

Evaluating potential conservation conflicts between two listed species: sea otters and black abalone

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Abstract. Population consequences of endangered species interacting as predators and prey have been considered theoretically and legally, but rarely investigated in the field. We examined relationships between spatially variable populations of a predator, the California sea otter, *Enhydra lutris nereis*, and a prey species, the black abalone, *Haliotis cracherodii*. Both species are federally listed under the Endangered Species Act and co-occur along the coast of California. We compared the local abundance and habitat distribution of black abalone at 12 sites with varying densities of sea otters. All of the populations of abalone we examined were in the geographic area currently unaffected by withering disease, which has decimated populations south of the study area. Surprisingly, our findings indicate that sea otter density is positively associated with increased black abalone density. The presence of sea otters also correlated with a shift in black abalone to habitat conferring greater refuge, which could decrease illegal human harvest. These results highlight the need for a multi-species approach to conservation management of the two species, and demonstrate the importance of using field-collected data rather than simple trophic assumptions to understand relationships between jointly vulnerable predator and prey populations.

Key words: adaptive management; black abalone; Endangered Species Act; multi-species plans; predator–prey dynamics; recovery plans; refuge; sea otter; species interactions.

INTRODUCTION

As the lists of threatened and endangered species grow, there is an increase in the probability of situations in which species that interact as predator and prey are both depleted. Such cases have been explored theoretically and via expert panels, particularly where predator range expansion or recovery actions could threaten prey species (e.g., Chadès et al. 2012, Marcot et al. 2012). However, there have been no field-based studies explicitly quantifying relationships between endangered predator and prey populations. Although simple trophic theory predicts conservation conflicts in such cases, management actions based on theoretical assumptions may miss real-world complexities and increase the risk of unnecessary, or even harmful, interventions (Roemer and Wayne 2003). Successful conservation management necessitates a data-driven understanding of ecological

dynamics between federally listed predator and prey populations. Indeed, current legal guidance indicates that a multi-species approach should be used in recovery planning under the U.S. Endangered Species Act, or ESA (The Fund for Animals v. Lujan, Civ. No. 92-800, December 15, 1992; National Research Council 1995). However, such a management approach has not yet been applied to a situation comparable to that of black abalone and sea otters, in which trophic interactions between listed species could bring single-species management plans into conflict.

Along the coast of California (USA), two ESA-listed species with a predator–prey relationship co-occur: the California sea otter, *Enhydra lutris nereis*, and the black abalone, *Haliotis cracherodii*. There is potential for sea otter predation to further threaten or impede the recovery of black abalone populations. California sea otters are efficient predators that consume up to 30% of their body mass daily (Kenyon 1969, Costa 1982), mainly in rocky reef invertebrates, including abalone (Ostfeld 1982, Tinker et al. 2008). The small population

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and limited distribution (compared to its former state; Tinker et al. 2006), along with threats from disturbances such as oil spills, led the U.S. Fish and Wildlife Service to list it as threatened under the Endangered Species Act in 1977 (Estes et al. 1996).

Black abalone are large, long-lived gastropods found from northern California to Baja, Mexico, but severe declines led the National Marine Fisheries Service (NMFS) to list the species as endangered under the ESA in 2009. Once exceptionally abundant south of San Francisco, black abalone have virtually disappeared from southern California, due primarily to a fatal disease called “withering syndrome” (Lafferty and Kuris 1993, Richards and Davis 1993, Tissot 1995, Alstatt et al. 1996, Raimondi et al. 2002, Miner et al. 2006). Adult black abalone play an important role in determining community structure and maintaining favorable habitat for conspecific recruitment (Cox 1962, Douros 1985, Blecha et al. 1992, Miner et al. 2006), by reducing the cover of fleshy algae and macro-invertebrates in favor of bare rock and crustose coralline algae (Miner et al. 2006).

Sea otters are present over the entire range where black abalone are still abundant (Fig. 1), and thus otter predation has the potential for both demographic and distributional effects on this endangered species. While there is limited information on the predators of black abalone, the proclivity of sea otters for red abalone (Tinker et al. 2008) and evidence from shell damage patterns (Hines and Pearse 1982; P. T. Raimondi, *unpublished data*) suggest that, other than disease and human extraction (poaching in populations unaffected by disease is common; Butler et al. 2009), most observed adult mortality is the result of foraging by sea otters. In addition to the demographic consequences of predation, the presence of sea otters could drive shifts in black abalone microhabitat distributions, resulting in greater use of refuges such as deep cracks and crevices, a pattern that has been observed in other abalone species (Hines and Pearse 1982, Fanshawe et al. 2003).

In this study, we investigated the association between sea otter density and black abalone population density and habitat use. Abundances of *H. cracherodii* are highly variable across their range, with abalone restricted to patches of suitable rocky intertidal habitat. Otter abundance also varies along the coast, with differences in density explained in part by the spatial pattern of recovery over the last century (numbers are generally highest in the long-occupied range center and lower near the more recently occupied range peripheries; USGS-WERC 2014; Fig. 1) and partly as a result of local differences in sub-tidal habitat quality (Laidre et al. 2001). We assessed the potential for a negative correlation between sea otter density and black abalone density across sites. We also examined the effects of sea

otter density on the distribution of black abalone across intertidal microhabitats.

METHODS

We examined relationships between local otter density and black abalone population density, size distribution, and use of habitat refuges at 12 sites on the central California coast (Fig. 1) between January and December 2008. At each site, we sampled black abalone density and size distribution by counting and measuring individuals in a series of plots of known size (details can be found in Engle [2008]).

We interpolated average sea otter density at each site from a GIS layer of sea otter abundance based on annual range-wide censuses by the U.S. Geological Survey and California Department of Fish and Wildlife (Tinker et al. 2006; data and detailed methods available at USGS-WERC 2014). Raw data consisted of georeferenced sea otter sightings made by aerial and ground-based observers over two-week periods each spring. We binned data into contiguous “coastal sections” of habitat (defined as the benthos between the 0 m and 60 m depth contour), each spanning 500 m of coastline. To account for variability in survey conditions and the mobility of sea otters, we smoothed section sums using a 5-km moving window average, and then further averaged over three survey years (2005–2007). For our purposes, “sea otter density” hereafter refers to the mean number of sea otters per 500 m of coastline.

Since the availability and use of microhabitat refuges could modify the effect of otters on abalone, we also examined the value of each abalone’s location as a refuge from otter access. We pooled these data by site to assess the location-specific deviation from expected use of refuge based on sea otter abundance (see *Statistical approaches*). Quality of refuge from predation provided by a microhabitat is difficult to quantify by a single measurement because cracks are highly irregular. We therefore assigned each abalone a refuge value (high, moderate, or low) based on how difficult it would be for an otter to remove that individual. We used two morphological characteristics of the average adult otter to evaluate the likelihood of otter access to an individual abalone: arm reach and body width (45 cm and 16 cm, respectively; T. Fink and B. Hatfield, *personal communications*). We scored an abalone’s refuge as high value if the microhabitat was deep or narrow enough that it was unlikely for an otter to take the abalone by prying or cracking the shell; the methods otters generally employ (Cox 1962, Hines and Pearse 1982). We defined moderate refuge as habitat providing difficult, but possible, otter access. Locations providing little or no protection from otters were considered to be of low refuge value. At each site, we estimated the percentage of each refuge category available within the search area

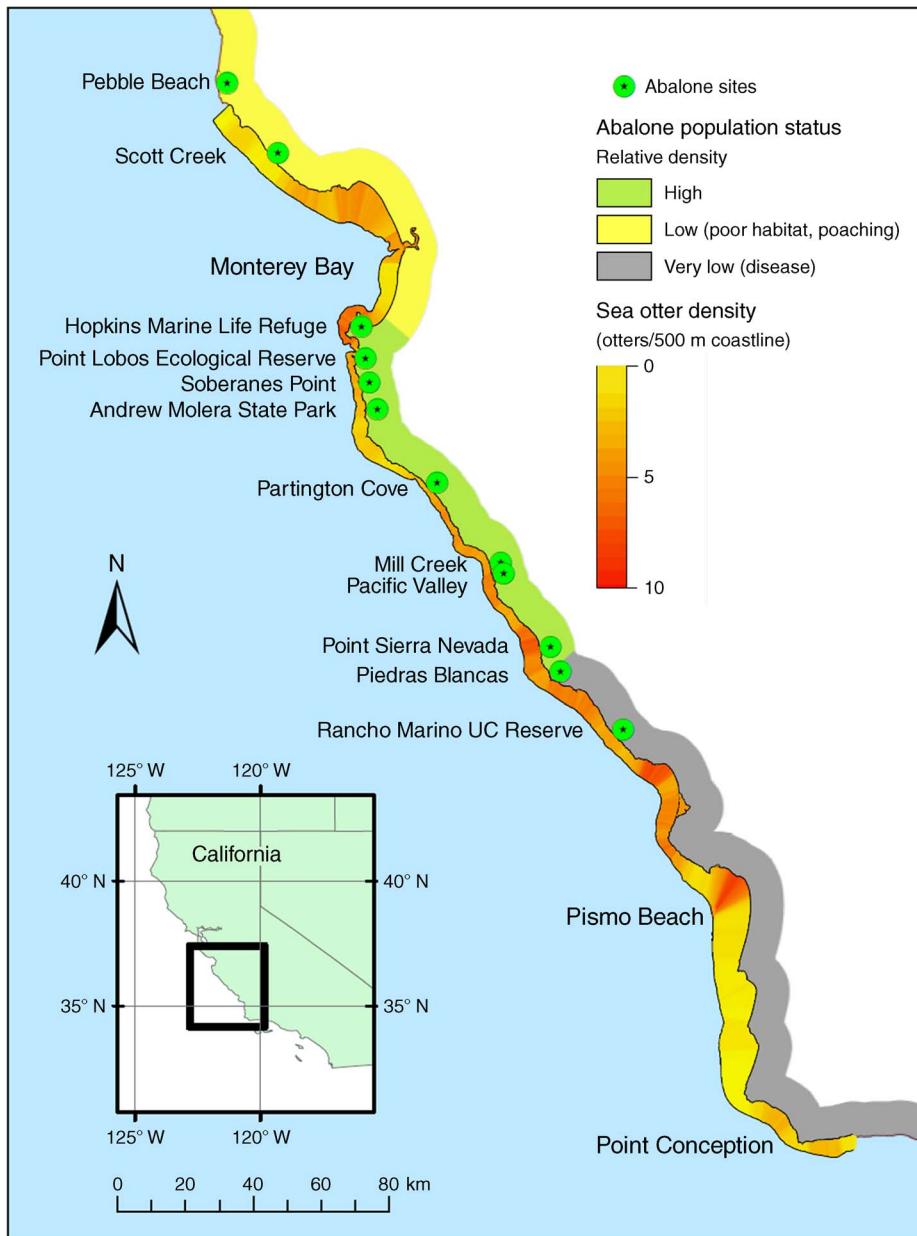


FIG. 1. Map of central California, USA study area showing locations of abalone sample sites, spatial variation in black abalone population status, and sea otter population distribution and density based on range-wide census data, 2005–2007.

in order to calculate the difference between the observed microhabitat distribution of abalone and that expected based on refuge availability.

Statistical approaches

We examined the effect of otter density and habitat refuge value on log-transformed black abalone density using a multiple regression model with site as the unit of replication. We included only the percent of high refuge

available at each site in the model because of colinearity with other percentages.

To assess the predictors of abalone distribution across microhabitats, we used a three-way analysis of variance, with abalone size, otter density (low or high), and refuge value (low, moderate, high) as predictor variables and the normalized deviation between observed and expected use of habitat refuge as the response variable, where “expected” was equivalent to the percentage of area

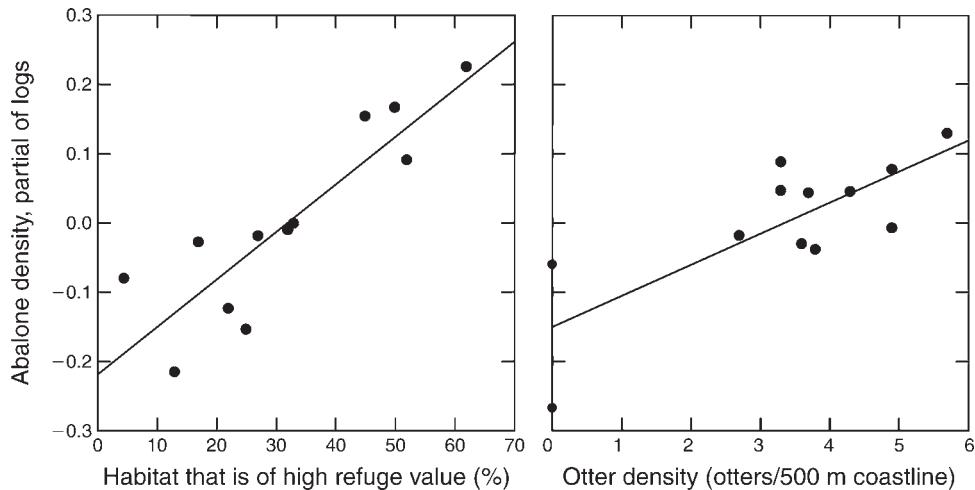


FIG. 2. The relationship between abalone density (partial residuals from the multiple regression model are shown) and (a) percent of habitat that is of high refuge value and (b) sea otter density. Increased abalone density is correlated with high refuge habitat and high otter density.

available in each refuge category at the site. Abalone size categories corresponded to juvenile (<50 mm), small adult (>50 and <90 mm), and larger adult stages (>90 mm). We defined low sea otter density as fewer than 1.5 individuals per 500 m, and high sea otter density as greater than 2.5 individuals per 500 m, corresponding, respectively, to areas where sea otters are found intermittently and rarely occur in large groups, vs. areas where otters frequently forage and rest in groups.

RESULTS

As predicted, high-refuge microhabitat was positively related to black abalone density, but unexpectedly, so was otter density (Fig. 2; model $F=29.801$, $df=2,9$, $P<0.001$, $r^2=0.84$; habitat quality $t=5.84$, $P<0.001$, partial $r^2=0.62$; otter density $t=3.89$, $P=0.004$, partial $r^2=0.22$).

There was no evidence that the size class of abalone affected their microhabitat distribution (Table 1). However, there was a significant interaction between local otter abundance and refuge value, indicating that the relationship between abalone abundance and refuge value varied as a function of otter density (Fig. 3). Specifically, at sites with high otter abundance, black abalone were more likely to be found in locations that conferred high refuge value and less likely to be found in locations with low refuge value.

DISCUSSION

Contrary to our expectations, our results did not support the idea that sea otter density would be negatively related to black abalone abundance. Instead, our findings indicate that in this region where sea otters have been present for over 40 years, they may now have

a net positive, rather than negative effect on black abalone populations. This result seems counterintuitive because otter foraging has been shown to decrease local abundances of red abalone (*Haliotis rufescens*; Wendell 1994, Fanshawe et al. 2003).

There are at least three plausible hypotheses for the observed positive relationship between sea otters and black abalone. First, rocky habitat that supports sea otter foraging is also likely to have refuges suitable for black abalone. Second, the species may co-occur in areas with high kelp densities. Black abalone eat kelp detritus and their growth was found to be fastest on a diet of kelp (Leighton and Boolootian 1963). As might be expected, kelp detritus is positively associated with local abundance of living kelp (Gerard 1976, Dayton 1985, Harrold and Reed 1985) and sea otters also use kelp forests as resting areas and as foraging habitat (Riedman and Estes 1990). Indeed, the bulk of sea otter diets in central California are composed of kelp-dependent macroinvertebrates (Tinker et al. 2012), and equilibrium densities of sea otters are highest in areas dominated by

TABLE 1. ANOVA results for the relationship between distribution of abalone and refuge value, otter density, and abalone size.

Source	df	SS	F	P
Otter abundance (O)	1	0.001	0.0000	1.0000
Refuge value (V)	2	24.449	27.7277	<0.0001
Abalone size (S)	2	0.001	0.0000	1.0000
O × V	2	9.921	11.2521	<0.0001
O × S	2	0.001	0.0000	1.0000
S × V	4	0.846	0.4802	0.7502
O × V × S	4	0.429	0.2434	0.9130
Error	99	43.647		

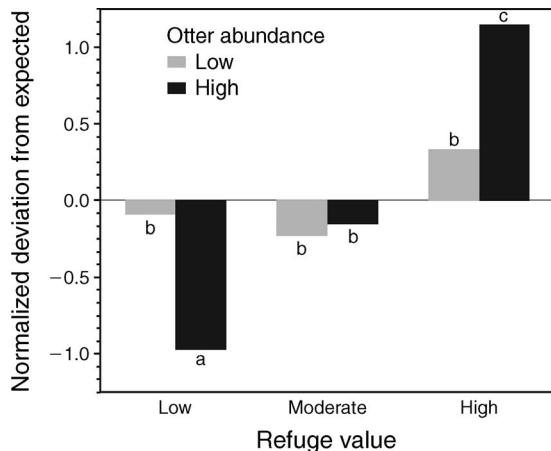


FIG. 3. The relationship between habitat refuge value and abalone microhabitat distribution (normalized deviation from expected based on available habitat) at sites with different levels of otter abundance. Abalones are concentrated more in high-value refuge habitat than expected where otter density is high. Positive values correspond to greater use of the microhabitat refuge type and negative values to less use than expected. Letters signify significantly different groups (REGWQ post-hoc test, $P < 0.05$) for both comparisons among treatment combinations and also relative to zero.

sub-tidal rocky reefs and extensive kelp canopy (Laidre et al. 2001, Lafferty and Tinker 2014). Third, sea otters could actually increase the availability of kelp detritus for black abalone via the well-documented indirect, positive relationship between sea otter and kelp abundances, which occurs when otter predation controls sea

urchins that forage on kelp (Estes and Duggins 1995). For a net positive relationship between sea otters and black abalone to occur, population increases from enhanced kelp abundance must be greater than mortality from otter predation.

Predation refuges could enhance the positive relationship we found between black abalone and sea otter abundances. Even if black abalones are taken by otters, the rate of predation could be considerably reduced by the microhabitat configuration. In areas of high otter abundance, abalones were much more likely to occur in deep, narrow crevices that conferred high refuge value (see Plate 1), and much less likely to be found in open locations with low refuge value. Where otter densities were low, there was no such shift in distribution (Fig. 3). Additionally, our findings imply that by increasing the proportion of black abalone in difficult-to-access refuges, otters could indirectly reduce mortality from poaching, which is a substantial threat to the species (Neuman et al. 2010).

Taken together, results of this study call into question the efficacy of predator removal as a strategy for enhancing abalone recovery. By applying simple trophic assumptions, sea otter range expansion has been considered a likely threat to northern abalone (*H. kamtschatkana*; Chadès et al. 2012, NOAA 2014), and otter control actions have been discussed as a potential solution (Gardner et al. 2000). Such an approach has been used in other systems. For example, evidence that Golden Eagle (*Aquila chrysaetos*) populations on the Channel Islands in California were reducing populations of the endangered island fox (*Urocyon littoralis*) led

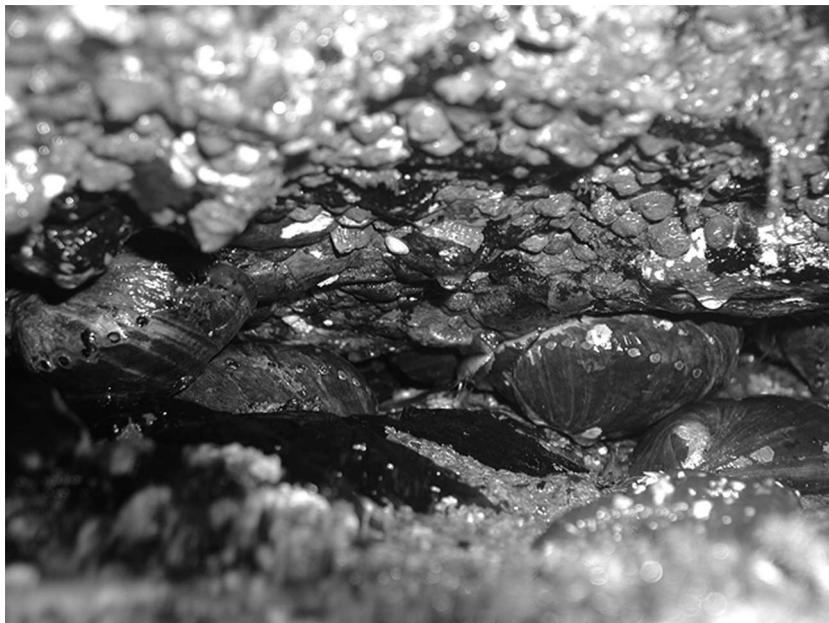


PLATE 1. Black abalone deep in a crack, which provides refuge from predation. Photo credit: Christy Bell.

managers to translocate Golden Eagles from Santa Cruz Island to the mainland in 1999 (Latta et al. 2005). Following the onset of the removal program, fox survival on the island increased to levels near those measured pre-decline (Latta et al. 2005). In contrast, our field-based results indicate that otter removal may not only be detrimental to otter populations, but could also fail to benefit abalone.

Our results suggest instead that management efforts directed at enhancing the sea otter population may also indirectly benefit black abalone populations. However, there are important caveats. We carried out this study in the last stretch of U.S. coastline where black abalone densities appear unaffected by withering disease, in a region where both otters and black abalone are relatively abundant. To the south, otters are present but black abalone are nearly (locally) extinct (Raimondi et al. 2002, Miner et al. 2006). If black abalone occur outside effective refuges in such areas, any additional losses due to sea otter predation are likely to be detrimental to the species' local recovery. Additionally, should withering disease move northward, population declines from disease could conceivably be further compounded by sea otter predation, although our results demonstrate that even this assumption would need to be tested. Our findings underscore the usefulness of a data-driven, adaptive, and spatially explicit multi-species management approach to these species, and in any situation where predators and prey are both species of high conservation concern.

Clearly, more studies aimed at teasing this relationship apart are needed before species-specific management actions are adopted, because as our results indicate such an action could reduce the abundance of one protected species and have little to no effect on the status of the other.

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