Indirect Benefits of Marine Protected Areas for Juvenile Abalone

LAURA ROGERS-BENNETT*‡ AND JOHN S. PEARSE†

*California Department of Fish and Game, Institute of Marine Sciences, University of California, Santa Cruz, Santa Cruz, CA 95064, U.S.A.

†Institute of Marine Sciences, University of California, Santa Cruz, Santa Cruz, CA 95064, U.S.A.

Abstract: *Marine protected areas (MPAs) designed to provide harvest refugia for red sea urchins* (Strongylocentrotus franciscanus) *offer a unique opportunity to study the indirect effects of urchin fishing on subtidal communities. Sea urchins may provide important cryptic microhabitat for juvenile abalone sheltering beneath urchin spines in shallow habitats worldwide. We investigated the abundance of juvenile (3–90 mm) red abalone, (*Haliotis rufescens) *and the rare flat (<90 mm) abalone (*H. walallensis) *on protected and fished rocky reefs in California. Abalone abundance surveys were conducted inside 24 × 30 m plots on three protected reefs with red sea urchins present and three fished reefs where red sea urchins were removed by commercial or experimental fishing. Significantly more juvenile abalone were found in 1996 and 1997 on protected reefs with urchins present than on fished reefs (χ² = 188, df = 1, p < 0.001). Juvenile red abalone abundance was not correlated with local adult red abalone abundance or habitat rugosity. One-third of the juveniles inside the MPAs were found under the urchins' spine canopy, as were a suite of unfished marine organisms. In the laboratory, juvenile abalone survived better (χ² = 7.31, df = 1, p < 0.01) in crab predation experiments in which red sea urchins were available as shelter. Fishing red urchins reduced structural complexity, potentially decreasing microhabitat available for juvenile abalone. This example demonstrates how MPAs designed for one fished species may help other species, illustrating their usefulness for ecosystem-based fishery management and marine conservation.*

Beneficios Indirectos de Áreas Marinas Protegidas para Juveniles de Abulón

Resumen: *Las áreas marinas protegidas (APM) diseñadas para proveer refugios contra cosechas de erizos marinos rojos (*Strongylocentrotus franciscanus) *ofrecen una oportunidad única para estudiar los efectos indirectos de la pesca de los erizos en comunidades de sub-mareas. A nivel mundial, los erizos pueden proveer microhábitat críptico importante para albergar abulones juveniles debajo de las espinas de los erizos en hábitats poco profundos. Investigamos la abundancia de juveniles (3–90 mm) de abulón rojo (*Haliotis rufescens) *y el raro abulón plano (*H. walallensis) *(<90 mm) en arrecifes rocosos protegidos y de pesca, en California. Los sondeos de abundancia de abulón fueron llevadas a cabo dentro de cuadrantes de 20 × 30 m en tres arrecifes protegidos con presencia de erizos marinos rojos y tres arrecifes con pesca donde los erizos marinos rojos fueron removidos por la pesca comercial o por pesca experimental. Encontramos significativamente más abulones juveniles en 1996 y 1997 en los arrecifes protegidos con erizos presentes que en los arrecifes con pesca (χ² = 188, gl = 1, p < 0.001). La abundancia de los abulones juveniles no estuvo correlacionada con la abundancia local de adultos de abulón rojo o con la rugosidad del hábitat. Un tercio de los abulones observados dentro de las APM fueron encontrados bajo el dosel de las espinas de los erizos, al igual que un grupo de organismos marinos no pescados. En el laboratorio, los abulones sobrevivieron mejor (χ² = 7.31, gl = 1, p < 0.01) en experimentos de depredación por cangrejos en los cuales los erizos marinos rojos eran una protección disponible. La pesca de los erizos rojos ha reducido la complejidad estructural, potencialmente disminuyendo el microhábitat disponible para los abulones juveniles. Este ejemplo demuestra el cómo las APM diseñadas para una especie pescada puede ayudar a otras especies, ilustrando su utilidad para el manejo y la conservación marina de pesquerías en base al ecosistema.*

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Introduction

Marine conservationists are increasingly concerned that fishing single species can have negative consequences for other species in marine communities (Dayton et al. 1995; Larkin 1996). One method for examining the indirect effects of fishing is to compare fished with "no take" or marine protected areas (MPAs). The establishment of MPAs has been advocated widely (Dugan & Davis 1993; Mangel et al. 1996; Roberts 1997 and references therein), but few empirical examples have demonstrated multispecies benefits beyond releasing the target species from fishing mortality. The use of MPAs as a fishery management strategy may be superior to single-species strategies if positive interspecific interactions (sensu Bertness & Leonard 1997) are maintained inside MPAs and lost in fished areas. Protected organisms may provide biological structure supporting habitat productivity and species richness (Jones et al. 1997), whereas fishing may reduce biological complexity and cause habitat degradation (Lenihan & Peterson 1998).

In the marine environment there are many examples of organisms structuring communities, including coral reefs (Reaka-Kudla 1997), kelp forests (Estes & Duggins 1995), and mussel beds (Suchanek 1978). Similarly, red sea urchins, (*Strongylocentrotus franciscanus*) enhance the structural complexity of subtidal communities, positively interacting with a suite of species (Tegner & Dayton 1977). Sea urchins have structurally complex spines that form a spine canopy under which organisms reside (Tegner & Dayton 1977; Rogers-Bennett et al. 1995).

Sea urchins are fished worldwide (Keesing & Hall 1998), but little is known about the indirect effects of urchin fishing on subtidal communities. In California, red urchins are one of the largest commercial fisheries where the state has removed in excess of 140,000 metric tons from 1988 to 1996 (Kalvass & Hendrix 1997). In northern California, heavy fishing pressure has resulted in a 10-fold decrease in red urchin landings from 1988 to 1996. Potential direct effects of recruitment overfishing include (1) poor urchin fertilization success (Levitan et al. 1992) and (2) poor juvenile urchin survival (Tegner & Dayton 1977; Sloan et al. 1987; Rogers-Bennett et al. 1998).

We examined the indirect effects of sea urchin fishing on benthic marine organisms in California. We compared the relative abundance of juvenile abalone between three MPAs where red urchins are abundant and three fished areas where red urchins have been removed by commercial or experimental fishing. We focused on the abundance of juvenile abalone for three reasons: (1) juvenile abalone have been observed in close association with the urchin spine canopy (Tegner & Dayton 1977; Kojima 1981; Tegner & Butler 1989; Rogers-Bennett & Pearse 1998), (2) the commercial abalone fishery has collapsed (Karpov et al. 2000) and is now closed (California Senate 1997), and (3) there is an active recreational fishery for red abalone in northern California. We examined two species of abalone: the fished red abalone (*Haliotis rufescens*) and the rare flat abalone (*H. walallensis*). We discuss the hypothesis that MPAs and urchin spine canopy are responsible for observed patterns as well as the implications for management and restoration.

Study Sites and Methods

Study reefs were located in rocky subtidal habitats along the central and northern California coast. Reefs ranged from 39° to 37° degrees latitude at the Caspar Urchin Closure (lat. 39°21′491″N, long. 123°49′475″W), Van Damme State Park (lat. 39°16′08″N, long. 123°47′58″W), Salt Point Urchin Closure (lat. 38°33′06″N, long. 123°19′45″W), the Bodega Marine Life Refuge (BMLR, north and south; lat. 38°19′03″N, long. 123°04′12″W), and Half Moon Bay (HMB; lat. 37°29′470″N, long. 122°29′690″W) (Fig. 1). Each site was 24 × 30 m (720 m^2) in an area of high-quality juvenile abalone habitat: shallow (5–8 m) rocky reefs with cryptic microhabitats, abundant algae, and little silt or sand. Red sea urchins were abundant at the three sites where commercial urchin fishing is prohibited—Caspar, Salt Point, and BMLR north—whereas Van Damme, BMLR south, and HMB, lacked urchins entirely. The north and the south sites of the BMLR are inside the MPA; at the south site we conducted an experimental urchin harvest, removing 533 urchins to examine the effects on juvenile sea urchin abundance (Rogers-Bennett et al. 1998). Neither recreational nor commercial fishing is permitted in the BMLR, which was established in 1965. The HMB site was heavily commercially fished, resulting in the removal of adult abalone and urchins. Recreational red abalone fishing is permitted (abalone >178 mm) at Caspar, Van Damme, Salt Point, and HMB.

We investigated whether the abundance of juvenile abalone differed in fished and protected sites at the regional scale in northern California. To do this, we determined juvenile abalone abundance at six sites (three fished and three protected) in early October 1996 and late August 1997. We invasively surveyed six parallel 4 × 30 m transects (720 m^2), searching all cryptic microhabitat: under red urchins, in rock crevices, under moveable cobble, and within coralline and fleshy red algae. The six transects were not statistically independent sampling units and were used simply for a complete search of the area. The relevant sampling unit is the 24 × 30 m site. We compared the number of juvenile abalone between the protected and fished sites using nonparametric chi-square in 1996 and 1997 because recruitment typically varies temporally. We recorded the spatial distribution of juveniles and their size in 1997 only to examine size-specific distribution patterns. All juvenile abalone were brought to the laboratory and killed for
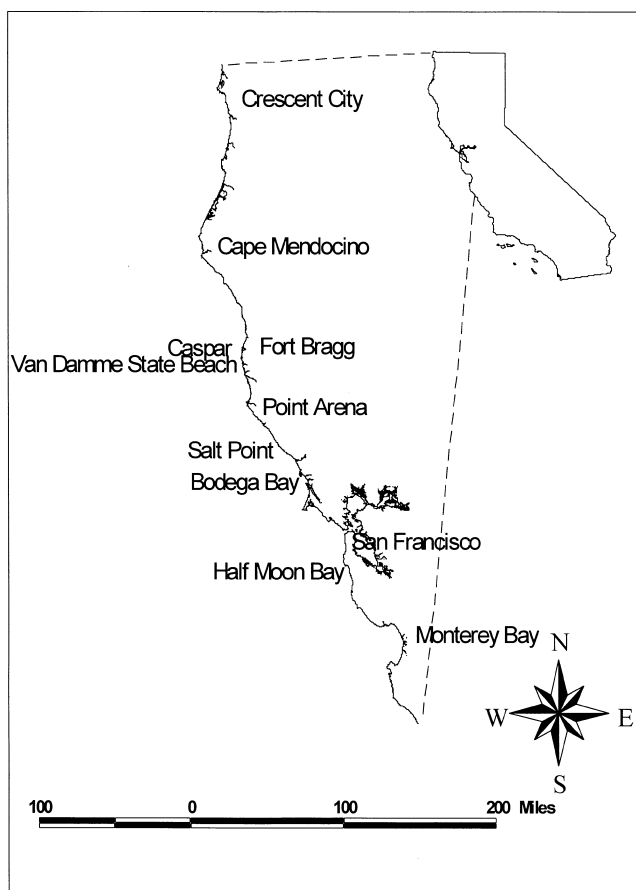
Figure 1. Map of six study sites in California. Three are marine protected areas (Caspar, Salt Point, and Bodega Marine Life Refuge South) in which red sea urchin fishing is prohibited, and three are heavily fished sites (Van Damme, Bodega Marine Life Refuge North, and Half Moon Bay).

species and size determinations; therefore juvenile abalone sampled in 1996 were not sampled again in 1997.

The number of red sea urchins and adult red abalone was quantified for one-third of the site and then multiplied by three. We ranked sites based on the abundance of juvenile red abalone, using Kendall rank correlation tau to determine whether juvenile abundance was correlated with adult abalone abundance. A relative measure of topographic evenness (rugosity = straight-line 30 m/contour distance) (Coyer & Witman 1990) was determined along three, 30-m transects at each site.

Laboratory experiments were conducted to test whether equal numbers of juvenile red abalone were eaten by crab predators with and without cover provided by adult red sea urchins. Two large circular tanks (3.25 m in diameter) with aereated static seawater (10–12ml/l; 12–13° C) at a depth of 18 cm were placed in a cold room. A combination of six large rocks (162–249 mm diameter) placed equidistant from each other and six adult red sea urchins (73–121 mm test diameter) were placed

in one tank. In the other tank, six rocks of comparable size were placed in the tank without adult urchins. Twenty juvenile red abalone ranging in size from 13 to 30 mm were added to the middle of the tank floor. Juvenile abalone were allowed to move into cryptic microhabitats; this acclimation period ranged from 6 to 12 hours. Three red rock crabs, (*Cancer productus*, 114–118 mm carapace width) or three green crabs (*Carcinus maenas*, 54–73 mm carapace width) were added to initiate the experiment and were allowed to feed until approximately half the juvenile abalone had been consumed. At the end of the trial, the locations of the surviving juvenile abalone were recorded and the juveniles were returned to holding tanks with running seawater to be used in future trials. Six replicate trials were conducted for each shelter treatment, three with red rock crabs and three with green crabs.

Results

In 1996 and 1997, juvenile abalone were found in high abundances inside MPAs on rocky reefs with red sea urchins present and in significantly lower abundances on reefs where urchins had been removed in both 1996 ($\chi^2 = 104.6$, df = 1, $p < 0.001$) and 1997 ($\chi^2 = 90.9$, df = 1, $p < 0.001$) (Table 1). Similarly, the number of flat abalone was also significantly greater inside the MPAs than outside the MPAs in both 1996 ($\chi^2 = 17.6$, df = 1, $p < 0.001$) and 1997 ($\chi^2 = 6.1$, df = 1, $p < 0.05$). Inside the MPAs, the sites with the greatest number of urchins also had the greatest numbers of juvenile abalone (Table 1). Juvenile abalone abundance was not significantly correlated with local adult abalone abundance (Table 2) or with mean rugosity. Salt Point exhibited the greatest mean rugosity, (30/42.6 m), HMB had the lowest mean rugosity, (30/34.9 m), and the other four sites fell in between (30/37 m).

In 1997, one-third of the juvenile abalone found ($n = 154$) in the MPAs were distributed under the spine canopy of red urchins (Fig. 2) and the remaining two-thirds were in other cryptic microhabitats. Small juvenile abalone (3–25 mm) were more abundant under urchins than large juvenile abalone (30–65 mm) in 1997 (Fig. 2). In 1996, 45% of the juvenile abalone ($n = 94$) were observed under the spine canopy of adult red urchins at Salt Point and BMLR north (the size and spatial distribution pattens were not recorded at Caspar). Overall, flat abalone were rare (14%) and were not found in the three southern sites.

A wide variety of small (<30 mm) marine organisms sheltered under the urchin spine canopy, including juvenile red and purple urchins, (*S. purpuratus*), juvenile sea stars, ophiuroids, snails (e.g., *Amphissa versicolor*), limpets, chitons, rock crabs, flat fuzzy crabs (*Hapalogaster cavicauda*), helmet crabs, hermit crabs, porcelain crabs, amphipods, scale worms, and polychaetes.

Table 1. Number of juvenile (3–90 mm) red abalone (*Haliotis rufescens*) and flat abalone (*Haliotis walallensis*) found in fished and protected sites (each 720 m^2) in northern California.

	Protected sites			Fished sites		
	Caspar	*Salt Point*	*BMLR North*	*Van Damme*	*Half Moon Bay*	*BMLR South*
1996						
H. rufescens	57	56	15	7	0	9
H. walallensis	11	12	0	2	0	0
Total		151			18	
1997						
H. rufescens	139	27	8	39	0	2
H. walallensis	18	5	0	9	0	0
Total		197			50	
No. of adult urchins	1011	600	66	0	0	0

In the laboratory, significantly more ($\chi^2 = 7.3$, df = 1, $p < 0.01$) juvenile red abalone survived predation experiments in which adult red sea urchins were available as alternate shelter (Table 3). More than one-third ($n = 30$) of all surviving juvenile red abalone that could be visually mapped at the end of each trial ($n = 76$) were found sheltered under adult red urchins. Both red and green crabs readily consumed juvenile red abalone. The duration of the predation trials differed between the crab species, with red rock crab trials ranging from 2.5 to 6 hours and green crab trials ranging from 9 to 12 hours, presumably as a result of differences in crab size and claw morphology.

Discussion

Our findings are consistent with the hypothesis that the biological structure (urchin beds) maintained inside protected areas, where sea urchin fishing was prohibited, had a positive effect on the abundance of juvenile abalone and possibly other benthic organisms. Fished sites in which red sea urchins were absent had significantly fewer juvenile abalone than protected sites, irrespective of differences in geography and habitat (rugosity). Juvenile abalone abundance was not correlated with local adult abundance (Table 2), despite the short planktonic

period (7–8 days). Furthermore, our field experiment in the BMLR showed that the site with urchins had more juvenile abalone than the site where we had experimentally fished out the urchins. Experimental removals of urchins in southern California (Tegner & Dayton 1977) and in South Africa (Tarr et al. 1996; S. Mayfield personal communication) also had negative effects on juvenile abalone abundances. In addition, urchin fishing has been shown to negatively affect juvenile urchin densities (Tegner & Dayton 1977; Sloan et al. 1987; Rogers-Bennett et al. 1998). Urchins also provided shelter for a suite of benthic organisms from several phyla. This suggests that other species residing in the spine canopy microhabitat may benefit from the shelter provided by red sea urchins in MPAs. The physical structure created by red urchins may be akin to that provided by mussel beds (Suchanek 1978; Witman 1985).

Flat abalone were more abundant inside MPAs. In our study, 14% of the abalone were flat abalone, whereas in a recent survey conducted in HMB, 5% were flat abalone (Karpov et al. 1997). More than a decade ago, flat abalone surveys indicated that this species was twice as
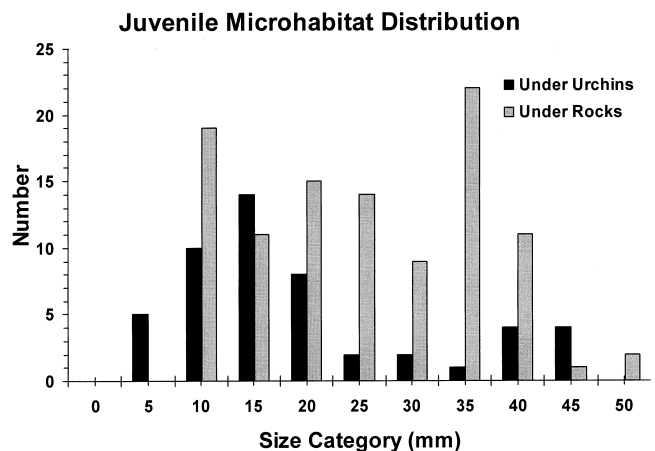
Table 2. Numbers of juvenile (3–90 mm) red abalone (*Haliotis rufescens*) and flat abalone (*H. walallensis*) in northern California in 1996 and 1997 compared with the total number of adult red abalone (>90 mm) found in fished and protected sites (720 m^2).

Site	No. juvenile abalone	No. adult abalone
Caspar	225	117
Salt Point	100	351
BMLR North	23	144
Van Damme	57	726
HMB	0	0
BMLR South	11	408

Figure 2. Spatial distribution of wild juvenile abalone in sites with red sea urchins present in 1997.

Table 3.   Number of juvenile red abalone surviving crab predation experiments conducted in the laboratory.*

	Shelter treatment	
Trial and crab predator	rocks and urchins	rocks alone
1. red rock crab	16	8
2. red rock crab	20	12
3. red rock crab	15	11
4. green crabs	5	1
5. green crabs	10	3
6. green crabs	6	8
Total	72	43

*Twenty juvenile red abalone were added at the start of each predation trial.

Table 4.   Abundance of flat abalone (*Haliotis walallensis*) compared with the total number of abalone observed in this and previous studies in California.

Investigators	No. flat abalone (total)	Flat abalone (%)
Lowry & Pearse 1974	25 (81)	31
Cooper et al. 1977	51 (135)	38
Hines & Pearse 1982	30 (112)	27
Karpov et al. 1997	2 (40)	5
This study	57 (416)	14

abundant (32%) (Table 4). White abalone (*H. sorensoni*) in southern California are nearly extinct (Davis et al. 1996; Tegner et al. 1996), and there has been serial depletion of five abalone species in southern California (Karpov et al. 2000). Restoration plans are now being formulated.

In the laboratory, more juvenile red abalone survived crab predation when adult red sea urchins were present, in addition to rocks than when rocks were the only shelter available (Table 3). Red rock crabs ate more juvenile abalone per hour than green crabs, which have smaller bodies and more slender claws. Green crabs, which have been recently introduced to California, are not found in open coast habitat with urchins and juvenile abalone. Experiments conducted in Japan have shown that the presence of urchins (*Anthocidaris crassispina*) increases the search time required by octopuses to find and eat juvenile abalone (*H. discus discus*) in aquaria and that juvenile abalone in the wild resided under the spines of urchins (S. Kiyomoto, personal communication). The presence of sea urchins also enhanced the recovery of hatchery-reared juvenile abalone stocked in the ocean in Japan (Kojima 1981) and in northern California (Rogers-Bennett & Pearse 1998).

Variance in the abundance of juvenile marine invertebrates, however, is difficult to attribute to a single factor. There were consistent patterns observed in 1996 and 1997, but this study was short term in nature thus should be continued. A latitudinal gradient in the abundance of juvenile abalone appeared in 1996, but this pattern did not hold in 1997. The relationship between latitude and fishing pressure could also play a role. An alternative hypothesis to explain the pattern we found is that juvenile abalone abundance is related to oceanographic features that supply larvae to sites. Although we found a poor relationship between the number of adults and juvenile abalone at each of the sites (Table 2) and although larval abalone dispersal may be limited, more work is needed to evaluate the role of larval supply.

Fishery Management Implications

We found that the positive sheltering interaction between adult urchins and juvenile abalone is maintained inside MPAs. Other examples of positive interspecific associations can be found in the ecological literature, but these are rarely interpreted in the context of fishery management. Concepts such as ecosystem health, ecological integrity, and intact communities are often poorly defined in the conservation literature (Simberloff 1998) and difficult for resource managers to implement. Nevertheless, managers are interested in identifying "essential fish habitat," defined in the Magnuson-Stevens Fishery Conservation and Management Act (National Marine Fisheries Service 1997) as "waters and substrate necessary to fish spawning, breeding, feeding, or growth to maturity." Our results suggest that the biological structure provided by urchins is essential fish habitat for juvenile abalone and possibly for a number of unfished species.

To preserve urchin spine-canopy microhabitat, managers could establish a system of MPAs or institute a maximum size limit to protect large urchins (T. Ebert, personal communication). Experiments show that without MPAs or a maximum legal size, 95% of the urchins in the San Juan Channel in Washington state are removed (Carter 1999). In southern California, however, many urchins smaller than the minimum legal size remain after fishing, albeit at low densities. Protecting urchin spine canopy in shallow habitats has been proposed as a management strategy for California's red urchin fishery (Rogers-Bennett et al. 1995). Our results illustrate how a management strategy including a system of MPAs could function to enhance more than one fished species, supporting multispecies or ecosystem-based fishery management and marine conservation (Norse 1993; Dayton et al. 1995; Larkin 1996).

Acknowledgments

Literature Cited

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78:** 1976–1989.

California Senate. 1997. Senate bill 463. Available from Senate Publications, Sacramento, California. (also available at www.senate.ca.gov).

Carter, S. 1999. Ecosystem effects of sea otter predation and commercial sea urchin harvest on nearshore benthic communities in northern Washington. M.S. thesis. University of Washington, Seattle.

Cooper, J., M. Wieland, and A. Hines. 1977. Subtidal abalone populations in an area inhabited by sea otters. Veliger **20:**163–167.

Coyer, J. D., and J. D. Witman. 1990. Underwater catalog: a guide to methods and research. Shoals Marine Laboratory, New York Sea Grant, Ithaca.

Davis, G. D., P. L. Haaker, and D. V. Richards. 1996. Status and trends of white abalone in the California Channel Islands. Transactions of the American Fisheries Society **125:**42–48.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems **5:**205–232.

Dugan, J. E., and G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences **50:**2029–2042.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs **65:**75–100.

Hines, A. H., and J. S. Pearse. 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology **63:**1547–1560.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78:** 1946–1957.

Kalvass, P. E., and J. M. Hendrix. 1997. The California red sea urchin, *Strongylocentrotus franciscanus*, fishery: catch, effort, and management trends. Marine Fisheries Review **59:**1–17.

Karpov, K., J. Geibel, and P. Law. 1997. Relative abundance and size composition of subtidal abalone *Haliotis* spp., sea urchin *Strongylocentrotus* spp. and abundance of sea stars off Fitzgerald Marine Reserve, Sept. 1993. Technical report 97–1. California Department of Fish and Game Marine Resources, Sacramento, California.

Karpov, K., P. L. Haaker, I. Taniguchi, and L. Rogers-Bennett. 2000. Serial depletion and the collapse of the California abalone fishery. Canadian Special Publication Fisheries and Aquatic Sciences **130:** 11–24.

Keesing, J. K., and K. C. Hall. 1998. Review of harvests and status of

worlds sea urchin fisheries points to opportunities for aquaculture. Journal Shellfish Research **17:**1597–1604.

Kojima, H. 1981. Mortality of young Japanese black abalone *Haliotis discus discus* after transplantation. Bulletin of the Japanese Society of Scientific Fisheries **47:**151–159.

Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. Reviews in Fish Biology and Fisheries **6:**139–164.

Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances the impacts of hypoxia on oyster reefs. Ecological Applications **8:**128–140.

Levitan, D. R., M. A. Sewell, and F.-S. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology **73:**248–254.

Lowry, L., and J. S. Pearse. 1974. Abalones and sea urchins in an area inhabited by sea otters. Marine Biology **23:**213–219.

Mangel et al. 1996. Principles for the conservation of wild living resources. Ecological Applications **6:**338–367.

National Marine Fisheries Service. 1997. Proposed rule. Magnuson Act Provisions: essential fish habitat (EFH). Federal Register **62:**19723–19732.

Norse, E. 1993. Global marine biological diversity. Island Press, Washington, D.C.

Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: a comparison with rain forests. Pages 83–108 in M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, D.C.

Roberts, C. M. 1997. Ecological advice for the global fisheries crisis. Trends in Ecology and Evolution **12:**35–38.

Rogers-Bennett, L., and J. S. Pearse. 1998. Experimental seeding of hatchery-reared juvenile red abalone in northern California. Journal Shellfish Research **17:**877–880.

Rogers-Bennett, L., W. A. Bennett, H. C. Fastenau, and C. M. Dewees. 1995. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. Ecological Applications **5:** 1171–1180.

Rogers-Bennett, L., H. C. Fastenau, and C. M. Dewees. 1998. Recovery of red sea urchin beds following experimental harvest. Pages 805–809 in R. Mooi and M. Telford, editors. *Echinoderms: San Francisco*. Proceedings of the 9th international echinoderm conference. A.A. Balkema, Rotterdam, The Netherlands.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? Biological Conservation **83:**247–257.

Sloan, N. A., C. P. Lauridsen, and R. M. Harbo. 1987. Recruitment characteristics of the commercially harvested red sea urchin *Strongylocentrotus franciscanus* in southern British Columbia, Canada. Fisheries Research **5:**55–69.

Suchanek, T. H. 1978. The *Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. Ph.D. dissertation. University of Washington, Seattle.

Tarr, R. J. Q., P. V. G. Williams, and A. J. McKenzie. 1996. Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. South African Journal of Marine Science **17:** 319–323.

Tegner, M. J., and P. K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science **196:**324–326.

Tegner, M. J., and R. A. Butler. 1989. Abalone seeding. Pages 157–182 in K. O. Hahn, editor. *Handbook of culture of abalone and other marine gastropods*. CRC Press, Boca Raton, Florida.

Tegner, M. J., L. V. Basch, and P. K. Dayton. 1996. Near extinction of an exploited marine invertebrate. Trends in Ecology and Evolution **11:**278–280.

Witman, J. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecological Monographs **55:** 421–445.