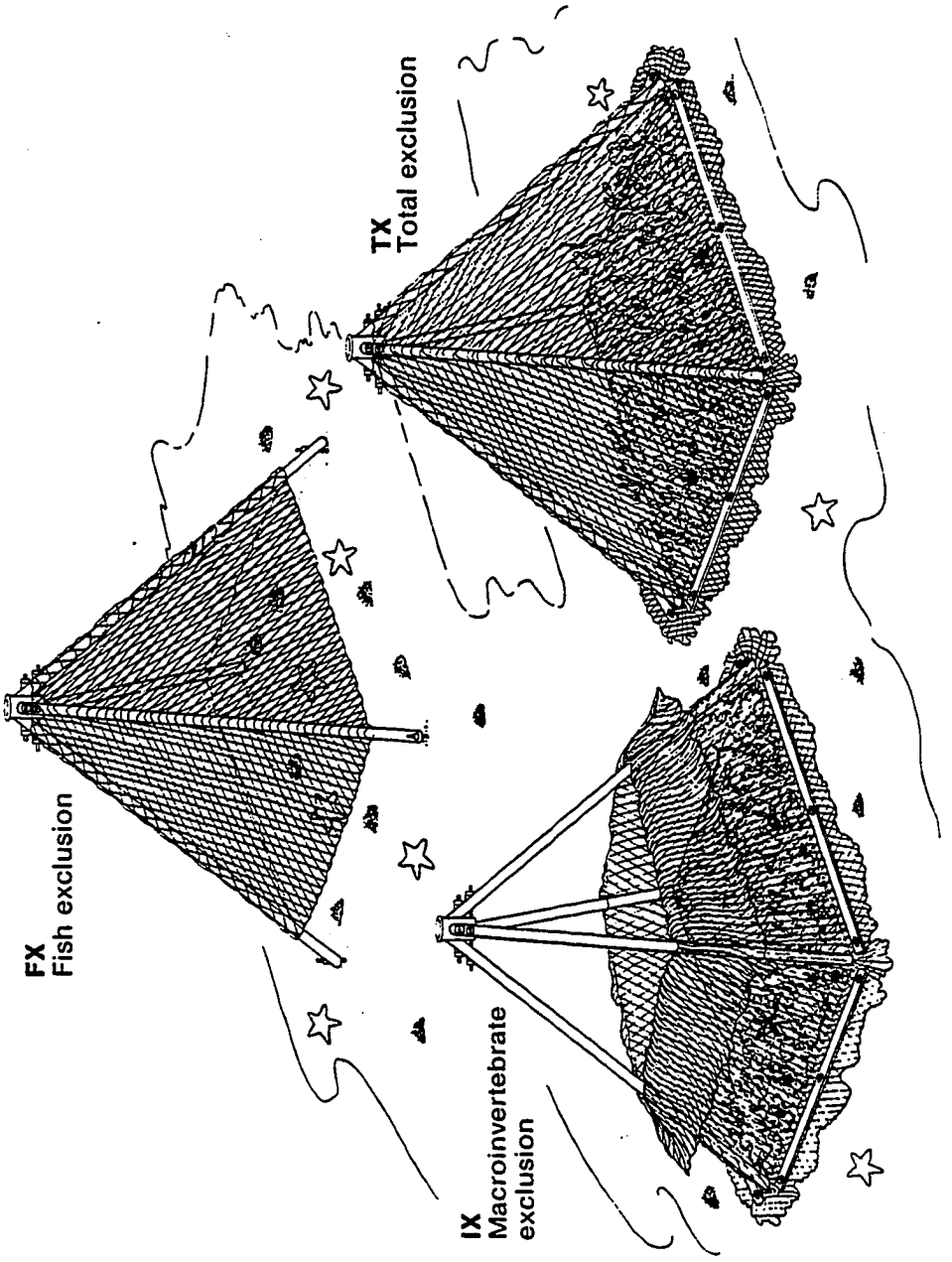

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Fig. 2

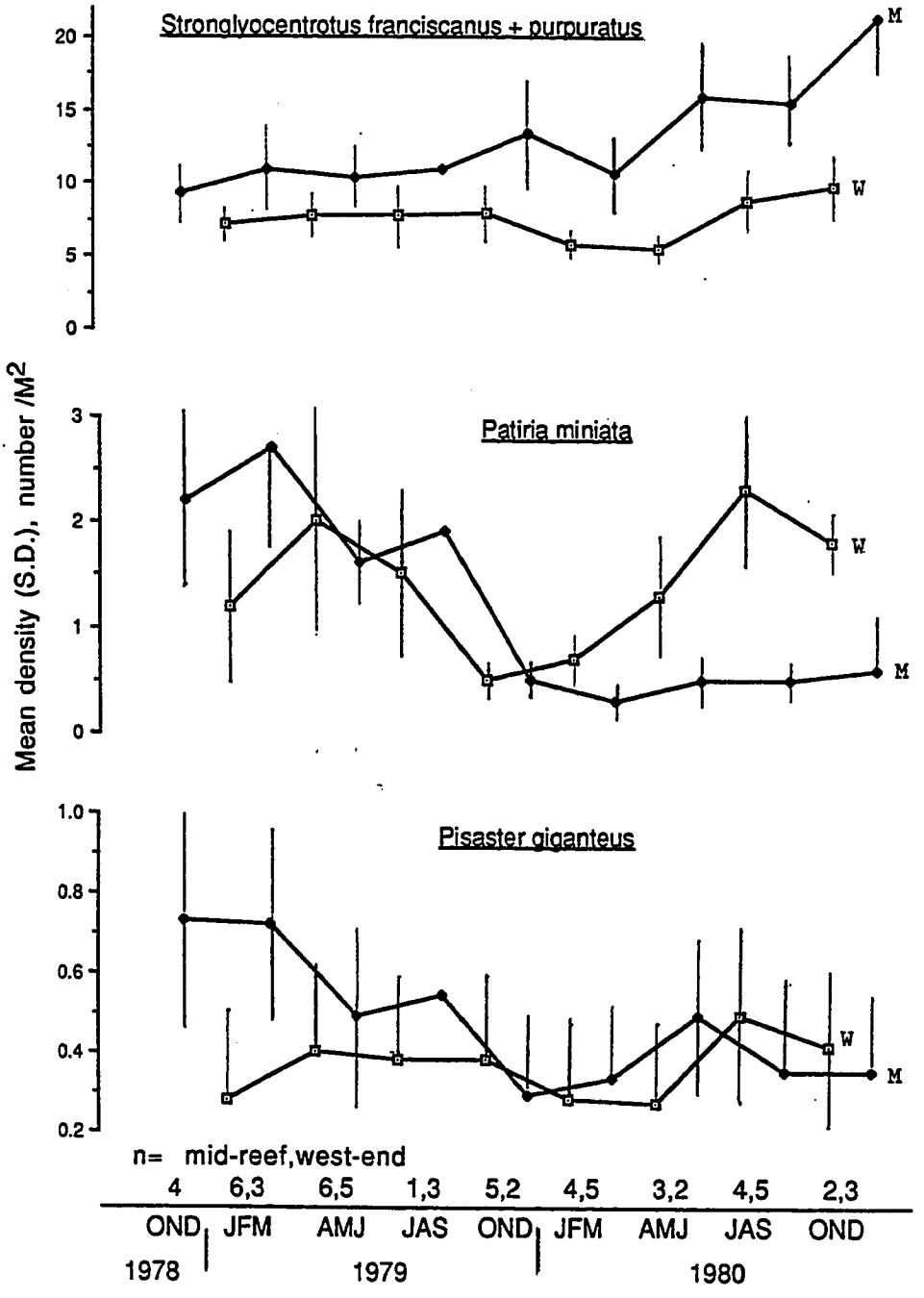

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Fig. 3

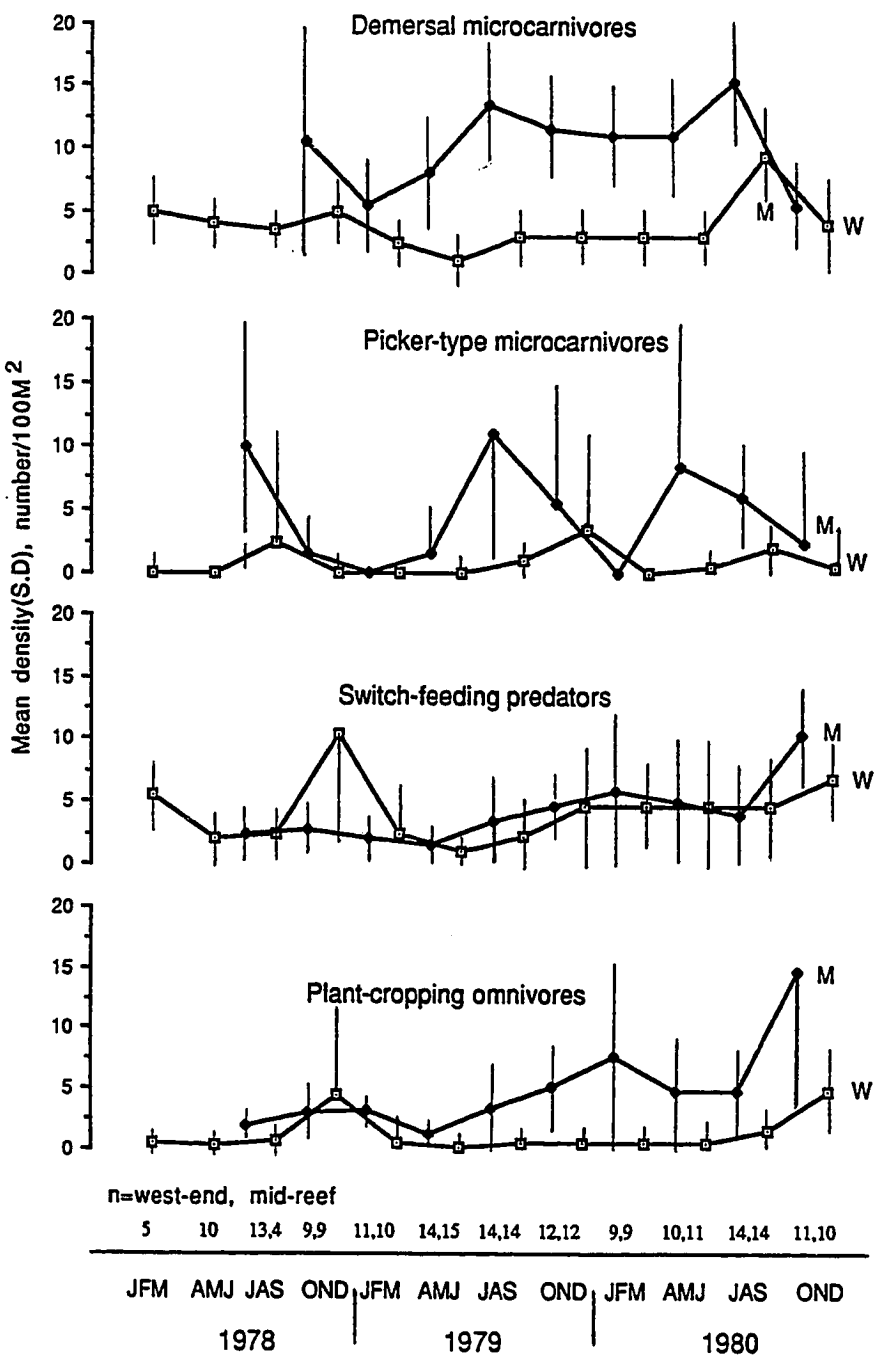

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Fig. 4

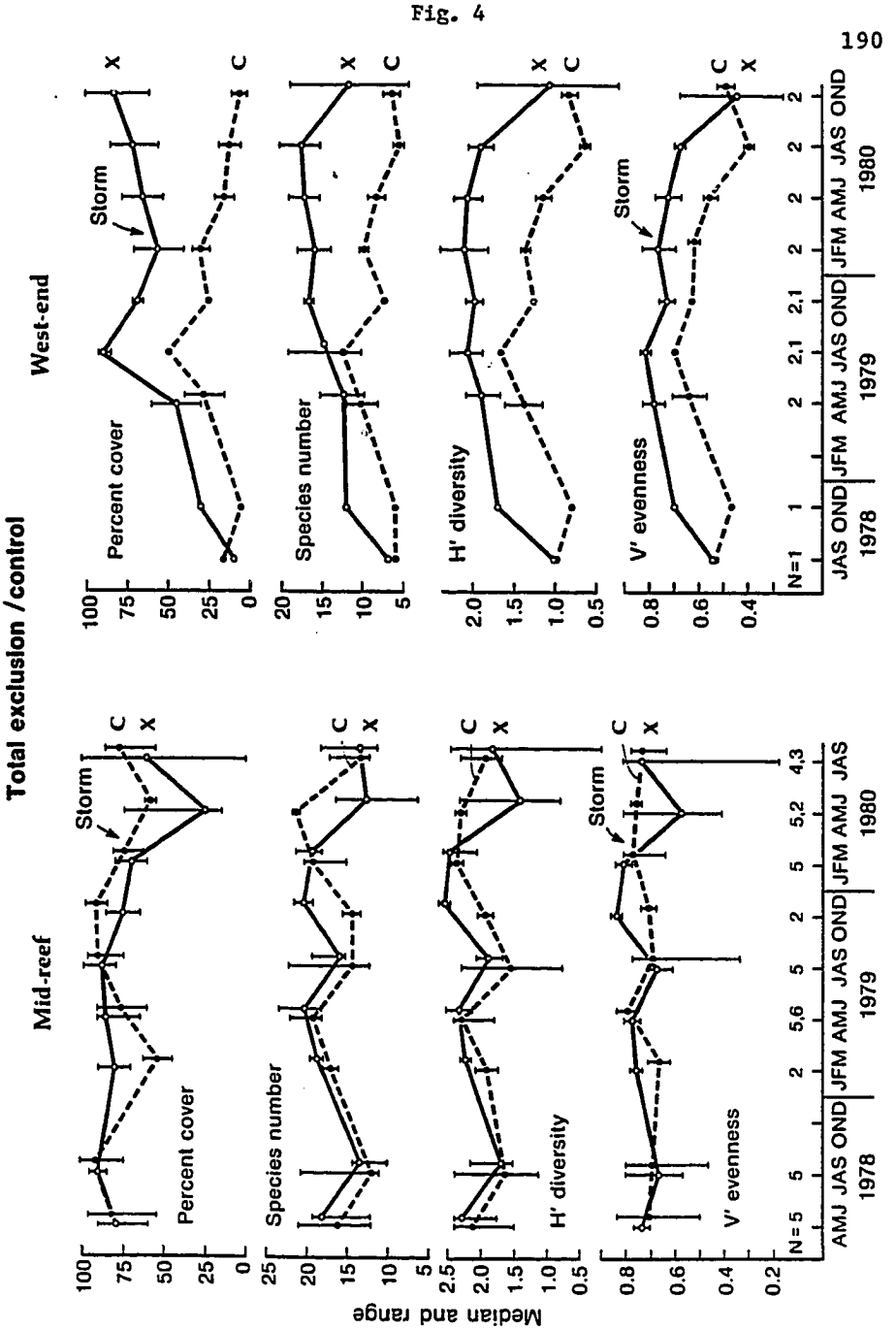

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Fig. 5

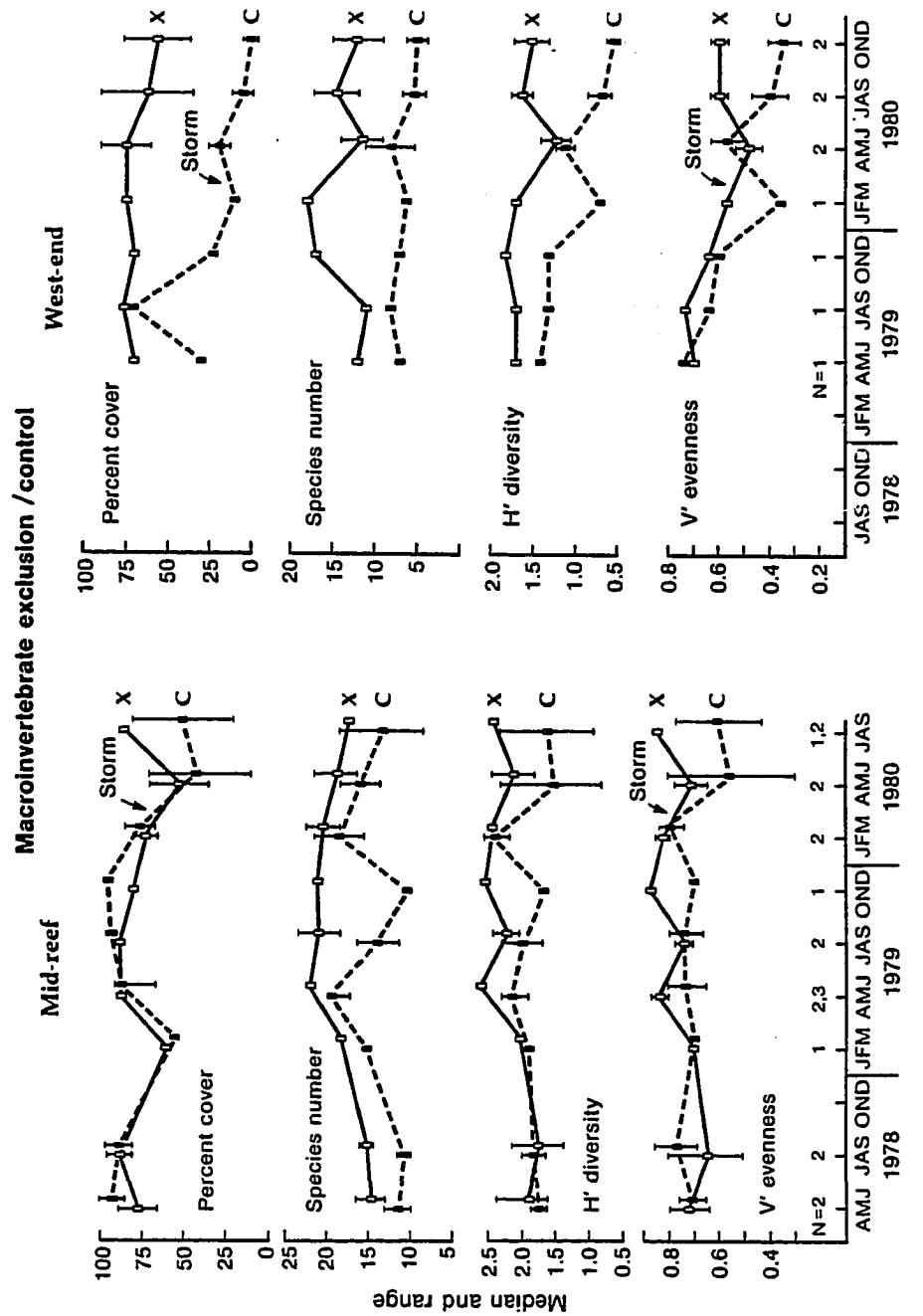

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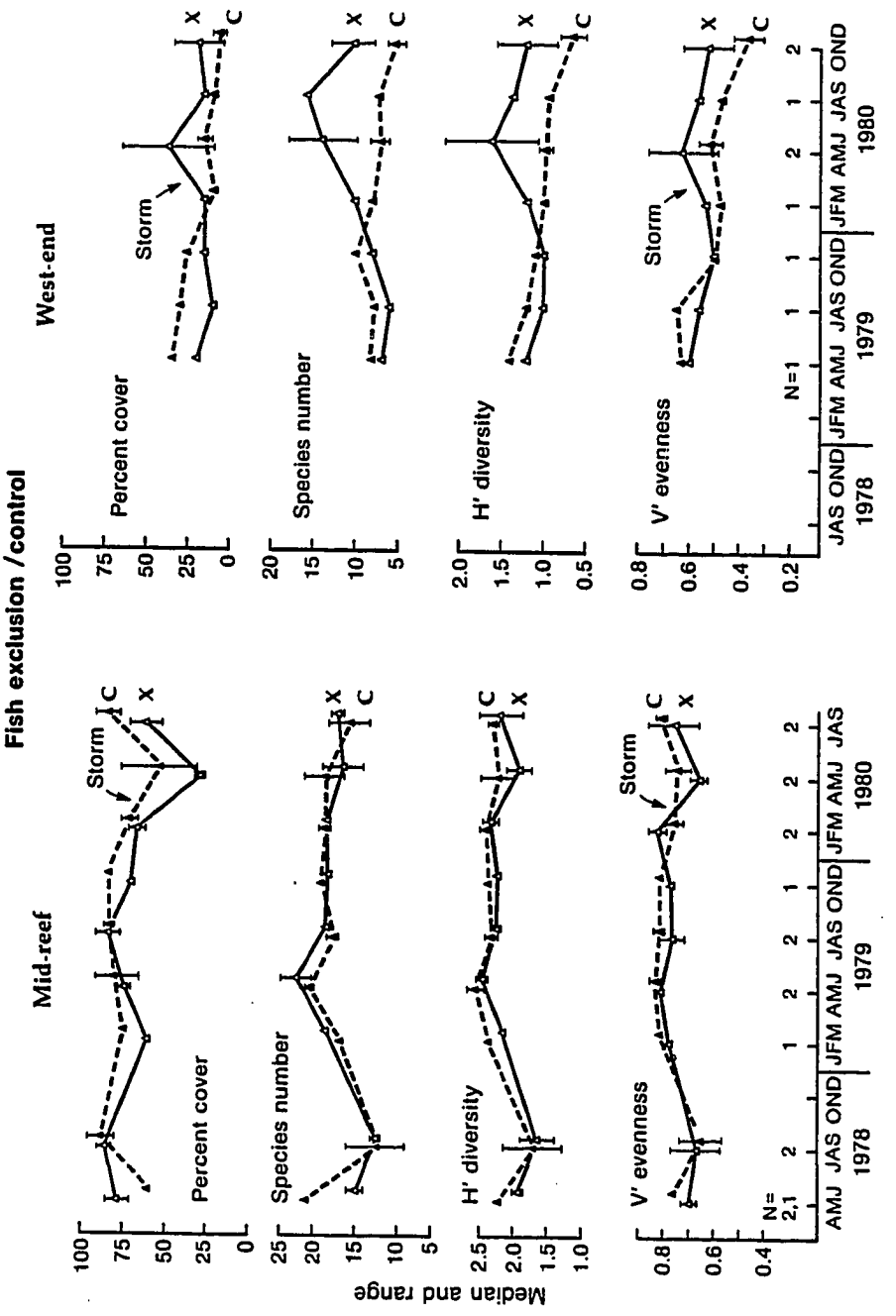
Fig. 6



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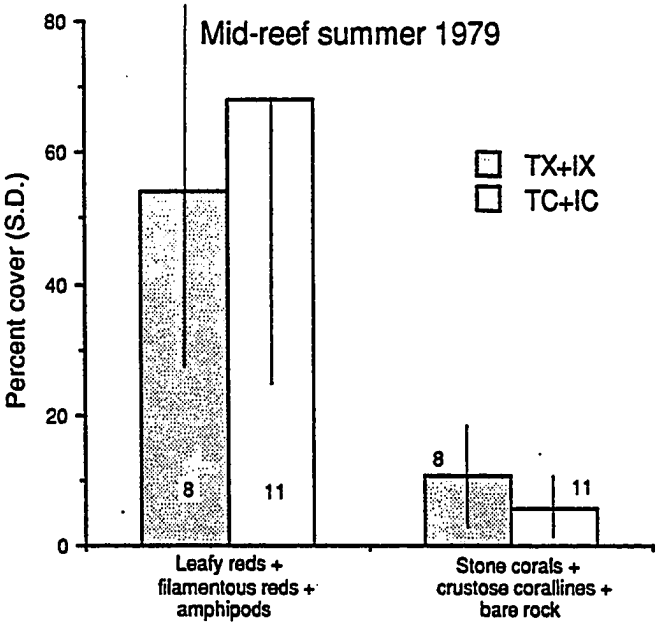

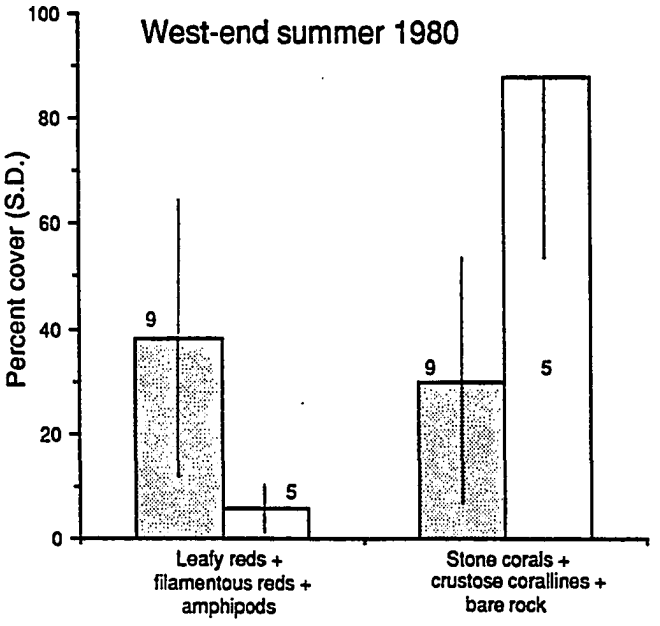

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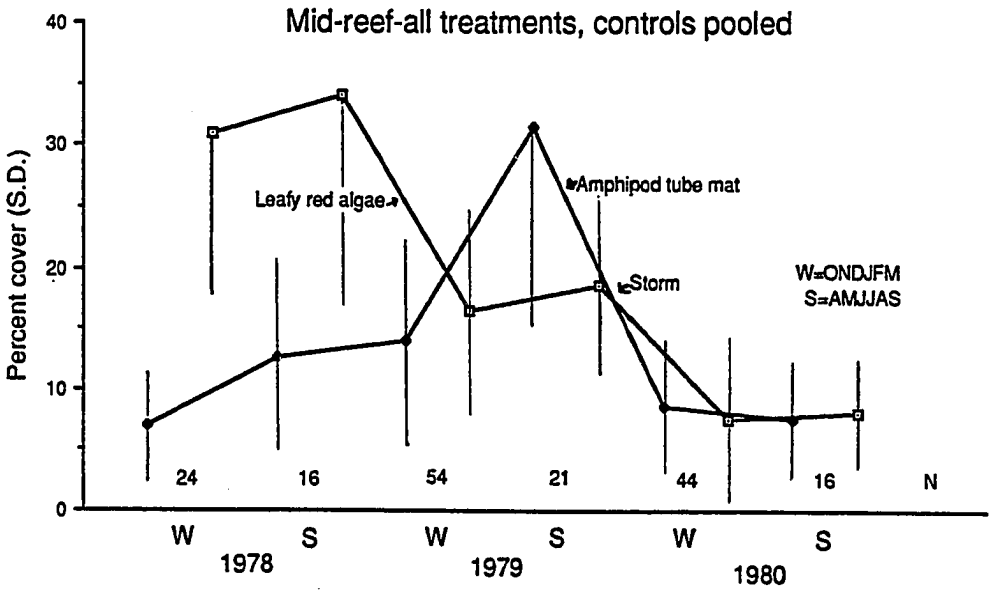
Fig. 8



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