Using Spatially Explicit Data to Evaluate Marine Protected Areas for Abalone in Southern California

LAURA ROGERS-BENNETT,* PETER L. HAAKER,† KONSTANTIN A. KARPOV,‡ AND DAVID J. KUSHNER§

*California Department of Fish and Game, University of California, Institute of Marine Sciences, University of California Santa Cruz and Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, U.S.A., email rogersbennett@ucdavis.edu
†California Department of Fish and Game, 4665 Lampson Avenue, Suite C, Los Alamitos, CA 90720, U.S.A.
‡California Department of Fish and Game, 19160 S. Harbor Drive, Fort Bragg, CA 95437, U.S.A.
§Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA 93001, U.S.A.

Abstract: *Abalone populations have declined dramatically in southern California. The white abalone (*Haliotis sorenseni*) is now (2001) on the federal endangered species list. To aid in the restoration of white, pink (*H. corrugata*), and green abalone (*H. fulgens*), productive marine protected areas need to be selected. We used spatially explicit fishery data (1950–1995) to identify the most productive marine areas in southern California. To assess the role of existing marine protected areas we compared fishery-independent data (1983–2001) inside protected and fished areas. San Clemente Island produced the greatest cumulative catches of white, pink, and green abalone, the most white abalone per hectare of deep reef (25–65 m), and the most green abalone per kilometer of rocky shoreline. Santa Barbara Island, however, produced 10 times more pink abalone per hectare of kelp canopy, making this area an excellent candidate for restoration and protection. Pink abalone surveyed in the Kelp Forest Monitoring Program were most abundant at three sites surrounding Anacapa Island: (1) protected, (2) protected but less visible, and (3) fished. The protected sites, despite having lower abundances of pink abalone initially (1983), had significantly more abalone (*$H = 9.0$; $df = 2$; $p = 0.011$*) than the nearby fished site over time. Size-frequency distributions revealed that the protected site had more (30%) commercial-size abalone (≥158 mm shell length) than the less visable site (6%) or the fished site (2%). Mean size was significantly larger at the protected site, yielding the highest estimate of biomass and potential egg production (2555 million eggs/site/year) of all the sites. Marine protected areas need to be selected and enforced so that abalone-restoration efforts can be enacted before remnant populations die. Restoration sites for a wide variety of depleted species can be selected based on previous levels of productivity identified by spatially explicit data.*

Utilización de Datos Espacialmente Explícitos para Evaluar Áreas Marinas Protegidas para Abalón en California Meridional

Resumen: *Las poblaciones de abalón han declinado dramáticamente en California meridional. El abalón blanco (*Haliotis sorenseni*) ahora (2001) está en la lista federal de especies en peligro de extinción. Para ayudar a la restauración del abalón blanco, el rosado (*H. corrugata*) y el verde (*H. fulgens*), se necesita seleccionar áreas marinas protegidas productivas. Utilizamos datos de la industria pesquera (1950–1995) espacialmente explícitos para identificar las áreas marinas más productivas de California meridional. Para evaluar el papel de las áreas marinas protegidas existentes comparamos datos independientes de la industria pesquera (1983–2001) dentro de áreas protegidas y áreas explotadas. La isla de San Clemente produjo las mayores capturas acumulativas de abalón blanco, rosado y verde, la mayor densidad de abalón blanco por hectárea de arrecife profundo (25–65 m), y la mayor densidad de abalón verde por kilómetro de litoral rocoso. Sin embargo, la isla de Santa Bárbara produjo 10 veces más abalón rosado por hectárea de quelpo, haciendo esta área un candidato excelente para la restauración y protección. Los abalones rosados examina-*

Paper submitted January 3, 2001; revised manuscript accepted April 3, 2002.

dos en el Programa de Monitoreo del Bosque de Quelpo fueron más abundantes en tres sitios alrededor de la isla de Anacapa: (1) protegido, (2) protegido, pero menos visible y (3) explotado. Los sitios protegidos, a pesar de tener menor abundancia de abalón rosado inicialmente (1983), en el largo plazo tenían significativamente más abalón ($H = 9.0$*; gl = 2;* $p = 0.011$*) que el sitio explotado próximo. La distribución de frecuencias de tamaño reveló que el sitio protegido tenía más (30%) abalón de talla comercial (≥158 mm longitud de la concha) que el sitio no regulado (6%) o el sitio explotado (2%). La talla promedio era perceptiblemente más grande en el sitio protegido, rindiendo la estimación más alta de biomasa y de producción potencial de huevos (2555 millones de huevos/sitio/año) comparadas con los otros sitios. Las áreas marinas protegidas deben ser seleccionadas y reguladas para poder decretar esfuerzos de restauración del abalón antes de que las poblaciones remanentes mueran. Los sitios de restauración para una amplia variedad de poblaciones agotadas se pueden seleccionar con base en los niveles de la productividad anteriores identificados por datos espacialmente explícitos.*

Introduction

Abalone fisheries are in decline around the world (Tegner et al. 1992; Shepherd & Brown 1993; see review by Campbell 2000). In southern California, there has been serial depletion of five abalone species (Dugan & Davis 1993; Karpov et al. 2000). Spatial depletion has also occurred, with the fishing grounds closest to port being depleted first (Karpov et al. 2000). Both California's commercial fishery and its recreational fishery south of San Francisco are now closed (California Senate 1997). Population declines have been so severe that white abalone (*Haliotis sorenseni*) now face extinction (Davis et al. 1996, 1998; Tegner et al. 1996) and have been designated (1997) an endangered species under the U.S. Endangered Species Act of 1973 (Hobday & Tegner 2000). White abalone densities averaged 2–10,000/ha on deep reefs in the 1970s (Tutschulte 1976). In 2000, submersible surveys found densities of <21/ha (P.L.H. et al., unpublished data). The black (*H. cracherodi*) and the green abalone (*H. fulgens*) are also likely candidates for the endangered species list. Restoration plans for pink (*H. corrugata*), green, and white abalone are mandated in California to be incorporated in an abalone restoration and management plan due in January 2003 (California Department of Fish and Game [CDFG] code, section 5522). Restoration work needs to be enacted now, however, before the remaining individuals die of natural causes.

One enhancement strategy that has been suggested as a tool with which to restore southern California's abalone is the aggregation of broodstock within closed marine protected areas (MPAs) (Tegner 1993; Tegner 2000). Aggregation has been proposed because fishery closure alone has not restored pink, green, and red abalone populations along the Palos Verdes Peninsula even after 15 years (CDFG, unpublished data), and recoveries of stocked juveniles have been low (Rogers-Bennett & Pearse 1998; Tegner 2000). Poor recovery at low population levels may be due to a combination of life-history traits such as poor fertilization success at low densities (Babcock & Keesing 1999) and a short planktonic period (6–9 days), which suggests that restoration through dispersal may be limited. Recovery may also be confounded by changes in community structure, such as the red sea urchin (*Strongylocentrotus franciscanus*) fishery being absent prior to 1971. Furthermore, sites where adult green abalone were aggregated showed enhanced recruitment compared with control sites in one study in southern California (Tegner 1993). These results suggest that abalone recovery may be enhanced with human intervention (Tegner 1993), but the selection of productive sites will be critical because abalone are rare and aggregating adults will be costly. Enforcement will also be important if abalone are aggregated because there will be an increased risk of illegal fishing (Daniels & Floren 1998).

One exception to this pattern of decline is red abalone (*H. rufescens*) in northern California. Landings from 1998–2000 averaged 1200 metric tons/year, and catch per unit effort estimates (25 years) in this recreational-only fishery remain high (CDFG, unpublished data). Management in this fishery includes size limits, bag limits, and season closures (Cox 1962). Divers are also prohibited from using SCUBA, resulting in a large de facto refuge in deep water (>8.4 m) (Karpov et al. 1998). Fisheries that are sustainable frequently include large spatial closures in which a portion of the population is excluded from the fishery, intentionally or unintentionally (Walters & MacGuire 1996). Although the California abalone fishery has had a history of both de facto and mandated closures (Edwards 1913), little work has been conducted to examine the efficacy of closed areas for abalone management and conservation.

We examined two aspects of abalone productivity: (1) spatial productivity of the commercial fishery to guide the selection of MPAs for abalone restoration and (2) potential egg production of abalone inside and outside of existing protected areas to assess the efficacy of MPAs for abalone restoration. We used a time series of fishery catch data, which is spatially explicit, to determine which areas historically have produced the largest catches of pink, green, and white abalone. To quantify biomass we determined catch per unit of appropriate habitat for each of the three abalone species. Next, we used an 18-year time series of fishery-independent data for pink abalone to examine the effectiveness of existing MPAs. Density and size-frequency information exists for pink abalone inside two "no-take" MPAs and one fished area on Anacapa Island in southern California. We compared the density, sizes, number of juveniles, and estimates of potential egg production at the three sites. We discuss the urgency of implementing pink abalone restoration areas and the role of enforcement.

Methods

Abalone Distribution and Commercial-Fishery Catch Data

We examined the spatial productivity (metric tons extracted per area) for three species of abalone from southern California. Fishery data exist for all three species in 12 catch areas. Each species has a unique depth distribution and habitat requirements. Pink abalone are distributed from 3 to 30 m primarily within kelp beds (Tutschulte 1976). Green abalone live predominantly in intertidal and shallow water areas (0–15 m) (Tutschulte 1976). White abalone are now a deep-water species frequently found at the interface between rock and sand on reefs and offshore banks at depths ranging from 25 to 65 m (Cox 1962; Davis et al. 1998). Historical evidence suggests that white abalone were found at shallower depths prior to and during the peak of the fishery in the early 1970s (B. Owen, personal communication). Fishery-independent data exist only for pink abalone. This species occurs within intermediate SCUBA depths (6–15 m).

We analyzed spatially explicit fishery catch data to determine the historic productivity of abalone fishing areas in southern California. We combined catches of pink, green, and white abalone from 1950 to 1995 in 12 catch areas in southern California: 3 southern mainland areas, 8 island areas, and offshore banks (Fig. 1). Catch data are reports by divers of the number of abalone fished from CDFG statistical blocks measuring 10′ latitude × 10′ longitude (linear measure approximately 18.53 km) in a day. Numbers of abalone are converted to weight based on a fixed average value for each species. Twelve pink abalone are 11.4 kg (25 pounds), 12 green abalone are 11.4 kg (25 pounds), and 12 white abalone are 9.1 kg (20 pounds) (Oliphant et al. 1990). At San Clemente Island, a productive island, we examined catch data on a finer scale to identify sites for restoration. We examined spatial patterns in the catch around this island at the scale of the CDFG statistical blocks. The data were taken from 10 CDFG blocks (828, 829, 830, 848, 849, 850, 851, 866, 867, and 868) that surround San Clemente Island. We determined which of the areas around the island historically produced the greatest cumulative catch.

We reviewed commercial passenger fishing vessel (CPFV) catch records for sport abalone landings to determine whether this segment of the fishery was a major factor in the numbers of pink, green, and white abalone caught. The CPFV abalone records exist from 1971 to 1993. Data from 1984 and 1985 are missing.

Fishery Productivity Estimate by Area

Productivity for the three abalone species in the fishing areas was estimated by dividing the metric tons of abalone caught by the amount of suitable habitat (Table 1). We had no data on other physical factors such as wave exposure or rugocity, although these and other factors influence distribution patterns. We used the number of hectares of canopy kelp observed from the surface to estimate pink abalone habitat. Aerial photographs of kelp canopy were taken during fly-overs of the southern California Bight in October 1989 by ECOSCAN for the CDFG. The number of hectares of surface canopy is summarized for each of the coastal mainland and offshore islands (Table 1). Pink abalone productivity is expressed as metric tons of pink abalone per hectare of surface kelp in the 12 catch areas.

We estimated green abalone habitat by determining rocky intertidal area, which in turn we estimated from the kilometers of shoreline along the mainland and around the islands that are classified as rocky by environmental-sensitivity index maps generated by the National Oceanic and Atmospheric Association in 1995 and ground-truthed by people walking the shoreline. Green abalone productivity, then, represents the metric tons of green abalone caught in each area, divided by the estimate of rocky intertidal habitat.

To estimate the amount of white abalone habitat, we determined the shelf area from 25 to 65 m in depth. We delineated a polygon bordered by the 25- to 65-m depth contours and then determined the total shelf area in hectares inside the polygon. Potential white abalone area was then assumed to be 3% of this total shelf area (Thompson et al. 1993), as per Davis et al. (1998).

Fishery-Independent Data

Abalone-density surveys, which are independent of the fishery, are conducted in southern California by the Channel Islands National Park's Kelp Forest Monitoring Program. This program has been monitoring 16 sites annually since 1986 (and 14 sites annually from 1983–1985) at five of the northern Channel Islands: San Miguel, Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara (Davis 1989). Within each site, 12 band transects for pink abalone are selected at random locations, perpendicular to

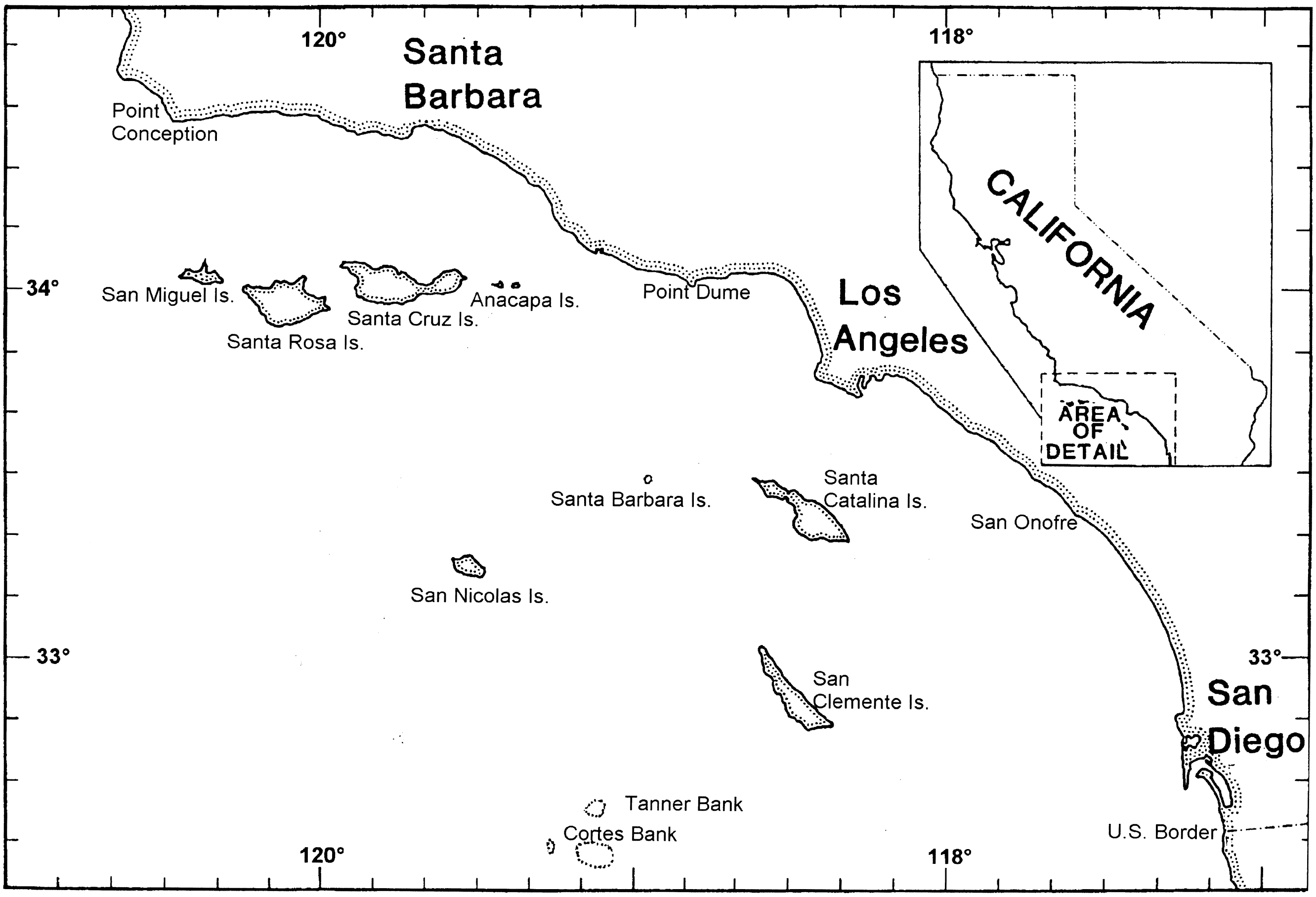

Figure 1. Map of 12 catch areas in the commercial abalone fishery along the mainland and islands of southern California.

a permanent 100-m line, by dive teams that survey two contiguous 3 × 10 m areas, which combine to form one 3 × 20 m band transect (60 m^2). In 1983 and 1984 only ten transects were examined at each site, and the transects were smaller in size (2 × 20 m). Therefore, the same area was searched in each of the three sites over the time series. These surveys were conducted at depths ranging from 10 to 15 m. Surveys at these depths target pink abalone, because green abalone are at shallower depths and white abalone are at deeper depths.

Of the five islands surveyed, the most pink abalone were found at Anacapa Island (Fig. 2). Three sites at Anacapa Island were surveyed from 1983 to the present. Two of the sites were within a no-take MPA that extends the length of the north side of east Anacapa Island (approximately 2500 m) to a depth of 20 m and was established in 1978 (McArdle 1997). Landing Cove inside the MPA is near the eastern end of the east island in an area that is well used and near a ranger station. Cathedral Cove, also inside the MPA, is in the middle of the island, has less traffic, and is presumably less protected. The fished site, Admirals' Reef, is on the southern side of west Anacapa Island and was a popular commercial fishing site prior to the close of the commercial fishery. In addition, more than half of the north side of middle Anacapa and a portion of the south side of west Anacapa are invertebrate no-take MPAs to a depth of almost 7 m (McArdle 1997).

We used a Kruskal-Wallis one-way analysis of variance on ranks to test for differences in density between the three sites at Anacapa Island. Pairwise multiple comparisons between all combinations of the sites were made with a Tukey test.

Size-frequency distributions were collected for pink abalone by divers 10 m on either side of the permanent 100-m transect (2000 m^2) per site per year from 1985 to 2001. Size information is not available for each of the abalone enumerated within the band transects used to determine density. These were emergent surveys, but some divers used invasive techniques to look for juvenile abalone, which are difficult to sample. Cathedral Cove had the most movable substrate, which facilitated searches for juvenile abalone. Minimum sport and commercial legal sizes were 152 and 158 mm, respectively. Using the size frequency data, we compared the number

Table 1. Estimates of cumulative commercial catch for three abalone species—pink, green, and white—in tons (1 ton = 1000 kg) from 1950 to 1995 by area for southern California (catch data for white abalone are missing for 1975).*

Location	*Pink abalone (metric tons)*	*Kelp area habitat (ha)*	*Productivity ([metric tons/ha] 100)*	*Green abalone (metric tons)*	*Shoreline distance habitat (km)*	*Productivity ([metric tons/km] 100)*	*White abalone (metric tons)*	*Deep habitat (ha)*	*Productivity ([metric tons/ha] 100)*
Southern mainland coast									
Point Conception to Pt. Dume	92	765	12	0.5	262	0.2	0.3	1773	0.0
Pt. Dume to San Onofre	1000	350	286	7	598	1.0	0.1	1444	0.0
San Onofre to Mexican Border	1037	739	140	103	406	25.0	4.0	1151	0.3
Southern islands									
San Miguel Island	114	471	24	4	126	3.0	0.2	378	0.0
Santa Rosa Island	143	604	24	3	87	3.0	0.2	754	0.0
Santa Cruz Island	2918	155	1883	10	128	8.0	0.2	449	0.0
Anacapa Island	682	27	2526	0.5	38	1.0	3.0	78	4.0
San Nicolas Island	144	218	66	7	44	17.0	0.6	499	0.1
Santa Barbara Island	2376	23	10330	16	33	47.0	4.0	47	9.0
Santa Catalina Island	1191	114	1045	171	109	157.0	2.0	123	2.0
San Clemente Island	9529	927	1028	1305	99	1317.0	241.0	167	145.0
Tanner and Cortez banks							35.0	129	27.0
Unspecified				89		39.0			
Total	19226	4393	17364	1716	1930	1618	291	6992	187
Average productivity ($\bar{x}$)			1579 (SD3025)			135 (SD375)			16 (SD41)

**See the section "Fishery Productivity Estimates by Area" in methods for explanations of how productivity and habitat area were determined.*

of juvenile pink abalone <50 mm in size among the three sites. Differences in abalone size-frequency distributions were compared with the Kolmogorov-Smirnov two-sample test (SYSTAT, Evanston, Illinois) among each of the three possible site combinations.

Potential Egg Production

To estimate egg production, we combined abundance and size information for pink abalone. From this estimate of biomass, we calculated egg-production estimates for pink abalone. Comparisons of egg production were then made between the two MPAs and the one fished site at Anacapa Island.

Lengths were available for pink abalone examined within quadrats at each of the three sites. The number of abalone measured was not consistent over time, and for some sites in some years <10 abalone were measured. To determine biomass estimates for these years at Cathedral Cove, we used the average adult size from the preceding year. At the Cathedral Cove site, where no size data were taken during 3 years (1987, 1988, 1999), biomass estimates were formed from the mean body weight from the preceding year. Lengths were not available for abalone enumerated along the density band transects. We did not account for potential gender differences in weight because abalone gender was unknown.

We converted abalone shell length to body weight based on the relationship of length (L) to body weight (w):

$$w_i = 0.0000291 \times L_i^{3.234}, \qquad (1)$$

as determined for pink abalone, $r = 0.9962$ ($n = 100$) (Tutschulte & Connell 1988). Only adult abalone (>49 mm) were used to determine the mean body weight, because juveniles do not contribute to reproduction. The juvenile size cutoff was selected based on observations that mid-size and large female pink abalone (>59 mm) have mature oocytes, whereas smaller females have only growing oocytes ($n = 50$; size range = 39–119 mm) (Tutschulte 1976).

We determined the average adult body weight (AW_s) for the three sites for each year:

$$AW_{st} = \sum_{i=1}^{x} (w_i X_i)/X, \qquad (2)$$

where s is site and t is year.

Average adult weight was converted to biomass (B_{st}) for each site for each year (t):

$$B_{st} = (AW_{st})(D_{st}), \qquad (3)$$

where D_{st} is density per hectare per site per year (D_{st} = [total count/60/N] × 10,000, where N is the number of transects that year). Biomass (grams per hectare) was then used to estimate egg production for each site for each year:

$$P_{st} = E(B_{st})S, \qquad (4)$$

where P_{st} is egg production per site per year, E is eggs produced per mature female pink abalone (determined as 3848 eggs/g female body weight/year at depths of 9 m [$n = 267$]; Tutschulte & Connell 1981); and S is sex

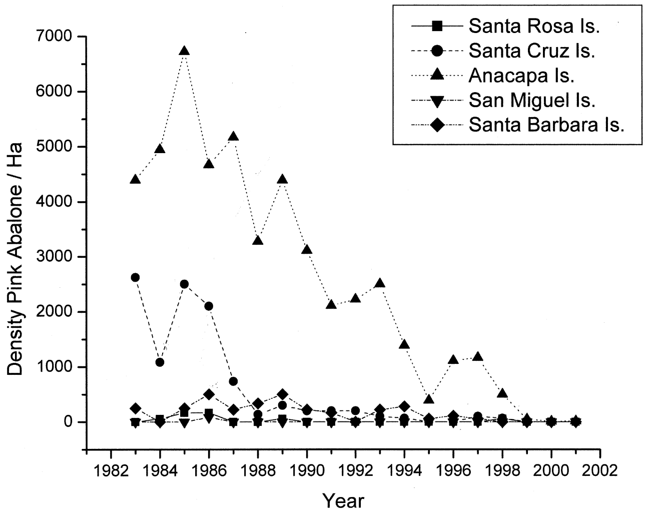

Figure 2. Density of pink abalone from 16 Channel Islands National Park sites at five of the northern Channel Islands: San Miguel Island, Santa Rosa Island, Santa Cruz Island, Anacapa Island, and Santa Barbara Island, 1983-2001.

ratio (0.5). Potential egg production in millions of eggs per site per year is reported.

Results

Spatial Productivity of the Fishery

San Clemente Island was the area of peak catches for all three abalone species, dominating the other 11 catch areas in southern California (Table 1). For San Clemente Island, pink abalone catches were high and variable prior to 1969 and then declined sharply. Most of the commercial green and white abalone landings from this island occurred during a short time period. Green abalone catches peaked in 1971, whereas white abalone catches peaked in 1972, peaks that lasted for only 3 years, after which both species declined rapidly. There are reports of white abalone landings prior to 1969, but because species codes were not available for white abalone landings may have been incorporated into pink abalone landing receipts (B. Owen, personal communication).

Catches from the San Clemente Island area accounted for 42.5% of all the pink abalone, 62.6% of the green abalone, and 82.8% of white abalone caught during the fishery from 1950 to 1995. Within San Clemente Island's 10 CDFG statistical catch blocks, block 850 off the west side of the island had the highest cumulative abalone landings for all three species. The next most productive site off the island was the southern tip (block 867), followed by the northern tip (block 829). This high level of production occurred despite the fact that a large portion of the island (the east side) is a steep, sloping, sandy area unsuitable for abalone. Although the San Clemente Island area produced the highest cumulative catches for all three species, it is also a very large island. The San Clemente Island area had the most kelp canopy of the 12 catch areas in southern California in 1989 (Table 1). Two of the mainland areas had the next most hectares of kelp canopy, followed by Santa Rosa Island.

An analysis of the productivity per unit of suitable habitat revealed that the San Clemente area was the most productive for green abalone per kilometer of rocky intertidal area and white abalone per hectare of deep rocky reef (Table 1). Areas around the smallest island, Santa Barbara Island, were the most productive for pink abalone per hectare of kelp habitat (Table 1). The Santa Barbara Island area, with only 23 ha of kelp canopy (assessed in 1989), produced 110 tons of abalone/ha of kelp, more than 10 times that produced near San Clemente Island (Table 1). The average production of pink abalone in each of the 12 catch areas per hectare of kelp canopy was 4.66 metric tons. Three of the southern and two of the northern Channel Islands areas produced more than this average, whereas none of the mainland areas were as productive (Table 1).

Abalone landings from CPFVs indicate that this segment of the sport fishery was relatively minor, representing <2% of the commercial fishery. Recreational divers fished 122 metric tons of green, 75 metric tons of pink, and 5.5 metric tons of white abalone from 1971 to 1993 (no data for 1984 and 1985). The Santa Catalina Island area had the highest CPFV landings of abalone during this time period.

Fishery-Independent Estimates of Pink Abalone Density

Densities of pink abalone at Anacapa Island at the start of the surveys at one site were >1000/ha; as for the other sites, however, densities at the island declined significantly over time. We used Anacapa Island to examine pink abalone density at a finer scale. Of the three sites on the island, Admiral's Reef, the fished site, had the highest densities of pink abalone initially (Fig. 3). Over time, as fishing continued, densities on Admiral's Reef declined to almost zero, whereas densities at the two MPAs were both >0 (Fig. 3).

Pink abalone density was normally distributed (p = 0.019), but the variances were unequal. A Kruskal-Wallis one-way analysis of variance on ranks indicated significant differences in density between the sites ($H = 9.0$; df = 2; $p = 0.011$). Landing Cove, the protected reserve, had significantly higher densities than the unprotected reserve, Cathedral Cove. Pairwise multiple comparisons among sites were significant only for the comparison between Landing Cove and Cathedral Cove ($q = 4.2$; $p < 0.05$). Tests comparing Landing Cove with Admiral's Reef ($q = 1.7$; $p > 0.05$) and Cathedral Cove with Admiral's Reef were not significant ($q = 2.5$; $p > 0.05$).

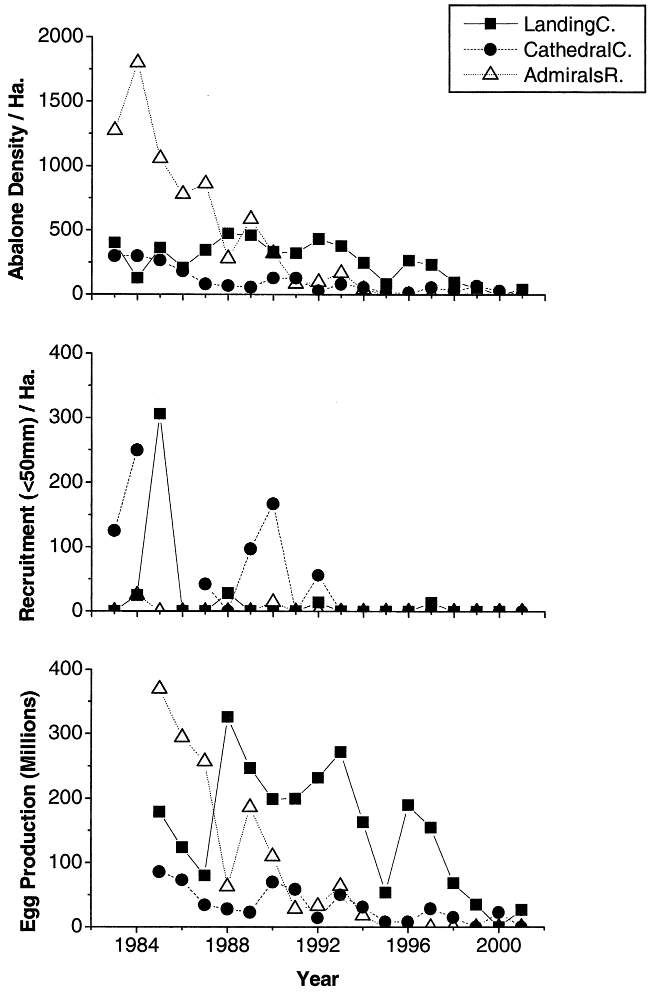

Figure 3. Total number of abalone observed per hectare (density), total number of juvenile abalone, and egg-production estimates for pink abalone at three Anacapa sites: two marine protected areas, Landing Cove (LandingC) and Cathedral Cove (CathedralC), and one fished site, Admiral's Reef (Admiral'sR), 1983-2001.

Estimates of Pink Abalone Egg Production

Despite declines over time in the abundance of abalone at the fished site, Admiral's Reef had the greatest cumulative (1983-2001) abundance of pink abalone when compared to the other two MPAs ($n = 224$ transects) (Table 2). An examination of the cumulative size frequency of pink abalone at these three sites shows that the protected reserve, Landing Cove, had the greatest percentage of large abalone ($\geq$158 mm) and the largest range of abalone sizes (Table 2). Landing Cove also had the largest pulse of new recruits (<50 mm), which occurred in 1987. Cathedral Cove, the unprotected MPA, had several small pulses of recruitment in 1985-1986 and 1991-1992, which accounted for this site having the greatest number of juvenile pink abalone. No recruitment events were detected at the fished site, Admiral's Reef, throughout the surveys from 1985 to 2001.

The mean length of abalone at the protected reserve was significantly greater than at the unprotected reserve ($t = 8.23$, df $= 740$, $p < 0.001$) and significantly greater than at the fished reef ($t = 11.17$, df $= 885$, $p < 0.001$) (Fig. 4). The mean length of abalone at the fished reef was greater than at the unprotected reserve ($t = 3.12$, df $= 501$, $p < 0.002$) (Fig. 4). Based on the Kolmogorov-Smirnov test, there were no significant differences in the size-frequency distributions among any of the site combinations: protected and unprotected reserves ($p = 0.57$), protected reserve and the fished site ($p = 0.33$), or unprotected reserve and the fished site ($p = 0.57$).

An estimate of the relative egg production was greatest for the protected MPA, Landing Cove (2555 million eggs/site/year), compared with the other two sites (Table 2). Despite the fact that this reserve site had fewer abalone than the fished site, abalone in the protected reserve (Landing Cove) had the greatest mean length (Fig. 4) and therefore the greatest average adult weight (313 g). More than 15% of the abalone at this reserve site were greater than or equal to the commercial legal size (158 mm), and this translated into the greatest potential egg production of the three sites.

Discussion

Selecting Restoration Sites

Abalone populations in southern California are in need of immediate restoration. Whether restoration takes the form of aggregating wild broodstock or captive rearing

Table 2. Fishery-independent survey data (1983–2001) compared for pink abalone at three sites on Anacapa Island.

Anacapa site	*Landing Cove (protected reserve)*	*Cathedral Cove (unprotected reserve)*	*Admiral's Reef (fished site)*
No. abalone/13,040 m (1983-2001)	333	116	431
Legal size $\geq$158 mm (%)	29.5	5.9	1.8
Juveniles <50 mm (%)	4.7	21.6	0.6
Mean length, mm (SD, *n*)	146.9 (0.0385, 569)	133.9 (0.0168, 185)	121.5 (0.0329, 326)
Mean adult weight, g (1985-2001) (SD)	313 (60)	272 (59)	189 (37)
Cumulative potential egg production (millions of eggs) (1985-2001)	2555	550	1423

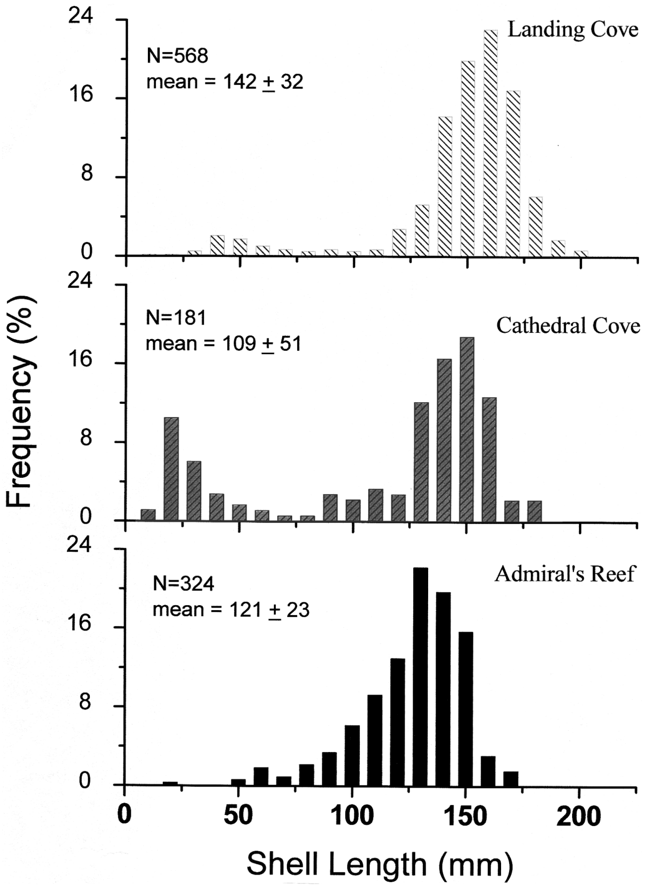

Figure 4. Size-frequency distribution (±SD) of pink abalone at two marine protected areas (Landing Cove and Cathedral Cove) and one fished site (Admiral's Reef) on Anacapa Island, 1985-2001.

and seeding, these methods require selection of sites where success can be maximized. Spatially explicit fishery data can serve as a quantitative measure of the productivity of specific sites. The San Clemente Island area had the greatest productivity (cumulative catch 1950–1995) of pink, green, and white abalone in southern California (Table 1), despite dramatic differences in life-history traits and depth distribution. The mechanisms responsible for historic productivity are unknown, as is whether these sites would be as productive today. Pink abalone abundances at San Clemente Island declined dramatically over time, and by 1998 only 50 legal-size abalone (>158 mm) were found during 40 hours of searching (P.L.H. et al., unpublished data).

Restoration efforts typically must take into account multiple biological, social, and economic concerns, so the largest areas may not be available for conservation. Smaller areas rich in resources may be more suitable for sequestering in protected reserves. The Santa Barbara Island area, despite its small size, had 10 times the productivity of pink abalone compared with San Clemente Island per hectare of kelp canopy (Table 1). Santa Barbara Island may also have a lower risk of predation by sea otters (*Enhydra lutris*) if they become reestablished south of Point Conception. Reoccupation of central California habitats by sea otters dramatically reduced abalone and shellfish populations (Wendell 1994). The extraordinary productivity of Santa Barbara Island suggests that this small island is an excellent candidate for protection, restoration, and enforcement.

Restoration efforts could be enhanced if MPAs are sited in source areas (sensu Pulliam 1988). Spatially explicit models suggest that the placement of MPAs in source habitats may benefit declining populations, whereas placement in sinks could be deleterious if fishing increases in source areas (Crowder et al. 2000). The spatial dynamics of marine invertebrate populations are poorly understood, but in some cases source areas can be identified. For example, shallow (5 m), food-rich habitats in northern California harbor red sea urchins at high densities (4 m^2), with 5 times the gonad indexes and 18 times the density of juveniles (<20 mm) compared with deeper habitats, making them likely candidates for source areas (Rogers-Bennett et al. 1995). High densities of reproductive adults enhance fertilization success (Levitan et al. 1992; Babcock & Keesing 1999). Source areas for abalone may differ substantially from those of other nearshore reef inhabitants because both the larval and adult stages may have limited dispersal capabilities. In this case, the net surplus appears to have gone to the fishery instead of repopulating other patches within the metapopulation (Gilpin & Hanski 1991). Roberts (1998) argues that establishing MPAs, which results in the accumulation of high densities of large individuals, may in effect create source areas.

Efficacy of MPAs for Abalone

Marine Protected Areas can have positive effects not only on abundance but also on the size structure of protected populations, which together may enhance reproductive potential (Roberts & Polunin 1991; Dayton et al. 1995; Paddack & Estes 2000). In this example, the more protected MPA had a greater average size and more large individuals than the other two sites (Table 2). In Tasmania, individual abalone (*H. rubra*) size was significantly greater in a large MPA (7-km coastline), whereas this effect was not seen in smaller MPAs (Edgar & Barrett 1999). In many marine invertebrates and fishes, the largest individuals may be most important for restoration because reproductive output is exponentially related to body size. Large animals are frequently preferred by fisheries (Dayton et al. 1995), however, and abalone fisheries are no exception. This conflict may necessitate the implementation of MPAs (Roberts 1997; Tegner & Dayton 2000) for broodstock protection.

The greatest reproductive potential came from pink abalone at the protected MPA, Landing Cove, which had more than four times the potential egg production of the unprotected MPA and almost twice that of the fished area (Table 2), despite lower initial and cumulative abundance. The protected MPA had the greatest reproductive potential because the site had more large adults (Table 2). We found no stock-recruitment relationship for pink abalone at the scale (sites) of our investigation. Recruitment was temporally sporadic, although this may be common for abalone. For example, Tegner (1989) found only one recruitment peak for red abalone around Santa Rosa Island during a 5-year study.

In British Columbia, northern abalone (*H. kamtschatkana*) inside a well-enforced MPA had a larger mean size (>130 mm) and higher abundance than in unprotected closed areas (Wallace 1999). Potential reproductive output of northern abalone was greatest in the closed area that was heavily protected. Despite the total closure of the abalone fishery in British Columbia in 1990, only the well-enforced MPA (near a prison with 24-hour armed guards) had more large abalone (Wallace 1999), and populations have not rebounded despite the closure (Campbell 2000).

In southern California, the impacts of large-scale regime shifts (Mantua et al. 1997; McGowan et al. 1998) and multiple fishery interactions will have to be considered when abalone restoration plans are developed. Kelp abundances may have played a role in the decline of pink abalone at Anacapa Island, but abundance data are lacking. It is likely that kelp declined at Anacapa Island, because kelp canopies at Santa Cruz Island declined (<25% maximum) in the 1980s, as did densities at Santa Rosa Island in the 1990s (International Specialty Products, Alginates, kelp data). Frequent and intense El Niño events, coupled with storms, reduced both the quantity and quality of kelp resources in the past two decades (Tegner et al. 2001).

There may also be interactions among multiple fisheries inside MPAs. Red sea urchins are heavily fished (Kalvass & Hendrix 1997), and their spine canopy may be important for the survival of juvenile abalone (Tegner & Dayton 1977). In northern California, MPAs with red sea urchins had significantly more juvenile red and the rare flat abalone (*H. walallensis*) than did fished sites (no sea urchins), and one-third of the juveniles in the MPAs were associated with sea urchins (Rogers-Bennett & Pearse 2001). Despite this positive association, red sea urchins may also compete with adult red abalone. In northern California, the abundances of these species are negatively correlated at the scale of the transect (60 m^2) (Karpov et al. 2001). In Tasmania, however, abalone density was 30% lower inside an MPA because there were fewer juveniles, perhaps as a consequence of intraspecific competition with large abalone and/or interspecific interactions with lobsters, which increased dramatically in abundance (260%) inside the MPAs (Edgar & Barrett 1999). Therefore, the efficacy of MPAs is affected by interactions among the biological and physical components of the community.

Spatially explicit data exist for many fished species. If the abundance of large reproductive adults can be used as a surrogate for the identification of source areas, then these data may aid in the selection of MPAs and restoration sites. Fishery-independent data from inside and outside MPAs, although rare, are critical for evaluating the effects of fishing. We provide an example of how MPAs may function to enhance the reproductive potential of pink abalone. If effective restoration is to be enacted before depleted abalone stocks senesce and die, we will need to glean as much useful information as we can from existing data sets.

Acknowledgments

We dedicate this paper to the memory of M. J. Tegner, who taught us about abalone and friendship. She also knew intuitively that Santa Barbara Island is prime abalone habitat. We thank S. Shepherd for suggesting that we look at fishery data as a method of determining spatial productivity. We especially thank N. Wright and J. Kum for kelp, intertidal, and deep-area estimates. We thank P. Wolf, M. Bergen, E. Larson, and the Marine Region of the California Department of Fish and Game for supporting this work and the University of California, Davis Bodega Marine Laboratory for logistic support to L.R.-B. This research was supported in part by the National Sea Grant College Program of the U.S. Department of Commerces' National Oceanic and Atmospheric Administration (grant NAO6RG0142, project R/CZ-69PD), through the California Sea Grant Program. The views expressed herein do not necessarily reflect the views of any of these organizations. This is contribution number 2161 of the Bodega Marine Laboratory, University of California, Davis.

Literature Cited

Babcock, R., and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. Canadian Journal of Fisheries and Aquatic Sciences **56**:1668–1678.

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

Campbell, A., editor. 2000. Preface to workshop on rebuilding abalone stocks in British Columbia. Canadian Special Publication on Fisheries Aquatic Sciences **130**:xii–xiv.

Cox, K. W. 1962. California abalones, family Haliotidae. Fish bulletin **118**. California Department Fish and Game, Sacramento.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science **66**:799–820.

Daniels, R., and R. Floren. 1998. Poaching pressures on northern Californias' abalone fishery. Journal of Shellfish Research **17**:859–862.

Davis, G. E. 1989. Design of a long-term ecological monitoring program for Channel Islands National Park, California. Natural Areas Journal **9:**80–89.

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.

Davis, G. E., P. L. Haaker, and D. V. Richards. 1998. The perilous condition of white abalone *Haliotis sorenseni*, Bartsch, 1940. Journal of Shellfish Research **17:**871–876.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation Marine 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.

Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology Ecology **242:**107–144.

Edwards, C. L., 1913. The abalone industry in California. Pages 5–15 in Fish bulletin **1**. California Department of Fish and Game, Sacramento.

Gilpin, M., and I. Hanski. 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Hobday, A. J., and M. J. Tegner. 2000. Status review of white abalone (*Haliotis sorenseni*) throughout its range in California and Mexico. Technical memorandum. National Marine Fisheries Service, South West Fisheries Center, La Jolla, California.

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. A., P. L. Haaker, D. Albin, I. K. Taniguchi, and D. Kushner. 1998. The red abalone, *Haliotis rufescens*, in California: importance of depth refuge to abalone management. Journal of Shellfish Research **17:**863–870.

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

Karpov, K. A., M. J. Tegner, L. Rogers-Bennett, P. E. Kalvass, and I. K. Taniguchi. 2001. Interactions among red abalones and sea urchins in fished and reserve sites of northern California: implications of competition to management. Journal of Shellfish Research **20:**743–753.

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.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific-interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society **78:**1069–1079.

McArdle, D. A. 1997. California marine protected areas. California Sea Grant College System, University of California, La Jolla.

McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science **281:**210–217.

Oliphant, M. S., P. A. Gregory, B. J. Ingle, and R. Madrid. 1990. California marine fish landings for 1977–1986. Fishery bulletin **173**. California Department Fish and Game, Sacramento.

Paddack, M. J., and J. E. Estes. 2000. Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. Ecological Applications **10:**855–870.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Nationalist **132:**652–661.

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

Roberts, C. M. 1998. Sources, sinks, and the design of marine reserve networks. Fisheries **23:**16–19.

Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries **1:**65–91.

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., and J. S. Pearse. 2001. Indirect benefits of Marine Protected Areas for juvenile abalone. Conservation Biology **15:**642–647.

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.

Shepherd, S.A., and L.D. Brown. 1993. What is an abalone stock: implications for the role of refugia in conservation. Canadian Journal of Fisheries and Aquatic Sciences **50:**2001–2009.

Tegner, M. J. 1989. The California abalone fishery: production, ecological interactions, and prospects for the future. Pages 401–420 in J. F. Caddy, editor. Marine invertebrate fisheries: their assessment and management. Wiley, New York.

Tegner, M. J. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? Canadian Journal Fisheries and Aquatic Sciences **50:**2010–2018.

Tegner, M.J. 2000. Abalone (*Haliotis* spp.) enhancement in California: what we've learned and where we go from here. In A. Campbell, editor. Canadian Special Publication on Fisheries and Aquatic Sciences **130:**61–71.

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 P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. International Council for the Exploration of the Sea Journal of Marine Science **57:**579–589.

Tegner, M. J., J. D. DeMartini, and K.A. Karpov. 1992. The California red abalone fishery: a case study in complexity. Pages 370–383 in S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo, editors. Abalone of the world: biology, fisheries, culture. Fishing News Books, Blackwell Scientific Publications, Oxford, United Kingdom.

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

Tegner, M. J., P. L. Haaker, K. L. Riser, and L. I. Vilchis. 2001. Climate variability, kelp forests, and the Southern California red abalone fishery. Journal of Shellfish Research **20:**755–763.

Thompson, B., J. Dixon, and S. Schroeter. 1993. Benthic invertebrates. Pages 369–458 in M. D. Dailey, J. D. Reish, and J. W. Anderson, editors. Ecology of the Southern California Bight. University of California Press, Los Angeles.

Tutschulte, T. C. 1976. The comparative ecology of three sympatric abalones. Ph.D. dissertation. University of California, San Diego.

Tutschulte, T. C., and J. H. Connell. 1981. Reproductive biology of three species of abalones (*Haliotis*) in southern California. Veliger **23:**195–206.

Tutschulte, T. C., and J. H. Connell 1988. Growth of three species of abalones (*Haliotis*) in southern California. Veliger **31:**204–213.

Wallace, S. S. 1999. Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. Conservation Biology **13:**882–887.

Walters, C., and J. J. MacGuire. 1996. Lessons for stock assessment from the northern cod collapse. Review Fish Biology and Fisheries **6:**125–137.

Wendell, F. E. 1994. Relationship between sea otter range expansion and red abalone abundance and size distribution in central California. California Fish and Game Bulletin **80:**45–56.