The Community Ecology of Sea Otters

Edited by
G.R. VanBlaricom and J.A. Estes

With 71 Figures

Springer-Verlag
Berlin Heidelberg New York
London Paris Tokyo
7 Effects of Sea Otter Foraging on Subtidal Reef Communities off Central California

D. R. LAUR, A. W. EBELING, and D. A. COON

7.1 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, this Vol.). In the absence of otters, patches of kelp and other erect algae survive only on shallow pinnacles, crevices, and other high-relief zones of turbulence (Estes et al. 1978; VanBlaricom 1984), which are unstable platforms for sea urchins (Dayton 1985b; Laur et al. 1986). Thus, after otters return to their 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, this Vol.). For instance, North (1965) attributed enhancement of canopies of the giant kelp *Macrocystis pyrifera* to the otters' presence, but Miller and Geigel (1973) pointed out that kelp also regrow 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 linza* 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., Ostoff 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 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; see Lawrance 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 (see Foster and Soebel, this Vol.).

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 5 months after otters were first seen in the area during February (S. Bench, Bench Biological & Assoc., Ventura, CA., pers. commun.). 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 understorey 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.

7.2 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. Bench, Bench Biological & Assoc., Ventura, CA., pers. commun.). 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. Location of study reefs (upper arrows) where the effects of sea otters on reef communities were observed in central California north of Pt. Conception and where (lower arrows) the effects were simulated by macroinvertebrates exclusion cages in an urchin-dominated barren ground in southern California near Santa Barbara.

(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 Ebbling and Lauer, this Vol.).

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, cobbles, 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 to 9.0 m deep, sloping 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 had no surface canopy for at least 10 years before the sea otters came (R. Burge, Dep. of Fish and Game, pers. commun.). 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. 7.1). 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. 1980b). 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, Fucus californicus (Ebeling et al. 1985; Ebeling and Lau, this Vol.).

7.3 Methods

7.3.1 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 post-urchin baseline was limited to an initial reconnaissance, as winter’s rough weather prevented further diving before oysters arrived at the sites sooner than expected. Hence, post-urchin sampling in 1976 was limited to a total of only 2 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 surveys and transect construction was expended at LBR, which was to have been the only site monitored. Consequently, post-urchin sampling (macroinvertebrates, algae, benthiic cover) was performed, as originally designed, at LBR only, covering 4 days in July—August 1977 and 2 days in July 1978. By then it was obvious that LBR could show few indirect effects of oyster foraging, and that our remaining limited resources could be better spent elsewhere. Therefore, post-urchin 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 3 years. Observations were begun in 1979, when treatments were installed in a barren 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).

7.3.2 Macroinvertebrate Sampling

For all three sites, yearly samples of sea urchin, sea star, and 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 lens held at the length of a slender rod above a different point, such that about 1 m² of surface was covered. To measure the temporal consistency of macroinvertebrate densities 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.

7.3.3 Algae and Sessile Invertebrates

7.3.3.1 Central Californian Sites

Benthic cover was sampled yearly by photoquadrat. At LBR, 36-54 0.25 m² quadrats were positioned at random intervals along the transect line on reef slope. Coverage of each quadrat was from six 35-mm color slides taken by the Nikonos camera and 0.042 m² close-up film. 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 airlift 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 m²) 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: fleshly 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 (3.44 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 ursiformis, in 18-35 1.0 m² 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 quadrat.

7.3.3.2 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 m² plots of flat overgrazed substrate. In addition, macroinvertebrate densities were monitored yearly out-
Fig. 7.2. Structure of caged treatments for the urchin exclusion experiment at Naples Reef in southern California. A macroinvertebrate exclusion; B fish exclusion; C total exclusion.

inside the plots as explained above. Over the 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 m² base of the pipe frame. The three caged treatments consisted of teapot cages for macroinvertebrate exclusion, bottomless cages for fish exclusion, and complete cages for total exclusion (Fig. 7.2). 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 nonexclusion (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 photo-quadrate taken within the plots and pooled among years (see above).

7.3.4 Fish Sampling

Reef fish assemblages were sampled at LBR and SRR in cine-transects: 2.5-min, super-8, high-speed color movie films taken by divers swimming unidirectionally (Eheling 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 mid-water 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, although occasionally stopped to film all fish sighted in a school. Coverage averaged some 211 m² of projected area (see Ebeling et al. 1980b). Transects per sample ranged from 4-19, as time permitted.

7.3.5 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 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 most 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 dinotransects.

The varying sizes of sampling units presented further problems in statistical comparison, especially between sites. For example, sampling units for macroinvertebrates were either 37 m² (LBR) and 13 m² (SRR, NR) transect bands or 1 m² 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 m² (LBR) vs. 0.042 m² (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 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 arc sine 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 inter-
val 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).

7.4 Results and Discussion

7.4.1 Macroinvertebrates

In April 1977, evidence of sea otter foraging — scattered broken red abalone (*Haliotis rufescens*) shells and red sea urchins (*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, Bench Biological & Assoc., Ventura, Ca., pers. commun.). Subsequent results indicated that the otters continued harvesting abalones and urchins from LBR during the entire 15-month study period. Total exposed red abalones counted in all six transects declined from 26 (0.12 m⁻²) in 1976 before otters arrived, to 4 (0.02) in 1977 three months after, and zero a year later in 1978, when the only abalone seen were 11 individuals located deep in cracks and crevices. This compares with a drop of from 0.75 to 0.01 m⁻² after otters first arrived at Pt. Estero, about 40 km to the north (Estes and VanBlaricom 1985). Post-otter densities of exposed red sea urchins also decreased to nil (0.55 to 0 m⁻²), and purple sea urchins (*Strongylocentrotus purpuratus*) were always rare (Fig. 7.3). Like abalones, the surviving red urchins found refuges, with numbers in crevices increasing from zero in 1976 to 27 in 1977 and 37 in 1978 (as compared with the total of 123 exposed individuals counted in 1976). Similarly in the 1960's after otters returned to reefs near Monterey, broken shells and tests littered the bottom, as abalones and urchins were eventually restricted to crevices (Lowry and Pease 1973; Cooper et al. 1977; Hines and Pearse 1982).

Apparently, however, the otters had not depleted available supplies of abalones and urchins to the point of diversifying their diet to include sea stars (see Riedman and Estes, this Vol.). 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. 7.3). Presumably, otters take sea stars only after the preferred urchins, abalones, and crabs are no longer available (Estes 1968; Estes et al. 1981; Ostfeld 1982).

Even before otter foraging, LBR supported a much lower density of urchins than the larger sites (Fig. 7.3). This may be typical of small high-relief reefs where strong wave action (Linsen 1980) and steep 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, pre-otter SRR had high densities of exposed red urchins (5.2 m⁻²), but within a year after otters arrived at SRR, densities had dropped 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 study in an environment without otters, kelp, or drift algae. 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
Fig. 7.3. Yearly densities of macro-invertebrates at the three study sites. Species are, from left to right: S.p.: purple sea urchin *S. purpuratus*; S.t.: red sea urchin *Strongylocentrotus franciscanus*; P.m.: bat star *Pisaster marmoratus*; P.p.: Pisaster *Pisaster* sea stars. Pooled. Bars: mean 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* = 5), and hatched for 1978 (*N* = 6); Santa Rosa Reef: clear for 1976 before otters (*N* = 361.6 m² photoquadrats), stippled for 1979 (*N* = 4 transects), and hatched for 1980 (*N* = 4); Naples Reef: clear for 1978 (*N* = 3 transects), stippled for 1980 (*N* = 27), and hatched for 1981 (*N* = 29).

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).

7.4.2 Algae and Sessile Invertebrates

7.4.2.1 Central Californian Sites

The flora of LBR was typical of a small exposed rugged reef without a permanent kelp canopy (see Foster and Schiel, this Vol.). Although scattered individuals of *Nereocystis* occurred in the area throughout the study, no obvious surface canopy formed on or about the reef during the post-otter period. Thus, the erect algal cover consisted mostly of low bushy forms and turf, as pavements of crustose coralline algae remained inconspicuous under the cover of erect forms (Fig. 7.4). Dominate species of bushy turf algae included *Gelidium robustum*, *Gigartina exasperata*, *Callophyllis plumosa*, *Rhodymenia pachyphylla*, and *Botryoglossum furcifolium*, all occurring together with articulated coralline algae such as *Calliarthus chelosporoides*. Species common at reef crest — *Gelidium*, *Calliarthus*, *Gigartina*, *Callophyllis*, and the understory kelp *Laminaria dentigena* — flourish in zones of strong water motion and high light levels (Burke and Schultz 1973; Foster and Schiel 1985).
At LBR, benthic cover showed little response because invertebrates had not overgrazed the pre-otter reef. Most components remained essentially unchanged (Fig. 7.4). A slight increase in fleshy red algae and other cover may have occurred independently of any effect of sea otters, 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; M. Foster (pers. commun.) observed similar recruitment pulses in other areas both with and without otters along the central Californian 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 erect-algal cover (Fig. 7.5). A carpet of fleshy red algae and sessile invertebrates, harboring greater abundances of tubicolous amphipods, overgrew the nearly continuous pavement of exposed crustose corallines (Fig. 7.4). A thick canopy of *Nereocystis* measuring some 80 × 100 m had reached the surface within 2 years. Stands of understory kelp (*Laminaria dentigena*), previously restricted to shallow areas of high relief and strong water motion, had spread over all deeper areas of reef flat within three years (Fig. 7.6).

---

**Fig. 7.4.** Yearly percent cover of four categories of benthic organisms at the three study sites. Bars measure back-converted mean percent cover with 95% confidence intervals: **Lone Black Reef**, clear for 1977 (*N* = 54 six-side photoquadrats) and stripped for 1978 (*N* = 56); **Santa Rosa Reef**, clear for 1976 before sea otters (*N* = 24 single-side photoquadrats), stripped for 1977 (*N* = 34), and harvested for 1980 (*N* = 63); **Naples Reef**, clear for the nomewotivation that allowed underwater to enter (*N* = 32 six-side photoquadrats), pooled among years and stripped for the urchin-exclusion plots (*N* = 192).

**Fig. 7.5A-C.** Photographs showing expansion of erect benthic cover on Santa Rosa Reef flat after sea otters arrived in winter, 1977. **A** exposed pavement of crustose coralline algae before otters; **B** fleshy red algae and amphipod tube-mass overgrowing the pavement after otters; **C** stands of the understory kelp *Laminaria dentigena* after otters. **A** and **B** include 0.042 m² of area.
7.4.2.2 Urchin Exclusion Experiment

This post-otter effect was simulated experimentally on a smaller scale at NR. All three categories of erect cover increased markedly in urchin-exclusion plots as the exposed crust was overgrown (Fig. 7.3). Even small kelp plants (Macrocystis pyrifera and Pterygophora californica) appeared in the exclusion cages and were eventually grazed by fish in the topless treatments. Continually grazed by urchins, the remaining plots retained a much larger exposed cover of coralline pavement.

7.4.3 Fish

The large drop in total fish abundance at LBR reflected the virtual disappearance of young rockfish (Sebastes mystinus and S. serranoides) from the post-otter reef between 1977 and 1978 (Fig. 7.7). Such crashes in rockfish recruitment are not unusual along California and may result from climatic shifts and variations in larval abundance, as well as from loss of plant cover in which the young hide from predators (reviewed in Ebeling and Lauer, this Vol.). The young fish had aggregated about the low foliage on the pre-otter reef. A noticeable increase in numbers of surfperch coincided with a vigorous growth of fleshy red algae, especially Gelidium robustum, on reef crest. Striped surfperch (Embiotoca lateralis) foraged about the crest, where they can pick amphipods and other small prey from the algal surfaces (Laur and Ebeling 1983, Schmitt and Holbrook 1984; Ebeling and Lauer 1986).

At SRR, a large maximum in fish abundance was recorded between 1977-1979 on the post-otter reef (Fig. 7.7). Although this may have been a reproductive response to a favorable climatic shift of which we were unaware, it is tempting to attribute the initial rise to an otter effect for two reasons. First, a canopy assemblage of fishes (senza Ebeling et al. 1985a) had begun to form: increasing numbers of seftons (Oxudris cali-
7.5 General Discussion and Conclusions

Sea otter foraging brought about changes in the Santa Rosa Reef (SRR) community similar to changes observed elsewhere off central California. After otters returned to...
the Monterey area during the 1940's and 1950's, 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 Reese 1973). Likewise at SRR, exposed abalones and sea urchins—the otter's preferred food—disappeared, as turf, kelp, and saccate 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 coralline; a canopy of Nereocystis luetkeana formed at the water surface, and an understory of Laminaria dentigena 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 re-establishment of Macrocystis canopies on barren grounds off central California. Using historical data collected from the area, VanBlaricom (1984) composed a qualitative model of this 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 matting system is invaded by Macrocystis, which forms a new surface canopy, has the potential of rapid vegetative regrowth, and may persist indefinitely. Hence at SRR, the Nereocystis canopy, which formed within 2 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 urchin replacement in understory patches requires at least 10 years in the Pt. Loma kelp off southern California, and major shifts 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 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 (this Vol.) contention that reef "types" 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 was 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 wave motion. Carter et al. (1985a) 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 (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/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 2. With steep sides buffeted by a heavy swell, therefore, the latter reefs would 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 the 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 Ebelling et al. 1980), including an obligate canopy species (Hapalichthys 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 abundance was not documented by transects made during the single day's sampling for 1980). As also observed in other Channel Islands localities (Miller and Geibel 1973; Bodkin et al. 1986; Bodkin 1986), blue rockfish (Sebastodes mystinus) were by far the most abundant species in the new SRR kelp forest (Fig. 7.6).

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 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; Bodkin 86).

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 oceanic currents and temperature patterns (Stephens et al. 1984; Cowen 1985; Bodkin et al. 1986; Ebelling and Laur, this Vol., Adult fishes that tap the detritus-based food chain or young fishes that recruit to shelter of the algal canopies are more likely to respond to revegetation (Quast 1966; Miller and Geibel 1973; Burge and Schultze 1973; Estes et al. 1978; Smenstad et al. 1978; Ebelling and Laur, this Vol.). Species are likely to seek cover in the canopies as young and eat tiny
gray living on bushy algae and in the carpeting turf as adults (Stouder 1983; Ebeling and Laur 1986). For instance, overall abundance of Embitterus lateralis increased at SRK as young found refuge in the understory kelp (see Ebeling and Laur 1985) and adults may have encountered greater food supplies related to the increasing algal abundance (see Hilton 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 northern ocean currents or increasing water temperature, as well as changes in cover (reviewed in Ebeling and Laur, this Vol.). Yet to our knowledge, no large shifts in weather pattern, such as El Niño episodes, occurred during the period of study (see Seymour et al. 1984; Ebeling and Laur, this Vol., Fig. 7.2).

The potential for kelp-related enhancement of reef-fish assemblages may be greater in central than southern California, as long as a complex rocky substrate is provided (review in Ebeling and Laur, this Vol.). During a 3-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, this Vol.). In fact, abundances of some species that do not always rely on the kelp forest for food and cover actually increased (see also Quast 1968b). These planktovores (Chromis punctipinnis) and “switch-feeder” (Girella nigricans, Menticirrhus californicus, Paralabrax clathratus) were southern species, rare in central Californian waters north of Point Conception. Although rank orders of fish species abundance for LBR and SRK 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 Schwartz 1973; Bockin 1986).

In perspective, Californian kelp forest 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 1983a; Foster and Schiel 1985, this Vol.; Estes and Harrold, this Vol.; Schiel and Foster 1986). 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 converse 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 disturbances” (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, this Vol.; Foster and Schiel, this Vol.).

7.5.1 Future Research

As pointed out by other authors in this Volume, 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 urchins are excluded from small barren plots are no longer needed to demonstrate this outcome (Foster and Schiel, this Vol.). There is also adequate evidence that urchins 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, this Vol.). 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, this Vol.). What physical settings present barriers to urchin settlement, recruitment, and immigration? (see Laur et al. 1986). Perhaps a reef's aspect ratio (depth of surrounding water/model reef height), average vertical slope (inclination from the horizontal), and percent unconsolidated substrate (gravel 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 comprehensive effect of urchins moving into a new area may be predictable from the distribution of reef types.

As recommended by Duggins (this Vol.), 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. comm.). Determining the role of the canopy's "edge effect" in enhancing fish populations is equally important (Dayton and Tegner 1984a, Dayton 1985). 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. comm.). If this is so, urchins 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 the effect of otter foraging on kelp-forest communities grazed 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 2 years, canopies of algal turf, understory kelp (*Laminaria dentigera*), and surface kelp (*Nereocystis leutheus*) overgrew pavements of crustose coraline 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 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 authors in this Volume, 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.

**Acknowledgments**: We thank J. Kates and G. VanBaren for their good services, and, along with M. Hixon and an anonymous referee, helpful manuscript reviews. M. Cart, D. Reed, and M. Foster provided stimulating discussions. R. Bray, A. Buelow, M. Hixon, R. Larson, M. Love, R. Resley, and G. Trinette helped with the field work. M. Hixon and D. Reed assisted with data analysis. N. Lanner and S. Anderson gave technical assistance with equipment and boat operations. The Marine Science Institute provided administrative support. This material is based on support by the California Department of Fish and Game under Agreement No. 1193 for the central California study and by the National Science Foundation under Grant No. OCE79-25006 for the urchin exclusion experiment.