Restored Top Carnivores as Detriments to the Performance of Marine Protected Areas Intended for Fishery Sustainability: a Case Study with Red Abalones and Sea Otters

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Abstract: *Marine protected areas are possible solutions to the problems of protecting the integrity of marine ecosystems and of sustaining harvested marine populations. We report demographic data for red abalones (* Haliotis rufescens*) at nine sites along the California coast. Six of our sites are within marine protected areas, and four of those six sites are occupied by sea otters (* Enhydra lutris*). Sea otters are known abalone predators and are believed to have an important role in facilitating biodiversity within coastal kelp forest communities along the North Pacific Rim. We asked whether marine protected areas intended to conserve ecosystems are compatible with use of marine protected areas for abalone fishery sustainability. We found that both sea otters and recreational harvest alter the density, size distribution, and microhabitat distribution of red abalones in qualitatively similar ways. Red abalone populations in marine protected areas outside the current sea otter range have higher density, are composed of larger individuals, and occur in more-open microhabitats compared with populations in locations lacking sea otters but subject to harvest and with populations in locations with sea otters. The effects of sea otters are stronger than the effects of harvest. Characterization of harvest effects on density may be confounded by other uncontrolled factors. We conclude that coastal marine protected areas off California cannot enhance abalone fisheries if, in the interest of ecosystem integrity, they also contain sea otters. Where restored top carnivores limit the sustainability of commodity harvest, it may be possible to resolve conflicts with two categories of spatially segregated, single-use marine protected areas, one focusing on ecosystem restoration and the other on fishery development.*

Carnívoros Restaurados como Detrimento del Funcionamiento de Áreas Marinas Protegidas para Pesquerías Sustentables: un Estudio de Caso con Abulón Rojo y Nutrias Marinas

Resumen: *Las áreas marinas protegidas son posibles soluciones a los problemas de protección de la integridad de ecosistemas marinos y del sostenimiento de poblaciones marinas explotadas. Presentamos datos demográficos de abulón rojo (* Haliotis rufescens*) en nueve sitios a lo largo de la costa de California. Seis de nuestros sitios están dentro de áreas marinas protegidas, y cuatro de esos seis sitios están ocupados por nutrias marinas (* Enhydra lutris*). Se sabe que las nutrias marinas depredan al abulón y se considera que tienen un importante papel en la facilitación de la biodiversidad en comunidades costeras de bosques de ocle a lo largo del Pacífico Norte. Nos preguntamos si las áreas marinas protegidas proyectadas para conservar ecosistemas son compatibles con el uso de áreas marinas protegidas para la pesquería sustentable de abulón. Encontramos que tanto las nutrias marinas como la extracción recreativa alteran la densidad, la distribución de*

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tamaños y la distribución del microhábitat de los abulones rojos de manera cualitativamente similar. Las poblaciones de abulón rojo en áreas marinas protegidas fuera del rango de distribución de nutrias marinas tienen una mayor densidad, están compuestas por individuos más grandes y ocurren en microhábitats más abiertos en comparación con las poblaciones de sitios carentes de nutrias pero sujetas a explotación y con poblaciones en sitios con nutrias. Los efectos de las nutrias son mayores que el efecto de la explotación. La caracterización de los efectos de la explotación sobre la densidad puede confundirse con otros factores no controlados. Concluimos que las áreas marinas protegidas en las costas de California no pueden incrementar la pesquería de abulón si, por interés en la integridad del ecosistema, también contienen nutrias marinas. En aquellas zonas donde los carnívoros superiores restaurados limitan la sustentabilidad de la extracción de recursos, podría ser posible resolver conflictos con dos categorías de áreas marinas protegidas espacialmente segregadas, de uso único, una enfocada a la restauración del ecosistema y la otra en el desarrollo de las pesquerías.

Introduction

Marine protected areas are segments of marine habitats within which human behavior is regulated for purposes linked to biological conservation, and they have become a common and widely acclaimed technique for achieving various conservation goals. Marine protected areas are created for many purposes, the most frequent of which are protection of habitats and ecological processes, preservation of depleted species, and conservation of harvestable resources for sustained exploitation (Agardy 1994; Jones 1994; Gubbay 1995; Clark 1996; De Fontaubert et al. 1996; Hockey & Branch 1997; Done & Reichelt 1998).

We considered abalones off California as a case study to examine the degree to which natural ecological processes acting across a wide range of environmental variation impose constraints on the performance of marine protected areas. Our study is of particular interest to marine conservation science because we investigated the possibility that multiple-use goals for single marine protected areas may be mutually exclusive as a result of natural ecological interactions.

Fisheries for abalones (gastropod mollusks of the family Haliotidae) are common in coastal marine habitats, particularly in temperate latitudes (Shepherd et al. 1992). Largely as a consequence of poorly understood life-history attributes and persistently intense consumer demand, abalone fisheries are prone to collapse (Estes & VanBlaricom 1985; Tegner 1989; Breen 1992; Tegner et al. 1992, 1996; Shepherd & Brown 1993). Marine protected areas have been offered in several locations as a possible solution to the problem of sustainability of abalone fisheries (Tegner et al. 1992, 1996; Tegner 1993; Shepherd & Brown 1993). Adult abalones in California are effectively sedentary, and protection of a broodstock from harvest within protected areas is seen as a method for promoting the export of planktonic larvae, enhancing the size and productivity of harvested populations in unprotected locations.

Sea otters (*Enhydra lutris* [L.]) are known to forage on abalones in coastal habitats off California (Ebert 1968; Wild & Ames 1974; Estes et al. 1981; Ostfeld 1982). Sea otters were hunted nearly to extinction throughout their range in the coastal waters of the North Pacific Rim in the eighteenth and nineteenth centuries but recovered following a hunting moratorium imposed in 1911 by Article V of the Convention between the United States, Great Britain, Russian and Japan for the Preservation and Protection of Fur Seals (1911; Ogden 1941; Barabash-Nikiforov et al. 1947; Kenyon 1969). Recovery of sea otter populations off California during the 1900s (Estes 1990) resulted in conflicts with commercial and recreational abalone fisheries that developed while sea otters were rare (Estes & VanBlaricom 1985). As a consequence, there is a widespread perception that fisheries for abalones are not sustainable in the presence of sea otters (Tegner et al. 1992; VanBlaricom & Hardy 1992). Red abalones (*Haliotis rufescens* Swainson) have been of particular concern because of their high commercial value and because their geographic range (west coast of North America from lat. 28° to 41° N; Geiger 2000) lies entirely within the original range of sea otters.

Quantitative documentation of the effect of sea otter predation on red abalone populations is limited to longitudinal studies in two locations. Near Point Estero (lat. 35.5° N, 121.1° W), Wendell (1994) presented survey data for a red abalone population that once supported a valuable fishery. The fishery collapsed soon after the recovering sea otter population returned to the area during the 1960s, and red abalones were observed to be a primary prey for sea otters at the time the fishery failed. Wendell's data indicate tenfold reductions in abalone densities in association with the return of sea otters. Wendell concluded that the decline in Point Estero abalone stocks was caused primarily by sea otters and not commercial harvesters. The second location is the Hopkins Marine Life Refuge, off Monterey County (Table 1). Data from the refuge (Lowry & Pearse 1973; Cooper et

Table 1. Locations, status of sea otter populations, and "no-take" status of sites sampled off California during the study.

	Location	*Presence of otters*	*Status as "no-take" area for abalones*	*Designation date as "no-take" area**
Sonoma County				
Gerstle Cove Reserve	38.6° N, 123.4° W	no	yes	1971
outside Gerstle Cove	38.6° N, 123.5° W	no	no	na
Stillwater Cove	38.6° N, 123.3° W	no	no	na
Bodega Marine Life Refuge	38.3° N, 123.2° W	no	yes	1965
outside Bodega Marine Life Refuge	38.3° N, 123.1° W	no	no	na
Monterey County				
Hopkins Marine Life Refuge	36.6° N, 121.9° W	yes	yes	1984
Pacific Grove Marine Gardens Fish Refuge	36.6° N, 122.0° W	yes	yes	1984
Stillwater Cove (in the Carmel Bay Ecological Reserve)	36.6° N, 121.5° W	yes	yes	1976
Point Lobos Ecological Reserve	36.5° N, 121.9° W	yes	yes	1973

**Abbreviation: na, not applicable.*

al. 1977; Hines & Pearse 1982; Pollard 1992) suggest that sea otters set an upper size limit and impose stringent microhabitat constraints on red abalone populations. Interpretation of data from the refuge is hindered by the lack of quantitative information on abalone demography gathered prior to the return of sea otters to the area in the late 1960s.

We evaluated the effects of sea otters and human harvesters on red abalone populations in California. Our goals were to (1) compare the demographic characteristics of red abalone populations among nine locations off California that vary in harvest intensity and sea otter presence; (2) use our results to determine whether marine protected areas can be an effective measure toward sustainable abalone harvest in biological communities with a full complement of trophic levels; and (3) consider the implications of our results for relating marine protected areas to the conservation goals of human coastal communities.

Methods

Study Locations

We surveyed red abalone populations at nine study sites (Table 1), five off Sonoma County and four off Monterey County. Six of the sites (two off Sonoma and all four of the Monterey sites) are protected areas where harvesting of abalones is prohibited (Table 1; McArdle 1997). At the remaining three sites, recreational harvesting of abalones is permitted and is subject to regulation by season, bag limit, size (legal minimum is 178 mm, measured as maximum shell length), and method of diving. Sea otters currently are absent from the Sonoma area, but all Sonoma sites are within the original range of sea otters. The four sites off Monterey County are occupied by sea otters, and there is no indication of variability among Monterey sites in accessibility to foraging sea otters.

Commercial harvest and the use of scuba gear for recreational harvest have been prohibited for red abalones off northern California, including all of our study sites, since 1945. The intensity of recreational abalone harvest likely varies among sites off Sonoma County according to accessibility, wave exposure, and threat of shark attack. Stillwater Cove, Sonoma County (we used a second site also named Stillwater Cove off Monterey County) is the most frequently harvested site, and the site outside the Bodega Marine Life Refuge is the least frequently harvested.

Six of the nine sites are comparable with respect to substratum and kelp community structure. Substrata at these sites are granitic boulders and outcrops, including numerous crevices and cryptic interstices interspersed with coarse sand and gravel. The six sites support canopy-forming kelps (*Macrocystis pyrifera* [L.] in Monterey sites, *Nereocystis luetkeana* [Mertens] in Sonoma), understory kelps, and ground cover and turf dominated by red algae, sponges, tunicates, and solitary corals.

Three sites differ from the general pattern. The site inside the Bodega Marine Life Refuge has lower relief than other sites, with predominantly sandy substrata between depths of 4.5 and 9 m. Canopy-forming kelps are lacking at this site, and unlike at other sites the predominant understory kelp is *Egregia* sp. At our site outside the Bodega Marine Life Refuge, the substratum is large, granitic platforms cut by long, narrow sand-covered channels running perpendicular to shoreline. Kelp abundance is low and sea urchin (*Strongylocentrotus franciscanus* [Agassiz]) abundance is high compared with those of other study sites (Pollard 1992). Sea urchin abundance also is high at our site outside Gerstle Cove, especially at depths between 7.5 and 10 m, where kelps are absent and urchin densities exceed 5 individuals/m^2.

Sampling

We sampled populations of red abalones during scuba dives between September 1990 and September 1991. Surveys were done in two depth strata, shallow (3–4.5 m) and deep (7.5–10 m). The shallow stratum was thought a priori to be well within the diving range of most recreational abalone fishers and the deeper stratum within the range only of well-conditioned experienced divers, a distinction subsequently documented by Karpov et al. 1998. Both strata are easily within the diving capabilities of sea otters (Kenyon 1969).

Sampling began with arbitrary placement of a 30-m line parallel to depth contours within the predetermined depth strata. The line was divided into six intervals 5 m in length. Within each interval a 10-m line was extended perpendicularly from a randomly selected point in a randomly selected direction. Abalones observed within 1 m on either side of the 10-m line were counted, measured with calipers (maximum shell diameter to the nearest 0.5 cm), and categorized by microhabitat. We used two qualitative categories of microhabitat, open and crevice-cryptic. The open category describes individuals on open rock faces, easily located and removed by human fishers or sea otters regardless of inclination. The crevice-cryptic category describes abalones in crevices judged to provide refuge both from human fishers and sea otters.

At each study site we completed samples of two replicate 30-m lines within each depth stratum. Thus we surveyed 480 m^2 of substratum at each site that was partitioned as follows: 2 depth strata $\times$ 2 transects per stratum $\times$ 6 plots (2 $\times$ 10 m each) per transect $\times$ 20 m^2 per plot. We were able to complete only 11 plots in the shallow stratum at the site inside Gerstle Cove. We were able to add a third replicate transect (6 additional plots) in the shallow stratum at Stillwater Cove, Sonoma County. We were not able to sample the deep stratum inside the Bodega Marine Life Refuge because of insufficient abalone habitat. We did not sample the shallow stratum outside the Bodega Marine Life Refuge because of safety considerations.

Analyses

We used analysis of variance (ANOVA) to determine whether there were differences in the density and size of red abalones among sites and depths. We did not sample locations open to recreational abalone harvesting with sea otters present because of limited access, limited range in our skiffs, and safety considerations. The number of replicate samples within each site was unequal, so ANOVAs were run twice, with each main factor considered first in one model. For each factor, we report the result for the analysis in which that factor was considered first. We evaluated the effects of sea otters, recreational harvest, and unidentified site factors on density and size with Scheffe's multiple contrasts. For density, the dependent variable ("count") was the number of individual abalones observed in 2 $\times$ 10 m transect segments as defined above. Because our count data were right-skewed, we log-transformed the data ($\ln[\text{count} + 1]$) before running the ANOVA. For size, the dependent variable ("size") was the measured maximum shell dimension in millimeters, rounded to the nearest 5 mm. Our size data did not require transformation to approximate normality. We used a significance level of $\alpha = 0.05$ for all analyses. All statistical analyses were conducted with S-Plus statistical software (MathSoft 1998). We did not conduct statistical analyses of the microhabitat distributional data because principal patterns in the data were obvious without the support of analysis. In addition, classification criteria for microhabitat categories included an arbitrary component. Thus, rigorous analysis of distributions across category seemed inappropriate.

Results

Densities of Red Abalones

Mean densities of abalones by site off Sonoma County ranged from 11.5 to 18.1 individuals per 2 $\times$ 10 m plot, excluding the site outside the Bodega Marine Life Refuge where no abalones were observed (Fig. 1). The highest local densities (26.1 individuals per plot) occurred at the site outside Gerstle Cove in the shallow depth stratum, but mean densities for sites, with depth strata lumped, were highest in reserve sites protected from human harvest. Means by site in Monterey ranged from 0.1 to 3.6 individuals per plot (Fig. 1). The highest local densities (5.7 individuals per plot) occurred in the Hopkins Marine Life Refuge in the 7.5- to 10-m depth stratum. Densities at the refuge were comparable to or greater than densities reported for otter-free areas historically subject to commercial abalone fishing (Tegner et al. 1989; Wendell 1994), although abalones in the refuge were smaller than minimum size limits for commercial or recreational harvest.

There was significant interaction between site and depth with regard to abalone density (Table 2). Thus, differences between sites were not consistent across depths, but two patterns were apparent (Fig. 2). In the absence of recreational harvest, the effects of sea otters on abalone density were greater in the shallow than in the deep stratum. In the absence of sea otters, access to recreational harvest had a greater apparent effect on densities in the deep than in the shallow stratum.

For both depth strata, multiple comparison tests (Table 3; Fig. 2) indicated significant effects of sea otters. Access to recreational harvest had a significant apparent effect only in the deep stratum for Sonoma sites. In the

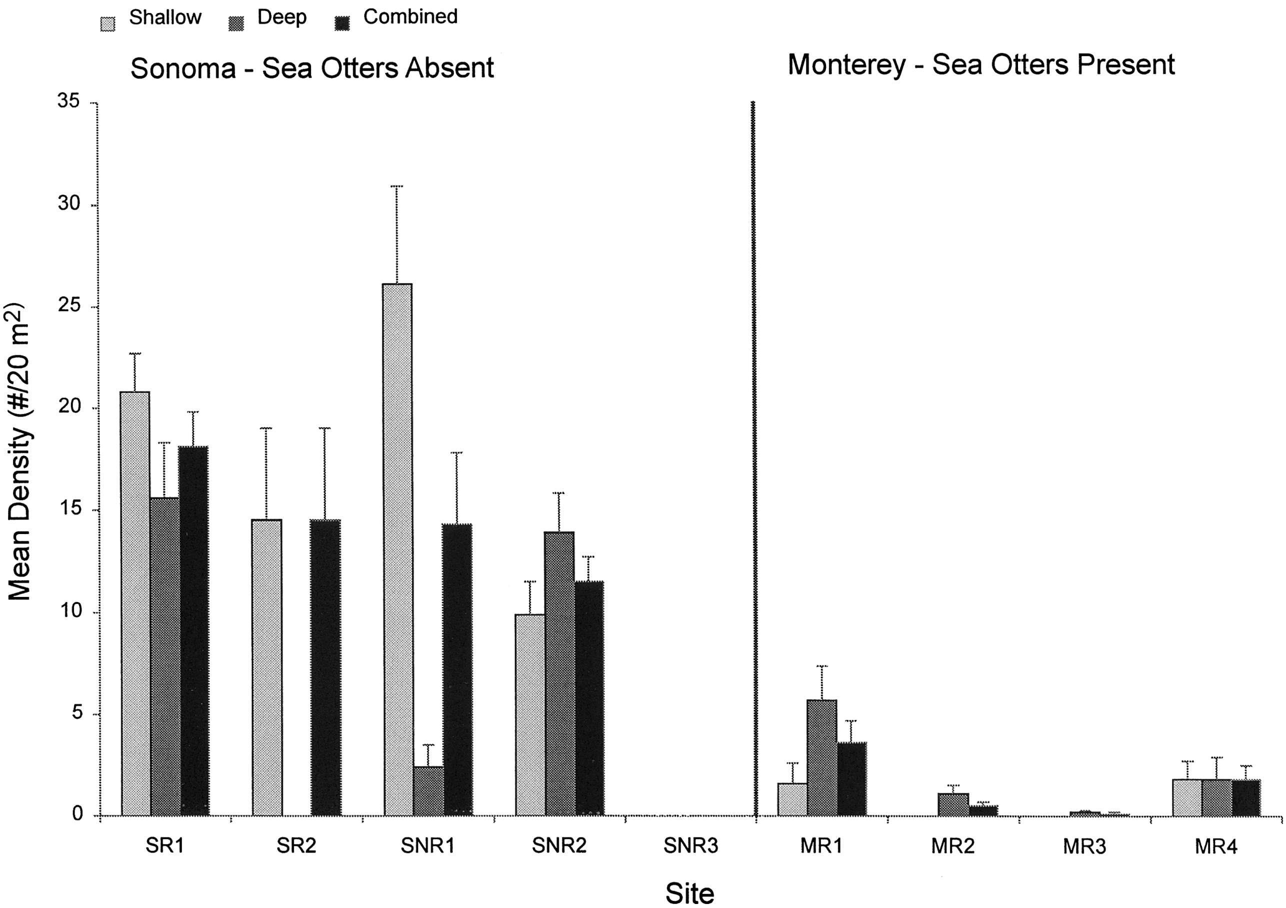

Figure 1. Mean densities (#, number) of red abalones, by stratum and site, observed during sampling in the study sites off California. Lines extending from bars indicate 1 SE. Sites SR1 (Gerstle Cove) and SR2 (Bodega Marine Life Refuge) are in "no-take" areas for abalones. Sites SNR1 (outside Gerstle Cove), SNR2 (Stillwater Cove-Sonoma), and SNR3 (outside Bodega Marine Life Refuge) are open to taking of abalones by recreational fishers. Remaining sites (MR1, Hopkins Marine Life Refuge; MR2, Pacific Grove Marine Gardens Fish Refuge; MR3, Stillwater Cove-Monterey; MR4, Point Lobos Ecological Reserve) are in no-take areas.

deep strata, the Hopkins Marine Life Refuge had significantly higher density than Stillwater Cove, Monterey County, within the Monterey sites, and Stillwater Cove, Sonoma County, had significantly higher density than other sites (outside Gerstle Cove and outside Bodega Marine Life Refuge) open to human harvest. There were no other differences between sites within treatment groups.

Size Distributions of Red Abalones

Data from shallow strata in sites outside of refuges off Sonoma County were dominated by smaller individuals, whereas data from shallow strata inside refuges indicated an accumulation of larger individuals (Fig. 3). The latter trend was particularly evident in data from inside the Bodega Marine Life Refuge, where the majority of individuals were larger than 178 mm. Abalones in the Bodega Marine Life Refuge also appeared to have much deeper shells than those from other sites. Deep, bowl-shaped shells may indicate individuals of advanced age (E. E. Ebert, personal communication).

Mean shell lengths by site in Monterey ranged from 58 to 99 mm (Fig. 3). We found only one individual (out of 132) larger than the legal minimum size for harvest (Fig. 3). Our measured mean lengths for the Hopkins Marine Life Refuge (111 mm for shallow strata, 96 mm for deep) were substantially higher than mean values reported previously (75 mm; Hines & Pearse 1982).

Mean shell lengths by site for Sonoma ranged from 142 to 190 mm (Fig. 3). Mean shell lengths exceeded the legal minimum in both refuge sites. Mean shell lengths for sites outside the refuges averaged 35 mm below the legal limit for harvest and were 38–48 mm smaller than means for sites within refuges. The proportion of individuals exceeding the legal minimum for harvest was higher in refuge sites (63–83%) than in nonrefuge sites (18–26%; Fig. 3).

Table 2. Results of analysis of variance (ANOVA) for abalone density data.

Analysis/factor	*df*	*Sum of squares*	*Mean square*	F	p
ANOVA 1*					
site	8	205.35	25.67	54.40	0
depth	1	0.41	0.41	0.87	0.35
site-by-depth interaction	6	41.88	6.98	14.79	0
residuals	181	85.41	0.47	—	—
ANOVA 2*					
depth	1	8.89	8.89	18.84	2.36×10^{-5}
site	8	196.87	24.61	52.15	0
depth by site interaction	6	41.88	6.98	14.79	0
residuals	181	85.41	0.47	—	—

**See text for additional details of analytical protocol.*

Table 3. Results of multiple comparisons for densities and sizes of red abalones.*

Category	*Marine protected areas without sea otters*	*Unprotected areas without sea otters*	*Marine protected areas with sea otters*
Mean abalone density in shallow stratum	17.5 (A)	15.4 (A)	0.9 (B)
Mean abalone density in deep stratum	15.6 (A)	5.4 (B)	2.2 (B)
Mean abalone size	183 (A)	142 (B)	94 (C)

**Data are mean values by indicated category. Densities are mean counts per 2 × 10 m plot. Sizes are maximum shell diameter (mm) rounded to the nearest 5 mm. Letter codes (A, B, C) indicate groups within which mean values are not significantly different.*

The main effects, site and depth, were significant in ANOVAs for abalone sizes (Table 4). Interaction was not significant (Table 4), so size data were combined across depth strata for multiple comparisons among sites. Results of multiple comparisons (Table 3; Fig. 2) indicated that abalones were significantly smaller outside of Sonoma marine protected areas than within, and that abalones were significantly smaller at Monterey sites than at Sonoma sites.

Microhabitat Distribution of Red Abalones

The pattern of microhabitat use by red abalones varied substantially between Monterey sites and Sonoma sites and between sites off Sonoma County (Fig. 4). About 90% of observed abalones in Monterey sites were categorized as crevice inhabitants. At Sonoma sites, the proportion of abalones in crevices was substantially higher at sites outside refuges than in refuge sites. For example, in shallow strata at the Gerstle Cove Reserve, 25% of observed abalones were categorized as crevice dwellers, whereas in shallow strata

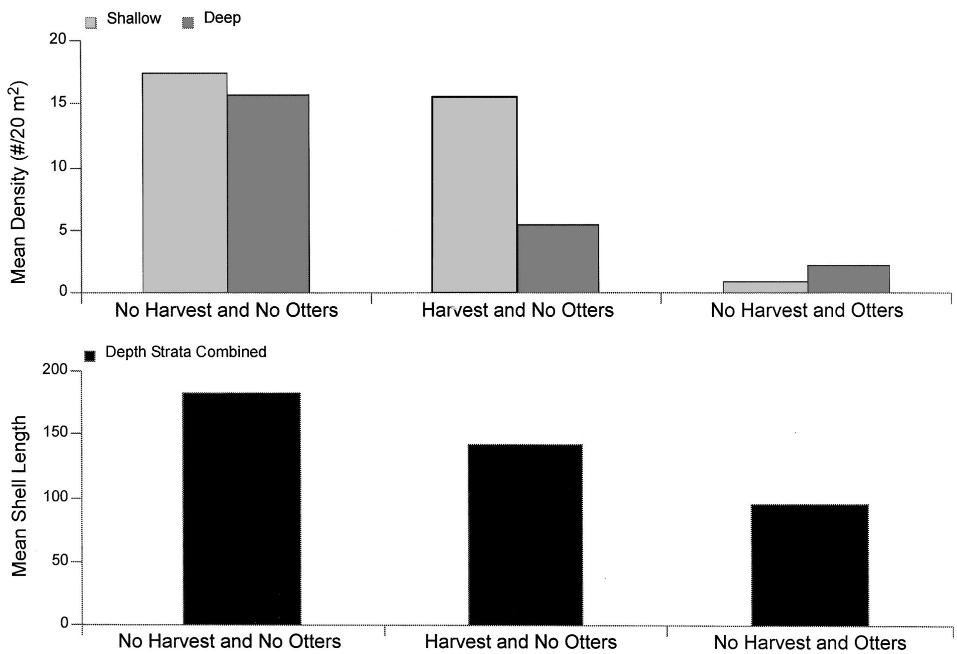

Figure 2. Mean densities (#, number) and mean shell lengths (maximum shell diameter in millimeters) by treatment category of red abalones observed during sampling in the study sites off California. Mean densities for shallow and deep strata are shown separately because of a significant interaction of sites and depths (see Table 2). Mean values of strata are combined for shell length because of the absence of significant interactions of site and depth.

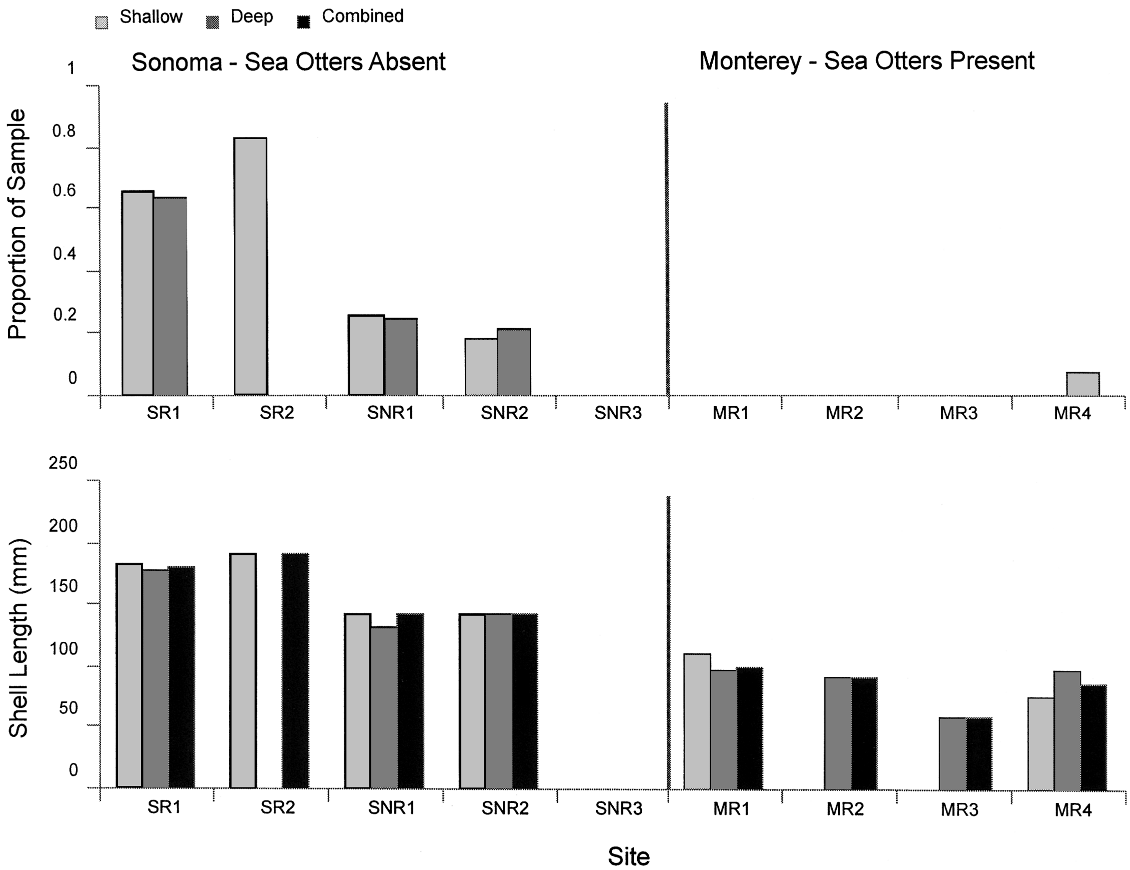

Figure 3. Mean proportions of sampled red abalones above the minimum shell length (178 mm) for legal recreational harvest (upper plots), and shell lengths (mean maximum shell diameter; lower plots) of sampled red abalones, by site and depth stratum, observed during sampling in the study sites off California. Site codes are defined in Fig. 1.

outside of Gerstle Cove Reserve, 63% were in crevices. At nonrefuge sites in Sonoma, the proportion of abalones in crevices was much higher in shallow strata than in deeper strata.

Discussion

Our results suggest that sea otters and recreational harvest have qualitatively similar effects on the population

Table 4. Results of analysis of variance (ANOVA) for abalone size data.

Analysis/factor	*df*	*Sum of squares*	*Mean square*	F	p
ANOVA 1 (with interaction)*					
site	7	1,064,380	152,054	116.14	0
depth	1	2,600	2,600	1.99	0.16
site × depth	4	9,272	2,318	1.77	0.13
residuals	1,320	1,728,212	1,309	—	—
ANOVA 1 (without interaction)*					
depth	1	54,060	54,060	41.19	1.92×10^{-10}
site	7	1,012,921	144,703	110.27	0
residuals	1,324	1,728,212	1,312	—	—
ANOVA 2 (without interaction)*					
site	7	1,064,380	152,054	115.87	0
depth	1	2,600	2,600	1.98	0.16
residuals	1,324	1,737,484	1,312	—	—

**See text for additional details of analytical protocol.*

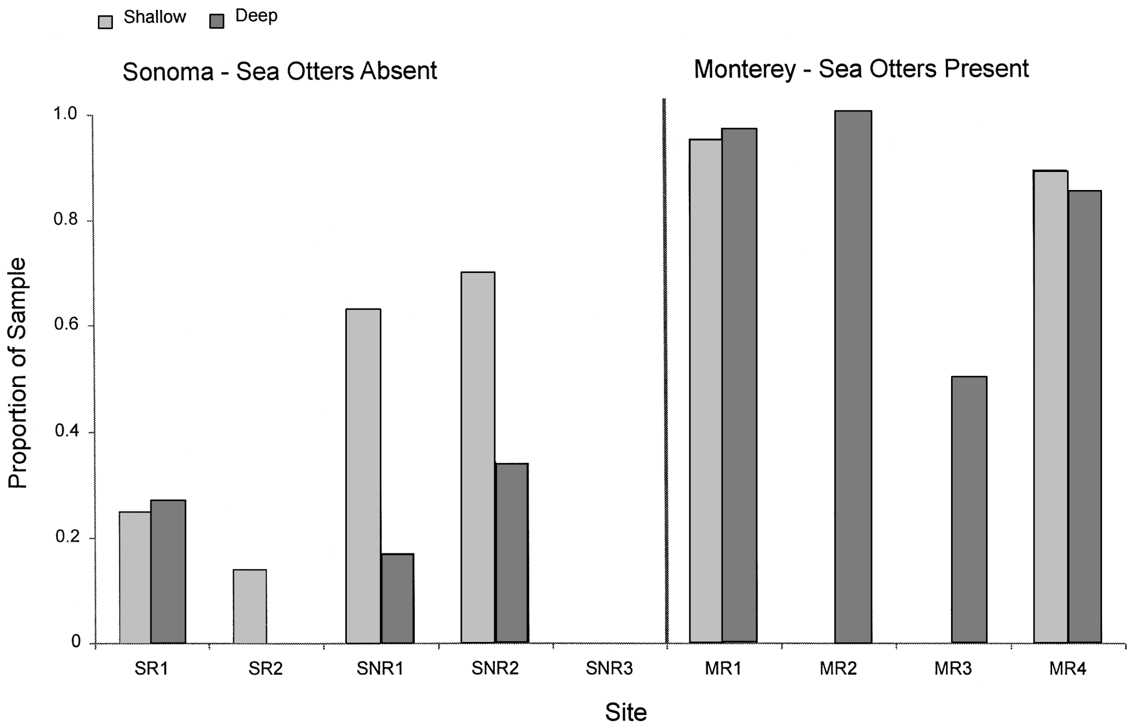

Figure 4. Mean proportions of sampled red abalones in cryptic microhabitats, by site and depth stratum, observed during sampling in the study sites off California. Site codes are defined in Fig. 1.

structure of and microhabitat use by red abalones. Both factors are associated with reduced density and truncation of larger size classes in red abalone populations. At face value, our data yield the counterintuitive result that harvest effects on abalone density in Sonoma sites were greater in the deep stratum than the shallow. Both sea otters and recreational harvest appeared to result in an increased proportion of individuals restricted to cryptic microhabitats. Our data suggest that sea otters have a quantitatively greater effect on abalone demography than recreational harvest.

Evidence that recreational harvest has greater effects on abalone density in deep strata than in shallow at Sonoma sites may be implausible, given documentation by Karpov et al. (1998) that the significance of abalone removal by breath-hold divers diminishes rapidly with depth. We suggest three alternative interpretations of the data. First, differences in habitat characteristics among study sites may produce a pattern that leads to a spurious conclusion of significant harvest effects. Our nonrefuge site outside the Bodega Marine Life Refuge had no abalones in transects and differed from other sites in many habitat characteristics. Inclusion of data from this site may have facilitated an inappropriate conclusion of a significant harvest effect in deeper strata. Second, the patterns in our data may reflect illegal harvest by scuba divers in deeper strata. Illegal abalone harvest by scuba divers has become a high-profile law enforcement issue off northern California in recent years. For example, measured abalone densities in the nonrefuge deep stratum outside of Gerstle Cove were 10 times smaller than densities within the same depth range in the nearby refuge. Illegal harvest by scuba divers in deeper nonrefuge habitats could produce such a pattern, although it is not clear why illegal harvesters would avoid harvesting in refuges. Third, breath-hold divers may be more efficient in deep strata and less efficient in shallow strata than we anticipated. The latter explanation seems to us less plausible than the former two.

Distribution of our study areas on a geographic scale may also be cause for caution in evaluating our data. All sites occupied by sea otters were in Monterey County, and all harvested sites were in Sonoma County. Sea urchin fisheries occur off Sonoma but not Monterey and may have indirect ecological effects important to red abalones. Large-scale differences in wave exposure and current pattern may also have been important. Evaluation of large-scale habitat effects were beyond the scope of our study but must be acknowledged as possible contributors to trends in our data.

In our Sonoma County sites, the significant effects of recreational harvest on size distribution, microhabitat use, and perhaps density indicate that marine protected areas may contribute to fishery sustainability. Abalones are larger, less cryptic, and possibly more abundant in reserve areas than in nearby areas. In abalones, fecundity scales geometrically to linear indices of body size. Thus, an increase in mean body size at the population level produces an exponential increase in fecundity and potentially in the production of larvae. To our knowledge, verification that Sonoma reserve populations actually contribute to harvest sustainability outside marine protected areas is not available.

Two marine conservation themes are heard frequently in California. One is the restoration and increased protection of sea otter populations. Prior to the period of excessive harvest for the fur trade, sea otters occurred in all coastal marine waters of California, including San Francisco Bay and the southern California islands (Ogden 1941; Kenyon 1969). Restoration advocacy for sea otters is most often based on the relatively small size and range of the current California population and its vulnerability to oil spills and other anthropogenic disturbances (VanBlaricom & Jameson 1982; Loughlin 1994; Benz 1996*a*, 1996*b*; Bonnell et al. 1996; Thomas & Cole 1996). As a result, the sea otter population in California has protected status under both state and federal conservation protocols, including a listing of "threatened" under the U.S. Endangered Species Act of 1973 (as in U.S. Code 1974) as amended. Two marine protected areas have been established specifically for the purpose of sea otter conservation and restoration. In addition, a major translocation project was undertaken in California in the late 1980s, with sea otter protection and recovery as primary goals (U.S. Fish and Wildlife Service 1987).

Interest in restoring and protecting sea otters is often linked to evidence that sea otters facilitate biodiversity and ecosystem health by controlling, through predation, benthic herbivores that otherwise overgraze and disrupt the structure and dynamics of coastal benthic communities in the North Pacific Rim (McLean 1962; Estes Palmisano 1974; Duggins 1980; VanBlaricom & Estes 1988; Estes & Duggins 1995). The contrarian view is that the effects of sea otters may be overgeneralized and oversimplified and that other ecological factors may complicate the ostensible top-down effects of sea otters in some locations (for California habitats: Schiel & Foster 1986; Foster & Schiel 1988; for other locations: Carter 1999; Gerber & VanBlaricom 1999; Dean et al. 2000; Konar 2000). Despite disparate views among researchers, there is broad popular acceptance of the view that recovering sea otter populations facilitate increased biodiversity and that restoration of pre-Columbian ecological function and biodiversity along the California coast ultimately will require full recovery of sea otter populations.

A second common theme in California marine conservation is the development of sustainability in coastal fisheries, including abalone fisheries. In recent decades, California abalone fisheries have been beset by a number of problems, among them excessive harvest, effects of natural predators and natural disturbances, and outbreaks of novel diseases (Estes & VanBlaricom 1985; Tegner 1989; Davis et al. 1992, 1996; Haaker et al. 1992; Tegner et al. 1992, 1996; Wendell 1994; Friedman et al. 2000). As a result of these problems, all commercial abalone fisheries in California are now closed. Only one recreational fishery remains open (north of San Francisco, which includes our Sonoma County study sites). Interest in abalone fishery restoration is a result of persistently high product demand from the consumer, the economic needs of the abalone fishers, and a strong appeal to the general populace, which appears to result from the long history and the perceived artisanal character of abalone fisheries in California.

Our data indicate that marine protected areas with sea otters restored as top-level carnivores cannot serve the dual purposes of biodiversity enhancement and abalone fishery conservation off California. In the restored case, abalones will be constrained by foraging sea otters to a small subset of available microhabitats and to densities and size distributions probably inadequate for significant contributions to regional fishery sustainability, although adequate for population persistence.

Our data indicate that, in at least some cases, calls for management of marine protected areas for multiple human uses (Agardy 1994; Jones 1994) may be ecologically naïve, creating unattainable expectations for performance of the protected areas. Klee (1999) describes a management dilemma for a marine sanctuary in American Samoa that parallels our case. Coral habitats were protected to facilitate recovery from an irruption of a coral predator, the crown-of-thorns sea star (*Acanthaster planci*). Klee reports the dismay of sanctuary management staff on learning that populations of the sea star within the sanctuary were to receive the same level of protection as the corals. Thus the sanctuary may be more effective in preserving a range of variable ecological processes, unpleasant and uncontrollable attributes included, than in specifically promoting recovery of coral populations from sea star irruptions.

A major implication of our results is the possibility that multiple categories of marine protected area may be required to meet multiple conservation goals. In cases such as ours, in which a desirable upper trophic level feeds preferentially on prey species targeted in desirable fisheries, generic multiple-use marine protected areas may be less effective than separate single-purpose categories of protected area for ecosystem restoration and for sustainability of commodity extraction, respectively. For example, managers of the Florida Keys National Marine Sanctuary have subdivided a large multiple-use protected area into segments, each with separate, more narrowly defined purposes (National Oceanic and Atmospheric Administration 1996). The management approach serves multiple needs that would be in conflict in a protected area managed homogeneously.

Dayton et al. (1998) lament the loss or depletion of species in coastal biological communities, noting the coincident loss of understanding about the behavior of natural systems. Tegner and Dayton (2000) argue further that knowledge about the ecological functions of depleted species requires the appropriate implementation of marine protected areas for ecosystem restoration. However, resurrection of the ghosts of communities past may be viewed as undesirable, and an incomplete ecosystem may provide greater value to human consumers than the more restored system. Species recoveries may be pleasing to ecologists and environmental advocates that yearn for the biological integrity of ecosystems but may be costly to human communities and economies and therefore politically untenable. The values and goals of human coastal communities are significant factors in the establishment and management of marine protected areas (Kelleher & Kenchington 1991; Agardy 1994; Gubbay 1995; Neis 1995; Hockey & Branch 1997) and should be weighed carefully when in conflict with the benefits of restored natural systems. One possible solution to such conflicts is implementation of arrays of spatially segregated single-use categories of marine protected areas.

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