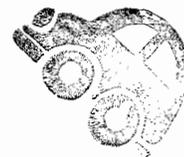


INTERACTIONS AMONG RED ABALONES AND SEA URCHINS IN FISHED AND RESERVE SITES OF NORTHERN CALIFORNIA: IMPLICATIONS OF COMPETITION TO MANAGEMENT

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ABSTRACT Red abalones (*Haliotis rufescens*), red sea urchins (*Strongylocentrotus franciscanus*), and purple sea urchins (*S. purpuratus*) share similar food and habitat requirements in northern California. Red abalones and red sea urchins also support important fisheries. Here we explore spatial interactions and apparent competitive effects among these species at an area where fishing has large impacts on both taxa, and at unfished reserve sites in which invertebrate density and food availability differ. There was an inverse correlation between adult red abalone and red sea urchin abundance at the scale of our transects when density of either or both species was high. In the poorest habitat for macroalgae, red abalones seldom occurred on the same transects with red urchins. The results suggest that differences in density, depth, and food availability play an important role in the observed spatial patterns of red abalones and red sea urchins. Purple sea urchins were not correlated to either of the other two species' distributions. An intense fishery for red sea urchins appears to have had a positive effect on kelp availability, and abalone growth and abundance. Aerial photographs during the period of intense urchin fishing (from 1982 to 1989), showed a dramatic increase in the surface canopy. Similarly, during this period, size frequency distributions of fished red abalones show an increase in the number of individuals in larger size classes. Modal progression in abalone size frequency distributions suggests a faster growth rate during this period when compared with a growth study, at the same location, conducted during the pre-urchin fishery years. Ultimately, red sea urchin removal apparently led to an increase in red abalone abundance even at a site that was heavily fished by recreational abalone fishers. Meanwhile, at a nearby reserve site where kelp populations are lower, red abalones have declined in abundance as red sea urchins increased. Our results suggest the need for multi-species ecosystem-based approaches to management of these valuable resources.

KEY WORDS: reserves, *Haliotis rufescens*, *Strongylocentrotus franciscanus*, *Strongylocentrotus purpuratus*, competition, spatial exclusion, ecosystem-based management

INTRODUCTION

Red abalones (*Haliotis rufescens*), red sea urchins (*Strongylocentrotus franciscanus*) and purple sea urchins (*S. purpuratus*) share similar food and habitat preferences in kelp forest communities along the California coast. In northern California, red abalones are found in rocky intertidal and shallow subtidal areas in high abundance at 7-8-m depths, but also occur down to 25 m in areas where drift algae accumulate in surge channels. Red and purple urchins are found from mid- to low- intertidal zones to depths in excess of 50 m. Both species prefer rocky substrates, particularly ledges, crevices and surge channels, and avoid sand and mud (Schroeter 1978, Kato & Schroeter 1985). In areas of high predation, red abalones show a preference for crevice habitat (Hines & Pearse 1982). Red abalones and red and purple urchins feed primarily on the same species of macroalgae (Leighton & Booloottian 1963), and have been described as potential competitors for food and space (Leighton 1968, Tegner & Levin 1982). Both urchins and abalones feed primarily on drift kelp, but sea urchins are well known for their destructive grazing on attached plants when drift becomes limiting. Schroeter (1978) presented evidence that red urchins out compete purple urchins for food and habitat, suggesting that the red urchin fishery could lead to an increase in populations of its smaller congener. Several authors have considered the potential of sea urchin populations being released from competition as abalones were fished down in southern California (North & Pearse 1970, Tegner 1980, Tegner & Levin

1982, Tegner & Dayton 2000). No one has examined the effects of red urchin removal in areas where red abalones are still abundant.

Red abalones and red sea urchins are both fished intensively in northern California. Red abalone take is restricted to recreational fishers who are prohibited from using SCUBA. Karpov et al. (1998) reported that this results in a "defacto" refuge for red abalone at depths greater than 8.4 m. Since 1985, Red urchins have been subjected to an intense commercial fishery at all depths (Kalvass & Hendrix 1997). Purple sea urchins are essentially unfished, comprising less than 1% of the total urchin landings.

The red abalone, the largest member of the genus, attains sizes of up to 312 mm in northern California (Department of Fish and Game -DFG- unpublished data). Legal minimum size for the recreational-only abalone fishery is 178-mm shell diameter. Red sea urchins, characterized by long spines in relation to test diameter (TD), attain sizes of 140 mm TD, and were first protected by a minimum size limit of 89-mm TD in 1991. Purple sea urchins have short spines relative to their TD, and maximum TD is about 85 mm. In northern California macroalgae are highly seasonal as a food source (Tegner et al. 1992). Wave energy is markedly higher in northern compared to southern California, and thus is likely to be a more important factor affecting the distribution of abalone and urchins (Deacon 1973).

Fishing effects, both direct and indirect, make field studies of competition difficult to conduct. Here we take advantage of three locations in northern California, one fished and two reserves closed to sport and commercial fishing, to examine biological and fishery interactions between red abalones, red sea urchins, and purple sea urchins. Differences in fishing regimes constitute a natural experiment, which offers an opportunity to examine the factors structuring this nearshore community, the potential produc-

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tivity of the three grazers, and the ecosystem effects of fishing. We compare observations of densities, size-frequency distributions, and spatial distributions of the three grazers and kelp populations over time. Two major questions are asked in this study: (1) Has intense red urchin removal by the fishery had an effect on the abalone resource, and (2) are there significant differences by habitat, density, or depth that indicate spatial exclusion between sea urchins and abalones.

Materials and Methods

Our study is focused in northern California on a fished area, Van Damme State Park (VDSP), and two unfished "control" areas: Bodega Marine Life Refuge (BMLR) and Point Cabrillo Marine Reserve (PCMR)(Fig. 1). VDSP is highly impacted by both the sport only abalone fishery and the commercial red sea urchin fishery. In this study, we used the same 120 dive stations examined for changes in emergent abalone abundance and size distributions during 1986, and from 1989–1992 by Karpov et al. (1998). In 1999, we added 34 more stations that were at comparable locations to those surveyed during earlier years. Red urchins were surveyed throughout these periods; purple sea urchins were added in 1989. As in the previous study (Karpov et al. 1998), we stratified our sampling into two strata, "shallow" and "deep", using 8.4 m as the dividing depth because free divers seldom dive deeper than 8.4 m to collect abalone. Thus, the VDSP study area represents a treatment of large-scale continued removal of red urchins at all depths and red abalones from shallow water. Two no-take reserves were also surveyed, PCMR and BMLR (Fig. 1). Parker et al. (1988) first surveyed 30 stations at PCMR in 1986. PCMR was re-sampled in 1988 for sea urchins at 14 stations and again in 1999 at 30 stations.

About half of the 1999 stations were in close proximity to locations sampled in 1986. Sampling was normally conducted during late summer months. Station depths throughout the study period ranged from 2 to 18 m. Sampling was conducted along 2 × 30 m transects randomly placed on rocky habitat. Transects were not sampled if they were placed on substrate with more than 50% sand.

PCMR, first established as a "no-take" reserve in 1975, is located 9 km north of VDSP. PCMR provides both a site for comparing spatial correlation for high densities of red and purple sea urchins to high densities of red abalone, as well as a nearby unfished control for comparison with the fished VDSP site. BMLR, located 130 km south of VDSP, was established as a no take reserve in 1966 (Fig. 1). In 1999, 33 stations at BMLR were sampled to examine spatial correlation in an area with no surface canopy of kelp in more marginal abalone and urchin habitat. We also examined this area on a smaller spatial scale. Stations were grouped into three sites of distinct habitat, designated Horseshoe Cove, Cave, and Points (North and South Point combined) (Fig. 2).

To compare the relative availability of food at each study area, percent cover of algae was estimated by divers on each quadrant and averaged in all three of the study sites during 1999. Algae and cover were classified in five categories: encrusting, coralline algae turf, foliose, understory, or canopy kelp. Understory kelp included brown algae such as *Pterygophera californica* and *Laminaria dentigera*. The primary canopy species in northern California was the annual kelp, *Nereocystis luetkeana*. Percentage cover at times exceeded 100%.

Size frequency distributions, weighted for density, were examined for patterns of recruitment of red sea urchins and red abalones at VDSP and PCMR. Size frequency distributions of red urchin catches were obtained from commercial samples. Estimates of

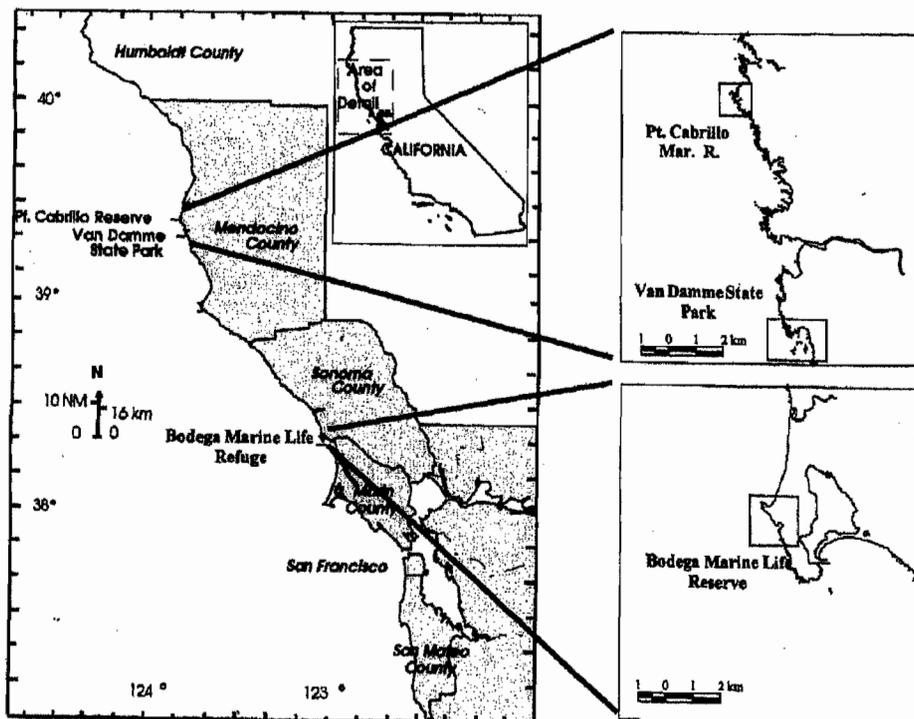


Figure 1. Location of Point Cabrillo Marine Reserve (PCMR), Van Damme State Park (VDSP), and Bodega Marine Life Refuge (BMLR) study areas in northern California.

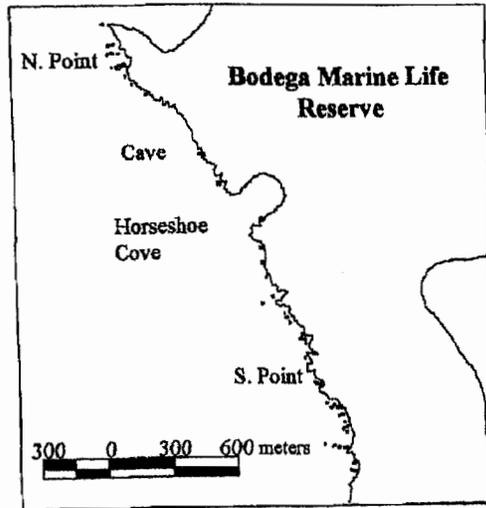


Figure 2. Detailed view of BMLR showing sampling areas.

urchin catch at VDSP were made from fishery logbook data. Creel surveys of sport-caught red abalones conducted during spring minus-tides from 1977 to 1994 at VDSP were used to construct size frequency distributions of the sport take.

Estimates of kelp surface canopy were obtained at VDSP from aerial infrared photographs taken each October from 1982 to 1991. Surface areas estimates were constructed from polygons drawn visually in Arc View GIS software.

Statistical Comparison

Red abalone and red sea urchin counts from 2 x 30 m transects at VDSP and PCMR were compared using two-way ANOVAs testing differences between year and depth strata. Densities were transformed using the method of Pearse and Hines (1987) (transformed density = ln (density + 1)). The non-parametric Spearman Rank Correlation test was used to examine inter-specific spatial correlation. Paired counts of each of the three species were used. The test produces a correlation coefficient (r_s) range 1-1. Transects with zero counts were excluded from these comparisons to avoid inappropriate habitat.

We used 1986 PCMR data to examine the effect of transect size on the observed inverse correlation between red abalones and red sea urchins. Since data that year were recorded on a finer scale, subdividing the 2 x 30 m transect into six 1 x 10 m segments, we examined spatial correlation by randomly selecting a 10, 20, and 60 m² segment from each of 26 shallow and deep transects. The inverse relation was significant at both 20 (r_s = -0.55, P = 0.004) and 60 m² (r_s = -0.43, P = 0.03) transect sizes, but not significant at 10m².

Red abalone and sea urchins were classified as having either low or high abundance at each of the three locations across the years examined, depth strata, and habitat types. This classification was used to create a matrix allowing the significance of the correlation coefficients related to high or low density of any of the species to be examined. The abundance of red abalone, red sea urchin, and purple sea urchin was considered high at greater than 0.4, 1.0, 1.0 m⁻², respectively. Similarly, inter-specific spatial correlation was examined at each of the three habitat types at BMLR and between the three study areas. Finally, correlation was also examined at VDSP and PCMR over time to determine if fishery

related abundance changes reflected spatial exclusion. Significance for all tests was set at α = 0.05.

RESULTS

During the 1999 survey, BMLR had the least macro-algae of the three study areas. While relative cover of foliose algae was comparable to the other two study areas, canopy was absent and understory much less abundant (Table 1). Horseshoe Cove had the largest standing stock of understory in BMLR. VDSP had the highest algal cover of all three study areas. Surface canopy covered 65% to 79% of shallow and deep stations. Understory and foliose algae were more abundant at shallow than deep stations. PCMR was intermediate between BMLR and VDSP in macro-algae abundance, with the highest abundance at the shallow stations.

BMLR

Red abalone were low in abundance throughout BMLR. They were the most abundant at Horseshoe Cove (0.4 abalone m⁻² SE = 0.1), followed by Cave (0.2 m⁻² SE = 0.1) and Points (0.1 m⁻² SE = 0.03) stations (Fig. 3). Almost all abalones were found at shallow stations, with only three encountered at deep (>8.4 m) stations. Red sea urchin densities were low in Horseshoe Cove (0.6 red urchin m⁻² SE = 0.2) but higher at both the Cave (1.2 m⁻² SE = 0.3) and Points (1.1 m⁻² SE = 0.2). Purple sea urchins were found in very low abundance throughout this reserve. No significant correlation in counts was found between purple urchins and either red abalones or red urchins at any of the three BMLR sites. Red urchin and red abalone counts, however, were negatively correlated on transects at each of the three sites (Fig. 3). Plots of the distribution of counts by station showed marked segregation by species at almost all the stations, with few containing both species. Patterns of segregation were similar among the three locations in the reserve irrespective of relative density decrease for abalones or increase for sea urchins.

PCMR

While generally higher than BMLR, red abalone densities at PCMR declined in both shallow water (from 1.2 SE = 0.2 to 0.6 m⁻² SE = 0.1) and in deep depths (1.2 SE = 0.2 to 0.1 m⁻² SE = 0.1) during this 13-year interval (Fig. 4, Fig. 5). ANOVA comparison showed the difference in density to be significant by

TABLE 1.

Percent cover of encrusting organisms and macroalgae at Van Damme State Parke (VDSP), Point Cabrillo Marine Reserve (PCMR), and Bodega Marine Life Refuge (BMLR) for 1999.

	N	Encrust.	Turf	Foliose	Under-story	Canopy
VDSP						
Shallow	21	62	39	41	53	65
Deep	11	44	18	31	30	79
PCMR						
Shallow	17	72	35	49	40	44
Deep	12	68	7	12	9	21
BMLR						
Horseshoe Cove	13	36	56	41	12	0
Cave	6	44	33	55	0	0
Points (NS)	12	41	24	33	3	0

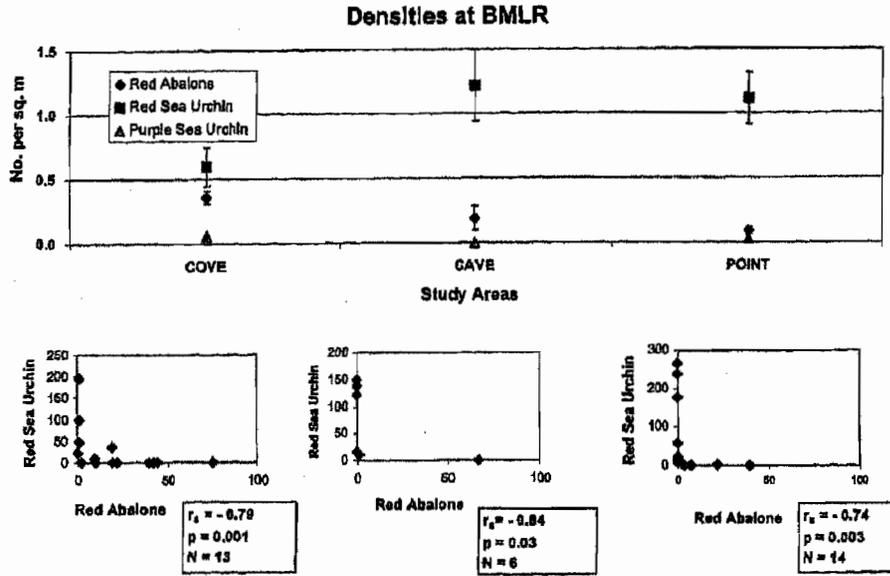


Figure 3. Red abalone, red sea urchin, and purple sea urchin densities (\pm se) by study area of BMLR with paired comparison of counts by species at each station with Spearman Rank correlation coefficients (r_s), statistical significance, and number of stations.

year, depth, and interaction (Table 2). Red sea urchin densities were significantly greater at depth and in 1999 (interaction was not significant). Size distributions reveal very little differences with large proportions of animals at both depths at or above legal sizes for both species (Fig. 6). Deep water red urchins showed evidence of recruitment in both years with bimodal distributions of YOY (<30mm) or small juveniles and large adults. Purple sea urchins, not surveyed in 1986, were at greatest abundance at shallow depths in 1999 (3.2 m^{-2} , SE = 1.0, Fig. 4 and Fig. 5).

Purple sea urchins at PCMR were not significantly spatially correlated to the other two species at the scale of our transects.

Correlation comparisons between red abalones and red sea urchins were significantly negative in both 1986 and 1999, when shallow and deep stations were combined. Comparisons at shallow depths were significantly negative in 1986 and 1999 (Fig. 4). Graphical comparison of correlation revealed more overlap or concurrence of both species on the same transects than observed at BMLR. At deep stations in 1986 the correlation was negative but not significant (Fig. 5). PCMR was the only area where high densities of both red abalones and red urchins were found in our study. Under these high densities both species were significantly negatively correlated ($r_s = -0.52$ $P < 0.0001$, Table 3).

Shallow (2.0 - 8.3 m)

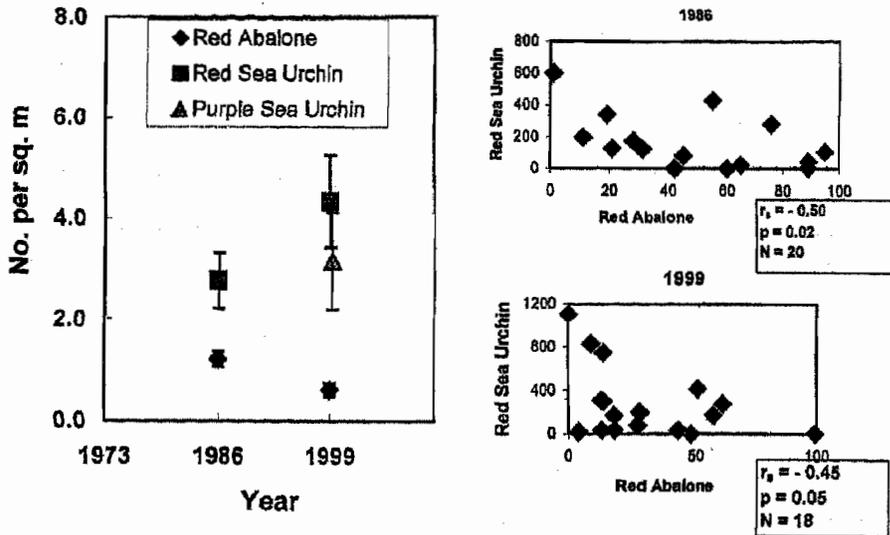


Figure 4. Red abalone, red sea urchin, and purple sea urchin densities (\pm se) at PCMR at shallow depth stations with paired comparison of counts by species at each station with Spearman Rank correlation coefficients (r_s), statistical significance, and number of stations.

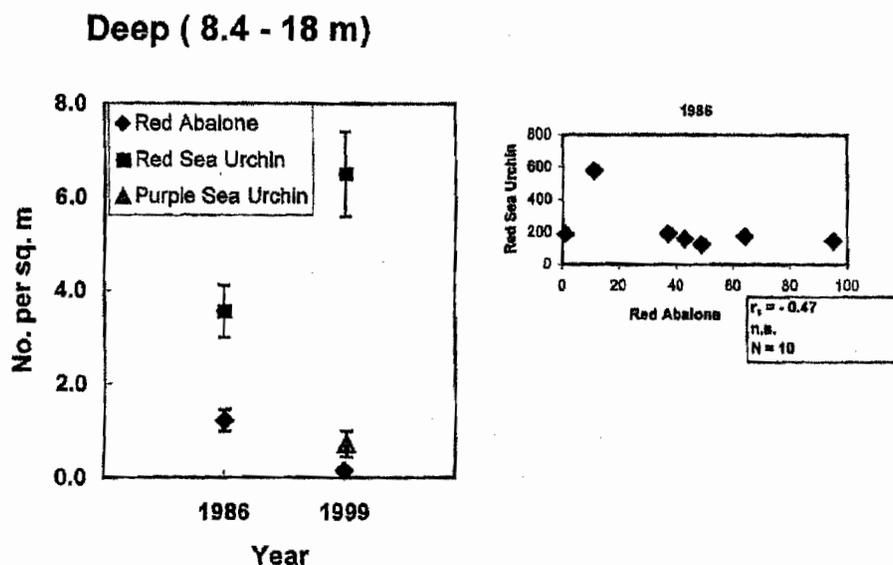


Figure 5. Red abalone, red sea urchin, and purple sea urchin densities (\pm se) at PCMR at deep depth stations with paired comparison of counts by species at each station with Spearman Rank correlation coefficients (r_s), statistical significance, and number of stations.

VDSP

In 1986 red abalone densities at VDSP were low in deep (0.1 m^{-2} SE = 0.1) and shallow depths (0.4 m^{-2} SE = 0.1), while red sea urchin densities were low at shallow (0.4 m^{-2} SE = 0.1) and high at deep stations (1.7 m^{-2} SE = 0.3) (Fig. 7, Fig. 8). Abalone densities had increased significantly to 0.8 m^{-2} (SE = 0.1) at shallow stations, and to 0.9 m^{-2} (SE = 0.2) at deep stations by 1992. Karpov et al. (1998) examined this difference using ANOVA and found the increase to be significant between years and depths (Table 2). During the same period, red urchin densities underwent significant decline by year and depth ($P = 0.04$ and 0.0001 respectively). By 1999, deepwater red urchin abundance had recovered to 2.4 m^{-2} (SE = 0.5), while red abalones had declined to 1986 levels (0.1 m^{-2} SE = 0.1). Repeating the ANOVA comparison revealed that the change in red urchin abundance was no longer significant by year, but still significant by depth. Purple sea urchins, first examined in 1989, underwent significant increases by depth and by year, increasing primarily at deep stations to 1.8 m^{-2} (SE = 0.7) in 1992 (Fig. 7, Fig. 8, Table 2).

VDSP data allowed comparison of species correlation at various combinations of density for each of the species (Table 3). Except at low densities of each, red abalones and red sea urchins were significantly inversely correlated ($P < 0.04$). Again, as in the other two study areas, no significant correlation was observed for purple sea urchins when counts were paired to either of the other two species.

Size distributions of both red abalones and red sea urchins at VDSP weighted for abundance were compared for evidence of recruitment by depth (Fig. 9). Red abalone size frequencies showed a clear pulse of juveniles at shallow depths in 1989. The mode in deep water appeared later, and grew into sizes larger than the sport size limit by 1992. In 1999, the deep water abalones remaining included few juveniles and resembled the 1986 and 1989 distribution. In shallow water, the distributions showed a large buildup of large adults over all previous years, with less evidence of recent juvenile recruitment than had been apparent in 1989 through 1992.

Size distributions of red sea urchins, first measured in 1990, showed a deep water peak at the minimum commercial legal size

TABLE 2.

Red abalone and red sea urchin two-way ANOVA probability values for log transformed density comparison by year, depth, and year*depth interaction at Van Damme State Park (VDSP) and Point Cabrillo Marine Reserve (PCMR). The first comparison at VDSP excludes 1999 data.

Comparison	Class Variable	Red Abalone	Red Sea Urchin	Purple Sea Urchin
VDSP (1986, 1989-1992) (Shallow, Deep)	Year	0.004	0.04	0.03
	Depth	0.005	0.0001	0.0005
	Year*Depth	n.s.	n.s.	n.s.
VDSP (1986, 1982-1992, 1999) (Shallow, Deep)	Year	0.0008	n.s.	0.03
	Depth	<0.0001	<0.0001	0.0001
	Year*Depth	n.s.	n.s.	n.s.
PCMR (1986, 1999) (Shallow, Deep)	Year	<0.0001	0.008	
	Depth	0.029	0.001	
	Year*Depth	0.034	n.s.	

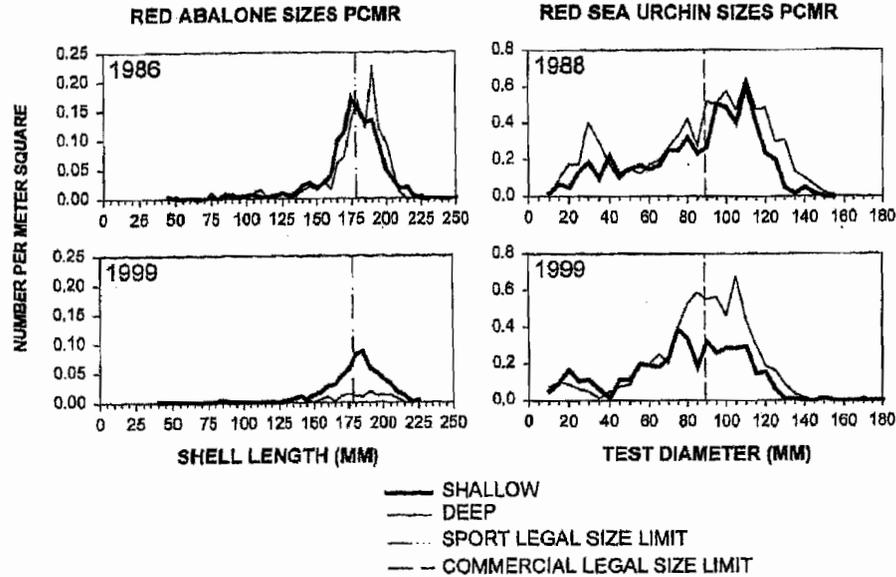


Figure 6. Size density of emergent red abalone and red sea urchin transects at PCMR at both shallow and deep depths. Years compared for red abalones are 1986 to 1999 and for red urchins 1988 to 1999. Vertical Lines represent minimum legal size for red abalone (178 mm) and red urchin (89 mm).

limit of 76 mm, first imposed in 1989 (Fig. 9). That mode declined through 1992 with little evidence of recruitment at either depth during that period. In 1999, a large cohort of red urchins, analogous to the earlier event for shallow water red abalones, had become established at deep depths with the peak, knife-edged, at the new 89 mm legal size limit, first imposed in June 1990.

Apparent Competitive Effects

Commercial landings of red sea urchins were first reported at the Van Damme area in 1985 (Fig. 10). Landings peaked at 800 mt in 1987, and declined along with CPUE (kg per diver day) through 1993. Size distributions of red urchins remained essentially flat from 1987 through 1990, becoming increasingly positively skewed by 1994 with few animals taken below the newly imposed size in 1990, and a decreasing number of animals larger than 120 mm taken (Fig. 11).

Surface kelp canopy at the VDSP area increased dramatically from 3 to 45 ha between 1982 and 1987. This coincided with increased red sea urchin removal (Fig. 10). *Nereocystis luetkeana* was the dominant kelp but the canopy also included *Macrocystis integrifolia*.

While the level of sport take was not monitored at VDSP, telephone surveys conducted from 1986 to 1989 estimated that

there were 30,000 to 40,000 sportsmen in the northern red abalone fishery (CDFG unpublished). In 1998, a \$12 stamp was instituted for the abalone sport fishery; 32,000 were sold in 1998, and 35,000 in 1999. VDSP is among the most highly utilized sport fishing sites in northern California. Creel surveys conducted at this site during spring and early summer since 1977 reveal continued high use with no decline in CPUE throughout our study period.

Red abalone size distributions from diver creels at VDSP can be segregated into pre- and post-onset of the sea urchin fishery. The first period, from 1977 through 1985, shows little change (Fig. 11). Size distributions during this period were highly skewed to the right, with the mode adjacent the sport legal size of 178 mm. Two of these years, 1983 and 1984, had the most positively skewed distributions with the lowest mean size of 188 mm. The second period (1986 to 1994) is characterized by dispersal into a flat distribution and an apparent modal progression from 182 mm in 1987 through 206 mm in 1992.

DISCUSSION

Spatial Interactions

There was a significant negative correlation between red abalones and red sea urchins at all sites and depths with the exception

TABLE 3.

Density matrix summarizing Spearman Rank Correlation test for red sea urchins compared to red abalones at low and high densities of each at Van Damme State Park (VDSP) and Point Cabrillo Marine Reserve (PCMR).

Species	Density	Red Abalones	
		Low	High (>0.4 per sq. m)
Red Sea Urchins	low	VDSP 1986 Shallow and 1989 Deep N = 29 n.s.	VDSP 1989-1992, 1999 Shallow and 1990-1992 Deep N = 101 $r_s = -0.22$ $p = 0.003$
	High (>1.0 per sq. m)	VDSP 1986 and 1999 Deep N = 18 $r_s = -0.63$ $p = 0.005$	PCMR 1986 and 1999 N = 60 $r_s = -0.52$ $p < 0.0001$

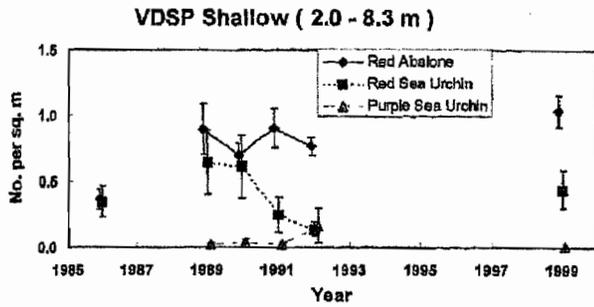


Figure 7. Red abalone, red sea urchin, and purple sea urchin densities (\pm se) at VDSP shallow depth stations in 1986, 1989 to 1992, and in 1999.

of deep-water stations at PCMR in 1999. This positive correlation is an artifact of data from only two stations; abalone were absent from 10 of 12 deep stations. The consistent negative correlation for all other comparisons suggests spatial interspecific exclusion between these two species. Deacon (1973) found a similar negative correlation between red abalones and red urchins in Sea Ranch, a northern California location between BMLR and VDSP. In 2000 we completed an additional 24 emergent transects, 13 deep and 11 shallow, at Salt Point State Park, located north of BMLR and south of VDSP (Bennett unpublished). Red urchins and red abalones were again negatively correlated in an area of high red abalone (0.84 m^{-2}) and low red urchin (0.90 m^{-2}) densities. Once more, red urchins were most abundant at deep and red abalones at shallow stations. Our finding of significant negative correlation at all but low densities of both red abalones and red urchins suggests that the observed spatial exclusion is density related. The increase in abalone abundance occurred during a period of increased surface

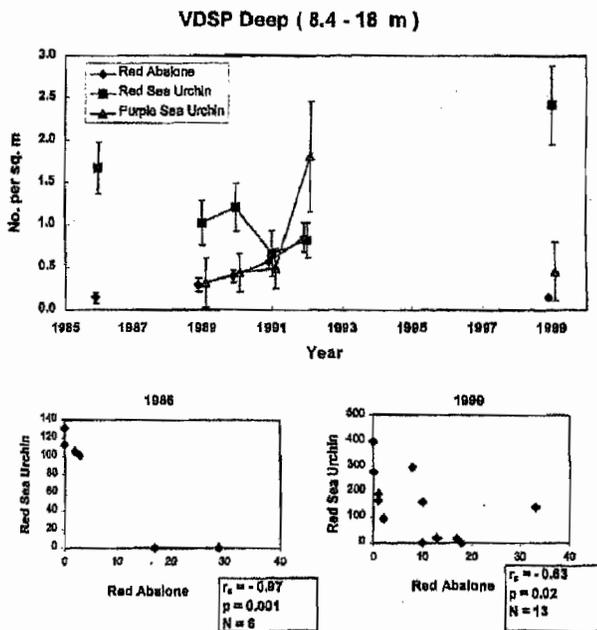


Figure 8. Red abalone, red sea urchin, and purple sea urchin densities (\pm se) at VDSP deep depth stations in 1986, 1989 to 1992, and 1999 with paired comparison of counts by species at each station with Spearman Rank correlation coefficients (r_s), statistical significance, and number of stations in 1986 and 1999.

canopy and therefore increased food abundance. Karpov et al. (1998) reported on the increase in abalone populations at VDSP at both depths from 1986 to 1992. Mechanisms responsible for this increase could include large-scale removal of potential competitors by the urchin fishery and positive effects on abalone growth due to increased kelp production.

The most profound lack of co-occurrence between red abalones and red sea urchins was at BMLR, the site with the least available macroalgae. This suggests competitive exclusion is greatest in habitat where food is limiting. It is likely that high silt loads from the Russian River (8 km to the north) and urchin grazing may limit kelp productivity in this area. Tegner et al. (1992) described areas adjacent to San Francisco Bay as marginal habitat, largely influenced by sediment loads from the bay. et al. (1997) reported comparable habitat to BMLR, with an absence of canopy and lack of understory algae below 13-m depth, off Fitzgerald Marine Reserve (another area near San Francisco Bay) in 1993. Canopy and understory kelps are the primary source of drift needed to support abalone as well as sea urchin populations (Deacon 1973, Tegner & Dayton 1991, Tegner et al. 1992).

The lack of correlation (positive or negative) between purple sea urchins and the other two species, at the scale of our transects, suggests that the spatial distribution of this species is not strongly correlated to the other two species. We note, however, that Schroeter (1978) found that the longer-spined red urchins exclude purple urchins from the most desirable habitat (within the m^2 scale) by spine fencing. The mechanism responsible for the increase in purple urchin abundance at both shallow and deep stations in VDSP may have been a release from competition for space as red sea urchin stocks declined due to fishing, or a strong coincident recruitment event. Off Sea Ranch, northern California, Deacon (1973) found a significant positive correlation between red urchins and purple urchins but no significant correlation between purple urchins and red abalones. Tegner et al (1989) observed significant increases in purple urchins at Johnson's Lee, Santa Rosa Island, an area that had also been subjected to intense fisheries for both red urchins and red abalones. Lafferty and Kushner (pers. comm.) reported periodic rapid increase and collapses of purple urchin populations off the northern Channel Islands in southern California from 1983 to 1998, with decreases due to starvation and disease following warming events. Our results and those of Tegner et al (1992) and Ebert and Russell (1988) are consistent with strong episodic recruitment for this species but do not clarify whether this follows release from competition for space.

Sea urchins are more adapted to periods of starvation than abalones, persisting for long periods on drift and microflora after macroalgae have disappeared from an area (Leighton 1968, Shepherd 1973, Tegner & Levin 1982). In spite of the overlap in their diet, red sea urchins have a more generalist feeding strategy than abalone (Leighton 1966). Abalones are essentially drift feeders, while sea urchins can act as drift feeders or can form feeding fronts that actively graze attached kelps when food is extremely limited (Harrold & Reed 1985). At both PCMR and VDSP, we found understory algae to be least abundant at deep depths, suggesting that food is more limiting at deeper depths. More drift algae at shallower depths have been observed at other sites in northern California (Rogers-Bennett et al. 1995).

The significant difference in red abalone and red sea urchin abundance by depth at VDSP and PCMR suggests differences in habitat preference between the two species. Greater numbers of red urchins were found at deeper stations and conversely greater num-

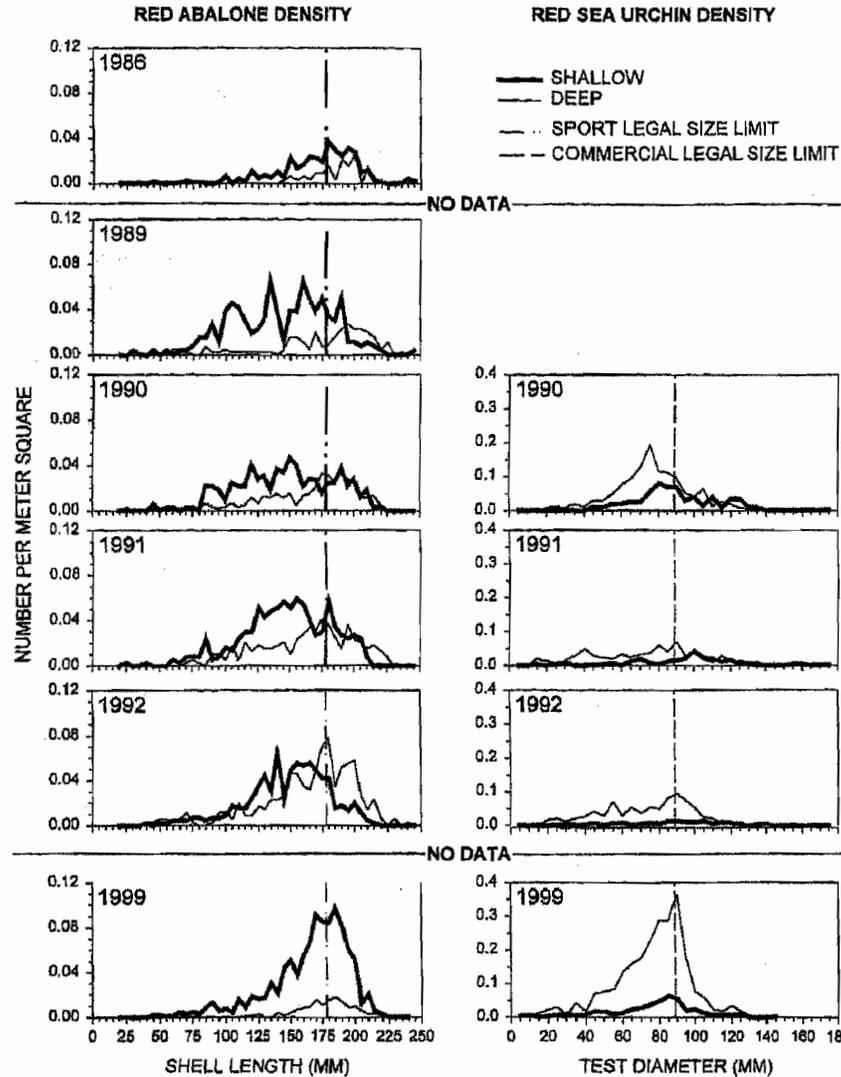


Figure 9. Red abalone and red sea urchin size density from emergent dive transects at VDSP at both shallow and deep depths. Years compared for red abalones are 1986, 1989-1992, and 1999; and for red urchins 1980-1992 and 1999. Vertical Lines represent minimum legal size for red abalone (178 mm) and red urchin (89 mm).

bers of red abalones at shallower depths. The absence of red abalones was most pronounced at deep depths off BMLR where food is most limiting, but was also apparent for abalones at VDSP, in spite of intense fishing pressure for abalone at shallow depths. The increased red abalone densities observed in deep stations at VDSP during the 1989 to 1992 period did not persist into 1999 and declined significantly following an increase in abundance of red urchins. A greater abundance of abalones at shallow depths in northern California may reflect their morphological adaptation to the high surge conditions found in shallow waters (Cox 1962, Deacon 1973). While both species prefer crevice habitats, especially in areas of high predation such as the sea otter range (Hines & Pearse 1982), urchins are more easily dislodged by wave action (Dayton 1973), and would be most vulnerable outside of crevices at shallow depths. In New Zealand, manipulative experiments reducing sea urchin densities enhanced the recruitment, survival, and growth of abalones (Andrew et al. 1998).

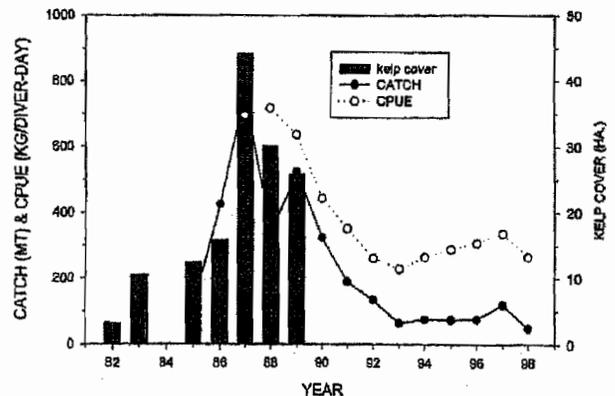


Figure 10. Commercial landings of red sea urchins, catch per unit effort (CPUE), and kelp canopy cover in the VDSP area.

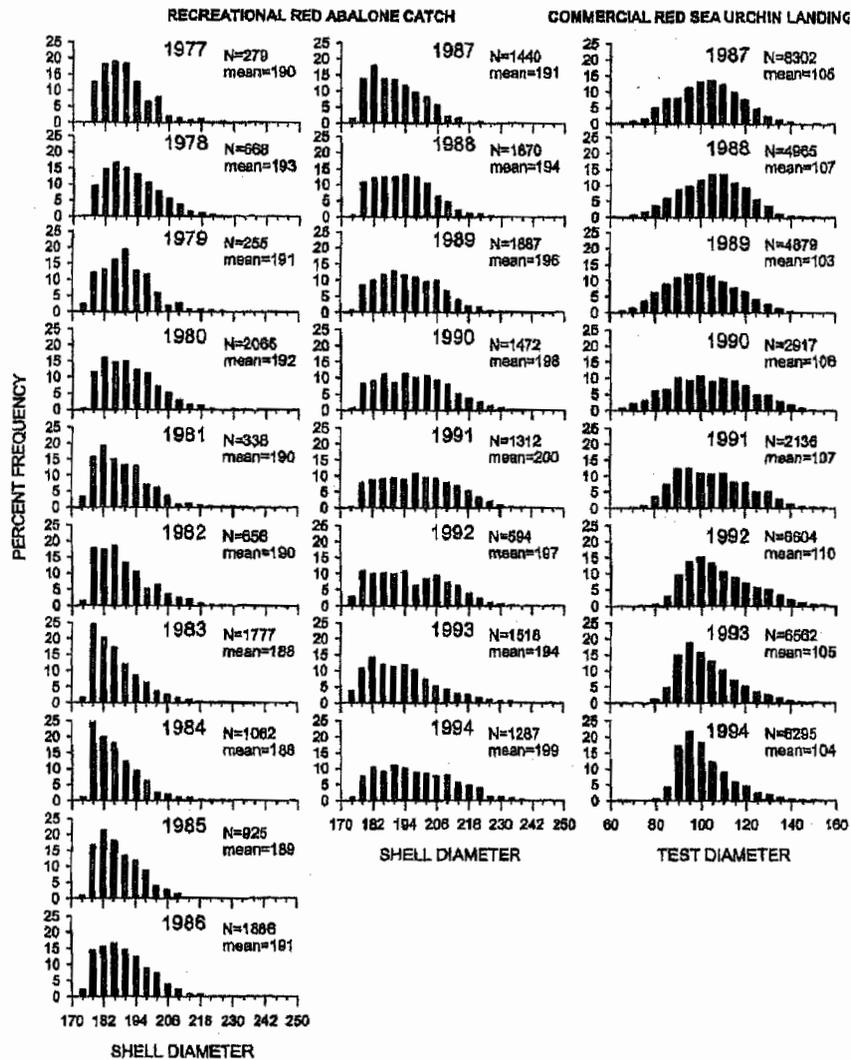


Figure 11. Size frequency distribution of commercial red sea urchins taken from the VDSP area from 1987 to 1994 with size of sport-diver-landed red abalones from 1977 through 1994. Legal minimum sizes are 178 mm for red abalones and 89 mm for red sea urchins.

Apparent Competitive Effects and Fishery Changes

Karpov et al. (1998) reported on the strong recovery in abalone populations in both depths at VDSP from 1986 to 1992. Both red sea urchin removal and enhanced abalone growth with increases in algal food are likely to have contributed to this increase in abalone abundance. Low kelp abundance observed at VDSP in 1982 and 1983 probably reflected the effect of grazing by an unfished population of red urchins. The rapid increase in kelp cover concurrent with high levels of urchin removal suggests kelp productivity and abundance increased along with removal of the sea urchins. Unfortunately, surface canopy aerial photographs were discontinued following 1989. Continued low levels of CPUE and increasingly skewed urchin size distributions in the fishery show that intense fishing continued throughout our study period.

Red abalone growth appears to be somewhat plastic and able to respond to increased food availability (Haaker et al. 1998). Modal progressions observed in size frequency distributions of sport-caught red abalones in the VDSP vicinity between 1987 and 1993

imply a growth rate of about 4 mm per year for abalone greater than about 180 mm shell length (SL) (Fig. 11). This growth rate is greater than observed in previous tag and recapture studies in northern California (Tegner et al. 1992) and southern California (Haaker et al. 1998). A DFG (unpublished) study at Van Damme from 1973 to 1977 based on 275 recaptured tagged red abalone showed an annual growth rate of <1 mm at sizes above 178 mm SL. While this is an area for more rigorous research, we propose a mechanism for this empirical observation of increased abalone growth at VDSP.

The importance of sea urchin grazing to the structure of kelp communities is well known (Nicholson 1970, Lawrence 1975, Harrold & Pearse 1987). Removal of an estimated 2,878 mt of red sea urchins from the VDSP area (approx. 3.5 km of coastline) from 1985 to 1993 coincided with an explosive increase in kelp canopy from 12.5 ha in 1985 to 44.2 ha in 1987 (Fig. 10). Concomitant with these events was a reduction in the larger size classes of red urchins. Red urchins ≥ 120 mm TD comprised 24.9% of the Mendocino County catch in 1992 (Mendocino County is used as a

proxy for the VDSP sea urchin catch, because of inadequate sampling at that location). By 1998, these sizes made up only 9.5% of the catch. This suggests a mechanism for the observed abalone growth rate increase, whereby removal of significant amounts of a primary macro-benthic grazer like sea urchins, as well as a continuing vigorous fishery for the abalones themselves, allowed release of the kelp canopy as well as subsurface kelps from grazing. This led to increased food availability for the remaining kelp grazers.

Red sea urchin size distributions by density at deep stations in 1999 showed peaks at 85–99 mm TD at PCMR and 80–94 mm TD at VDSP (Figs. 6 & 9). Based upon a combination of observational and experimental evidence, these peaks appear to be comprised primarily of a cohort that settled during the 1992–93 El Niño. Significant settlement events of red urchins were noted on artificial substrates monitored since 1990 at shallow subtidal stations at PCMR and Westport (about 30 km north of PCMR) in late spring and early summer 1992 and spring 1993 (Ebert et al. 1994). Subtidal surveys in the vicinity of PCMR in fall 1994 noted a strong cohort averaging 18 mm TD, 16 months following the spring 1993 artificial substrate settlement event (Kalvass & Hendrix 1997). Ebert (1997) developed a growth transition matrix for California red urchins with annual probabilities of transfer between 10 mm size groups. We applied these probabilities to the observed 1994 10–20 mm cohort and estimated that 63% would grow to the 80–100 mm size groups by the time we observed them in 1999 at both PCMR and VDSP. Growth of the observed cohort in 1994, from significant settlement events in 1992 and 1993, might account for much of the peak near the commercial red urchin minimum size limit of 89 mm TD observed in 1999 (Fig. 9).

Mechanisms

Our finding that red abalones are displaced from deep but not shallow depths at VDSP, combined with the negative correlation observed in abalones and red sea urchins at comparable densities in 1986, strongly suggests that competitive exclusion of red abalones has occurred. Disappearance of red abalone in deep water could have resulted from other mechanisms including illegal take (Daniels & Floren 1998), a major mortality event from disease (Lafferty & Kuris 1993), or movement to shallow depths during a period of successful red urchin recruitment.

Temporal changes in density at PCMR support the trend of exclusion of red abalones in deeper water but need to be interpreted cautiously. Densities were compared between two years bracketing a thirteen year interval and not a time series as sampled at VDSP. In addition, since only half of the same locations were resampled in 1999, spatial variations in habitat could have exaggerated (or underestimated) actual temporal differences in abundance (Thrush et al. 1994).

Red sea urchins in northern California appear to be much less mobile than red abalones. Ebert et al. (1999) tagged thousands of red urchins at 20 locations between southern California and south-east Alaska, for growth analysis. Recovery rates at these sites after approximately one year ranged from 13% to 76% for internally tagged urchins. These high recovery rates indicate that red urchins are relatively sessile. Conversely, red abalone tagging studies indicated abalone can move considerable distances. In a study at PCMR, Ault and DeMartini (1987) found that in an area of high abundance 11% of the tagged population moved over 90 m, with one animal moving 0.6 km. Similarly, high numbers of tagged red urchins (16–38%) were recovered after one year from sites in Salt

Point in northern California. Twice as many urchins were recovered from a shallow site compared with a deep site, suggesting urchins in shallow water are more sedentary (Rogers-Bennett 1994). Deacon (1973) also found that the vast majority of red urchins moved far less than red abalone, during movement experiments at Sea Ranch. In the spring of 1998 starving red abalone were reported by divers south of Noyo Bay, 14 km north of VDSP (Haaker & Karpov, unpub. obs.). They observed a marked absence of understory kelps with evidence of abalone undergoing unusual movements over foliose algae in search of food. One possible explanation for the decline in deep-water abalones off VDSP could be recent movement to shallow depths in search of food.

Continued low numbers of red sea urchins at shallow depths in Van Damme are expected, given the high density of red abalone remaining at shallow stations in 1999. Urchins could only survive at shallow depth in crevice areas protected from extreme sea conditions (Deacon 1973), and it is unlikely that red urchins could displace red abalones from such habitat once occupied. While we found that the removal of red sea urchins at shallow depths in VDSP appeared to enhance the abundance of adult red abalones, juvenile abalones are known to shelter under the spine canopy of red sea urchins, complicating the relationship between red abalones and red sea urchins (Tegner & Dayton 1977, Rogers-Bennett & Pearse 2001).

CONCLUSIONS

Our results suggest that spatial competition between red abalones and red sea urchins is density related and appears to be most pronounced in habitats where macroalgae are scarce. In kelp beds these species co-occur on transects more frequently but are negatively correlated when either species is in high abundance. Intense red urchin fishing at VDSP coupled with a major recruitment event of red abalones appears to have enhanced abalone density in both shallow and deep depths through 1992. This release from inter and intraspecific competition for space and food resulted in a large surplus abalone population at refuge depths through the early 1990s. However, significantly lower densities of abalone are now apparent at depth. A major recruitment event for red sea urchins appears to have depressed abalone populations at depth. We cannot rule out the possibility of movement, mortality, or poaching of deep water red abalones as causes for the decline. In the absence of fishing for both species, densities of red abalones at an adjacent PCMR reserve site are now below those found at the intensely fished area, while sea urchins have increased to greater numbers than fished abundance. With its high urchin abundance, PCMR kelp populations are also lower than at nearby VDSP. Together this suggests that fishing of both red urchins and red abalones at VDSP enhanced abalone densities. We therefore suggest that an ecosystem approach that takes into account multispecies interactions, should be an important consideration in managing these fisheries in northern California.

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