

The Community Ecology of Sea Otters

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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

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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, crests, 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 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, this Vol.). For instance, North (1965) attributed enhancement of canopies of the giant kelp *Macrocystis pyrifera* to the otters' presence, but Miller and Geibel (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 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 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, 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. Benech, Benech 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 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.

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. Benech, Benech 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 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 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 Ebeling and Laur, 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, 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 to 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 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, *Pterygophora californica* (Ebeling et al. 1985; Ebeling and Laur, 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 pre-otter baseline was limited to an initial reconnaissance, as winter's rough weather prevented further diving before otters arrived at the sites sooner than expected. Hence, pre-otter 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 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 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 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 3 years. Observations were begun in 1979, when treatments were installed in a barrens 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 × 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 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 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: 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 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-

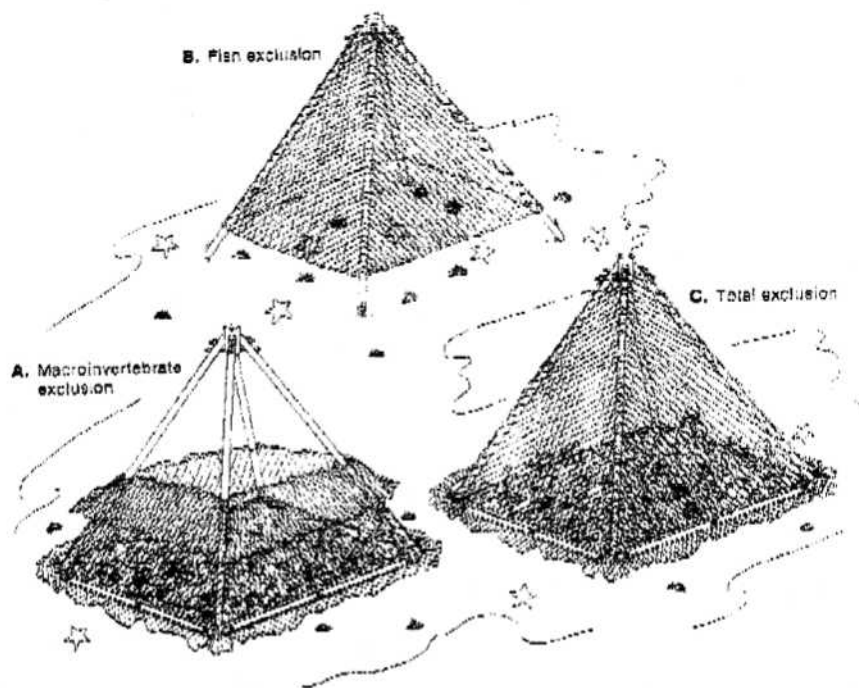


Fig. 7.2. Structure of caged treatments for the urchin exclusion experiment at Naples Reef in southern California. A macroinvertebrate exclusion; B fish exclusion; C total exclusion

side 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 topless 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-quadrats 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 cinetransects: 2.5-min, super-8, high-speed color movie films taken by divers swimming unidirectionally (Ebeling et al.

