ESTIMATING BASELINE ABUNDANCES OF ABALONE IN CALIFORNIA FOR RESTORATION

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Under our present laws the abalone is being exterminated.

—Dr. Charles L. Edwards, University of Southern California, 1913

ABSTRACT

Abalone populations in California have declined dramatically; however, reliable estimates of baseline abundances are lacking. The lack of sufficient time scales seriously limits the value of most baselines. We use historical data to define baselines for abalone in California and to evaluate current abundances and suggest restoration targets. Using the fishery as a "sampling tool," we estimate that baseline abundances for pink abalone (*Haliotis corrugata*) were 9.3 million, black abalone were 3.5 million (*H. cracherodii*), green abalone (*H. fulgens*) were 1.5 million, white abalone (*H. sorenseni*) were 360,000, and threaded abalone (*H. kamtschatkana assimilis*) were

Pierce Brothers Abalone processing shop, ca. 1933. © Pat Hathaway, <http://caviews.com>. Used by permission.

21,000. All of these species now number less than 1% of their estimated baselines. For species poorly represented in the fishery, we use survey data to estimate that baseline abundances for pinto abalone (*H. k. kamtschatkana*) were 153,000, and for flat abalone (*H. walallensis*) were 71,000. Our modern surveys suggest that pinto abalone populations have undergone a ten-fold decline and that flat abalone populations remain similar to their baseline. These baselines underline the dramatic declines in abalone populations and thus define the magnitude of the challenges we face in restoring formerly abundant species. The identification of rare species brings into question the wisdom of fishing species in the absence of baseline information. This approach may serve to help set restoration targets for other depleted species for which we have limited data.

INTRODUCTION

Abalone populations in California once supported a major commercial fishery, with landings exceeding 2,000 metric tons (t) a year (Cox 1962; Karpov et al. 2000); however, population declines forced the closure of the recreational and commercial fishery in the south in 1996 (CDFG Code 5521). Estimates of baseline abundances (or natural benchmarks) are desperately needed to assess population declines and to establish restoration goals (Dayton et al. 1998); however, estimating abundances is difficult because times series are rare and there is little information available on historical abundances (Dayton et al. 1998; Jackson et al. 2001; Pitcher 2001). Furthermore, our perspective of baseline levels can be distorted by what Pauly (1995) terms "shifting baseline syndrome," that is, the undocumented decline of population abundances that have been vastly reduced from historic baseline abundances over time. As a result of this lack of historical data, restoration targets are frequently set based on temporally limited monitoring studies that rarely span a career.

Changes in baseline abundance resulting from overfishing can include severe population decline, local extirpation, and even global extinction (Carlton et al. 1999; Jackson et al. 2001). Stellar's sea cow (*Hydrodamalis gigas*), for example, once heavily fished, has been globally extinct since 1768 (Anderson 1995). Sea turtles were once so numerous that they impeded the progress of Columbus's ships in the late 1770s, whereas today many species are in danger of extirpation (Jackson 1997). The large barndoor skate (*Raja laevis*) is now close to extinction as a result of trawling in the northwest Atlantic (Casey and Myers 1998). The Chesapeake Bay oyster (*Crassostrea virginica*) has declined more than 50-fold as a consequence of intensive mechanical dredging of Chesapeake Bay that began in the 1870s, pre-dating such threats as poor water quality and oyster disease (Rothschild et al. 1994). Spiny lobsters have declined in southern California such that 260 traps in 1888 once yielded the same biomass as 19,000 traps yielded in 1975 (Dayton et al. 1998). Abalone processors after World War II imposed buying limits of 100 dozen a day per hard-hat diver, and novice divers fished 50 dozen a day: abundances unimaginable today.[1] From these anecdotes of high baseline abundances (Pauly 1995) we can see that some modern nearshore communities have become nearly devoid of many exploited species and now resemble "ghost communities" (Dayton et al. 1998; Tegner and Dayton 2000) much like portions of the Amazon, which as a result of overhunting of large mammals and birds has become an "empty forest" (Redford 1992).

The seas were once perceived as inexhaustible and the fecundity of marine organisms boundless (Roberts and Hawkins 1999), creating the false notion that marine organisms are resilient to population declines. Scientists once upheld this notion regarding abalone; Heath (1925), for example, stated that "the life of the abalone is dependent principally upon the amount of seaweed, and as this is practically inexhaustible, there is a very remote possibility indeed that the shell fish will ever become extinct." We now know that the white abalone (*Haliotis sorenseni*) was not inexhaustible despite its being a broadcast spawner and one of the most fecund of all the abalone species in California, with each female producing an estimated 3.7–6.5 million eggs a year (Tutschulte 1976; Hobday et al. 2001). From 1971 to 1976 overfishing appears to have reduced the population of white abalone below a self-sustaining level (Hobday et al. 2001), and in 2001 it became the first marine invertebrate to be placed on the federal endangered species list.[2]

Abalone appear to be particularly susceptible to overexploitation, and in many parts of the world abalone fisheries have collapsed (Campbell 2000; Karpov et al. 2000; Shepherd et al. 2001). In California serial depletion occurred within the abalone complex as declines in red abalone (*H. rufescens*) and later pink abalone (*H. corrugata*) landings were bolstered by increased landings of rarer species and in distant fishing grounds, masking the inevitable collapse of the species complex (Dugan and Davis 1993; Karpov et al. 2000). In Alaska, pinto abalone (northern abalone, *H. k. kamtschatkana*) landings were not sustainable, which resulted in repeated reductions in fishery limits (quotas) from the peak of 172 t in 1979 to just 7 t when the fishery was closed in 1995 (Woodby et al. 2000). Likewise, pinto abalone landings in British Columbia peaked at 481 t in 1977 and then declined dramatically to the 47 t quota set in 1985, prior

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[1]D. Parker, pers. comm.

[2]*Federal Register* 66 (103) 29046, 29 May 2001.

to the fishery's closure in 1990 (Campbell 2000). Recent surveys in British Columbia show that even after the closure of the fishery populations have continued to decline except in "reserve" areas (such as those adjacent to a heavily guarded prison, a de facto reserve). This finding suggests that poaching may be widespread (Wallace 1999). Nowhere is poaching more problematic than in South Africa, where political and ecological factors have converged to negatively impact abalone populations (Tarr 2000).

Commercial extinction, the cessation of fishing when it becomes unprofitable (Safina 1998), was once thought to ensure that fished species would never suffer global extinction. This was not the case with abalone in southern California where sea urchin divers held dual permits allowing them to search for abalone during sea urchin fishing operations, a practice that sustained catch per unit effort (Dugan and Davis 1993). Today, sea urchin landings have also declined dramatically (Kalvass and Hendrix 1997), and the dive fishery is pursuing other invertebrate species. Despite the emerging dive fishery for wavy turban snails (*Megastrea undosa*, formerly *Lithopoma*), little information exists about the baseline abundance of this species (Taniguchi and Rogers-Bennett 2001).

Our purpose in this study was to determine baseline abundances for abalone in California. We combined peak fishery landings over a ten-year period to estimate baseline abundances of white (*H. sorenseni*), pink (*H. corrugata*), black (*H. cracherodii*), green (*H. fulgens*), and threaded (*H. kamtschatkana assimilis*) abalone. We assumed that abalone populations were at least as large as the numbers taken in the commercial and recreational fishery. For species that were poorly represented in fishery-dependent data, such as flat abalone (*H. walallensis*) and pinto abalone (*H. kamtschatkana kamtschatkana*), we analyzed fishery-independent density data from the past to estimate historic baseline abundances. To assess modern densities of flat and pinto abalone we conducted dive surveys in northern California and compared our results with previous density estimates. We assessed the status of each abalone species by comparing baseline estimates of abundance from the past with present day (fishery-independent) estimates of abundance, where possible. Finally, we discuss how population abundances have changed over time for each of the six species (and one subspecies) in California and the prospects for restoring abundances to baseline levels.

ABALONE EXPLOITATION IN CALIFORNIA

Abalone have a long history of human exploitation within coastal Californian ecosystems. Radio-carbon dating of abalone shells provides archaeological evidence that humans were exploiting abalone in the late Pleistocene (ca. 10,500 years B.P.) in the Channel Islands (Erlandson et al. 1996), 5,000 years B.P. in central California, and 1,000–2,000 years B.P. in northern California.[3] Red abalone (*H. rufescens*) shells in middens from Santa Rosa Island date from 5,370–7,400 years B.P. (Orr 1960). This evidence indicates that human fishing may have affected local abalone populations and kelp forest communities in prehistoric time (Erlandson et al. 1996).

THE INTERTIDAL FISHERY

Early records set the start of the abalone fishery in the 1850s when Chinese immigrants began gathering red, black, and green abalone in the intertidal zone off central California. Abalone were dried and consumed locally or exported to China (Bonnot 1930). The first-recorded commercial abalone venture occurred in 1853, when, according to the *Daily Alta California*, 500–600 Chinese men were gathering abalone (Lundy 1997). Croker (1931) reported that Chinese fishers set out to "gather every available abalone on the coast of southern California." This fishery peaked in 1879 at 1,860 t (Cox 1962; Cincin-Sain et al. 1977). Chinese fishers also collected abalone in Baja California, Mexico, in the 1860s, using San Diego as a base (Lundy 1997). In the 1880s, however, in an effort to reduce fishing pressure on abalone, the Mexican government began assessing a $60 annual tax on U.S. fishing boats fishing in Mexican waters. And in 1888 the U.S. Congress passed the Scott Act, making it illegal for Chinese workers to enter or re-enter the United States (Lundy 1997). These actions led to the demise of the Chinese fishing industry, and by 1893 only one Chinese junk was still fishing in San Diego County (McEvoy 1977). In 1900 concern in California regarding overfishing lead to ordinances prohibiting abalone fishing in shallow waters; in 1913 the export of abalone was banned, and by 1915 abalone drying was forbidden, ending the Chinese intertidal fishery for abalone (Bonnot 1930).

THE DIVE FISHERY

Japanese immigrants began commercial abalone operations in California in 1898 and introduced diving to the industry (Croker 1931; Lundy 1997). Initially the Japanese divers tried traditional free-diving gear, including goggles and shirts, but the cold waters of California forced them to use hard-hat helmets and deep-sea dive suits (Lundy 1997). In 1898 the Point Lobos Canning Company was started by Mr. Kodani, a marine biologist from Japan, and Mr. Allen, who owned land at Whaler's Cove at Point Lobos south of Monterey (Lundy 1997). They used three Japanese hard-hat helmet divers to fish for red abalone (Lundy 1997).

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[3]M. Kennedy, pers. comm.

During the early years of the industry it was not uncommon for divers to fish 40–50 dozen abalone a day (Lundy 1997). One account tells of diver Duke Pierce's first dive experience, when he came up with 50 dozen abalone (Lundy 1997). Divers typically worked in shifts, with six to seven men topside and one diver below. The boats worked approximately 15 days a month for six to eight hours a day. In 1903 a group of Japanese divers moved to the Mendocino area (Dark Gulch) in northern California. One diver working six hours could collect an average of 2,300 red abalone a day (Lundy 1997). In 1913 Japanese divers began diving in Baja California, Mexico. One fisher described what these divers saw: "Abalone [were] found in abundance. It was common to find them in layers of twelve or thirteen. . . . At that time the divers used to catch five to six tons a day" (Estes 1977).

Abalone imported into California from Baja California, Mexico, increased from 1,724 t in 1923 to 3,357 t in 1929 (Bonnot 1930). In 1913, with red abalone stocks declining, Japanese divers began fishing for the smaller green and pink abalone. These abalone, according to Edwards (1913), were extremely abundant. One observer stated, "I have seen the diver send the net up, filled with about fifty green and corrugated (pink) abalones, every six or seven minutes. During his shift below the diver gathers from thirty to forty basketfuls, each containing one hundred pounds of meat and shell, or altogether one and one-half to two tons."

The first abalone cannery opened in 1915 in Cayucos, California, and two years later five canneries were operating, from Monterey to San Diego (Cox 1960, 1962). By 1928, however, the number of canneries was down to three, and in 1931 the only cannery still open—Point Lobos, at Monterey—was closed (Cox 1960, 1962). In 1907 the first abalone reserve was established in central California, the Monterey Bay Shellfish Refuge between Point Piños and Seaside, Monterey County; the take of all shellfish was prohibited within the reserve. There was also an abalone closure at Venice Beach, Los Angeles County, California (Edwards 1913). By 1930 several laws had been passed establishing restricted districts for abalone fishing, outlining fishing methods, imposing minimum size limits and maximum bag limits, and providing for a closed season (Croker 1931; Lundy 1997). According to Croker (1931), "the passage of these laws, which was a gradual evolution, came too late to preserve the abalones of southern California in numbers sufficient to support a commercial fishery, but there are enough left to provide shellfish for amateur fishermen."

THE RECREATIONAL FISHERY

Around 1915 recreational abalone fishing became increasingly popular in California. According to a California Department of Fish and Game (CDFG) report, "For every commercial diver, there are 1,000s of sportsmen. . . . Partial policing results in many arrests and confiscation of many 1,000s of undersized abalone. . . . It is not difficult to understand why the abalone has literally disappeared from the littoral zone." It was at this time that a daily catch limit was imposed on sport takers (Lundy 1997). By 1930 recreational abalone fishing was thriving. Croker (1931) reports that at every low tide during the open season "many hundreds of tourists and ranchers can be seen going over every accessible reef and ledge with a fine-toothed comb. State and county authorities are hard-pressed to enforce the laws on limits and minimum size which are so easily broken by thoughtless people."

The 1970s and 1980s brought a huge surge in the number of recreational scuba divers as gear became safer and easier to use and as training became more available. Between 1965 and 1985 the number of recreational scuba divers searching for abalone increased by 400%, and the catch increased by 250% (Coastal Ecology Group 1985). In northern California recreational divers and shorepickers took an annual average of 533,000 red abalone (906 t) from 1985 to 1989 (Tegner et al. 1992).

THE MODERN FISHERY

In 1928, 11 dive permits were issued in the Monterey area; by 1937 the number had risen to 27 and by 1954 to 294; in 1960, CDFG issued 505 commercial permits (Cox 1962). The number of permits issued peaked at 880 in 1966 and then declined to 119 prior to the closure of the fishery in the mid-1990s. Japanese-American divers dominated the California red abalone fishery until World War II when many were sent to internment camps (Cox 1962). During the war many areas previously closed to commercial abalone fishing were opened to meet the wartime demand for protein sources. In 1945 more than 77,465 red abalone (132 t) were landed in Sonoma and Mendocino Counties in northern California. Northern California towns such as Bodega Bay had a commercial fishery during the war[4] as did such southern California cities as Newport Beach, Avalon, and Santa Barbara (Lundy 1997). These newly opened areas in the south contained large numbers of pink, green, white, and black abalone rather than the red abalone that comprised most of the commercial catch from northern areas.

In 1893 the U.S. Commission of Fish and Fisheries reported commercial landings of abalone at 141 t (Lundy 1997). Landings gradually increased, and in 1916 CDFG reported that the commercial fishery landed just under 454 t. Prior to 1940 only red abalone were documented in records of commercial landings. Green, pink, white,

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[4]R. Mantua, pers. comm.

and black abalone first appear in records in 1940, 1944, 1959, and 1956, respectively. Little information is available for white abalone landings prior to 1959 because landing receipts did not contain a specific category for white abalone so this species may have been recorded as pink abalone.[5] Landings for pink abalone peaked in 1952 at 1,509 t; for green abalone, in 1971 at 511 t; for white abalone, in 1972 at 65 t; and for black abalone, in 1973 at 868 t. Green and white abalones continued to be fished even after their landings fell in 1985 to less than 12,000 and 300 animals, respectively. White abalone landings fell to such a low level that in 1978 mandatory reporting requirements for this species were dropped (Tegner 1989), further exacerbating problems documenting the decline of this species.

Fishery closures were not enacted in California until the mid 1990s despite severe declines in landings. The commercial and recreational fisheries for black abalone were closed in 1993 due to severe population declines caused by commercial fishing pressure and the devastating effects of the lethal abalone disease Withering Syndrome (Haaker et al. 1992). The commercial and recreational fishery for green, pink, and white abalone was closed in 1996 (effective in 1997) south of San Francisco (CDFG Code Sec. 5521). Today, an Abalone Restoration and Management Plan is being drafted in California (CDFG Code Sec. 5522), and a federal recovery plan is being drafted for white abalone (NOAA, NMFS).

METHODS FOR ESTIMATING BASELINE ABUNDANCES

We generated estimates of baseline abundances for abalone in California by combining landings from the commercial and recreational fisheries over a ten-year peak period (fig. 1, tab. 1). We assume that abalone populations were at least as large as the number taken in the fishery. There is information available for commercial landings of red, pink, green, black, white, and threaded abalone from 1950 to the close of the fishery, and for recreational landing from 1971 to the close of the fishery (except for 1984 and 1986). Prior to 1950 red abalone dominated the landings records. Landings were recorded in pounds, using conversions from numbers of abalone to pounds as follows: 45 lb represented a dozen animals for red abalone; 25 lbs, a dozen pink, green, and black abalone; 20 lb, a dozen white abalone; and 15 lb, a dozen threaded, pinto, and flat abalone (Pinkas 1974). Prior to 1959 the conversion factor was 35 lb per dozen for pink abalone and 50 lb per dozen for red abalone (Cox 1962).

We made two simplifying assumptions about abalone populations during the ten-year time period used to gen-

[5]B. Owen, pers. comm.

TABLE 1
Commercial and Recreational Abalone Landings in California During the Peak Landings Decade

Species	Peak decade	Commercial landings	Peak decade	Recreational landings
Pink	1950–59	9,318,587	1950–59	—[a]
Green	1966–75	1,473,732	1971–75	30,947
Black	1972–81	3,537,126	1972–81	6,729
White	1969–78	354,973	1971–78	5,503
Threaded	1971–80	21,066	1971–80	—[a]

Note: Recreational landings are from commercial passenger dive vessels.
[a]No data available.

erate all the baseline estimates. First, we assumed that the fishery over a ten year period in effect "sampled" all size classes of the population. Even though the fishery was forced to take only large legal-size animals because of minimum legal sizes, the majority of juveniles and sublegal adults present in the first year of the time period grew to legal size and were subsequently taken in the fishery by the end of the ten-year time period.

Second, we assumed that we were not sampling abalone that had been added to the population by reproduction during the ten-year time period because newly settled abalone typically take more than ten years to grow to the minimum legal size. Abalone grow slowly (Tutschulte 1976; Haaker et al. 1998), and estimates (using the von Bertalanffy growth model) of the age at which abalone reach commercial legal size range from 20 years for green abalone at 178 mm to 9 years for white abalone at 159 mm in length (Tutschulte 1976; Tutschulte and Connell 1988). The length of time may be even longer since the von Bertalanffy growth model overestimates juvenile growth (Yamaguchi 1975; Ebert 1999).

We were unable to construct baseline information for abalone that also occur in Mexico because we were unable to acquire complete commercial fishery records (but for white abalone, see Hobday et al. 2001). Flat and pinto abalone are not well represented in the commercial fishery data. For these species we used fishery-independent data to determine baseline estimates of abundance from 1971, the earliest subtidal surveys we are aware of in northern California.

WHITE ABALONE

A conservative estimate of baseline abundance of white abalone, using landings data during the peak of the fishery, 1969–78, is 360,476 animals; this includes the 5,503 abalone taken in the recreational fishery (tab. 1). We assumed that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. This species is estimated to have a maximum life span of 35–40 years (Tutschulte 1976), and individuals are likely to attain older ages.

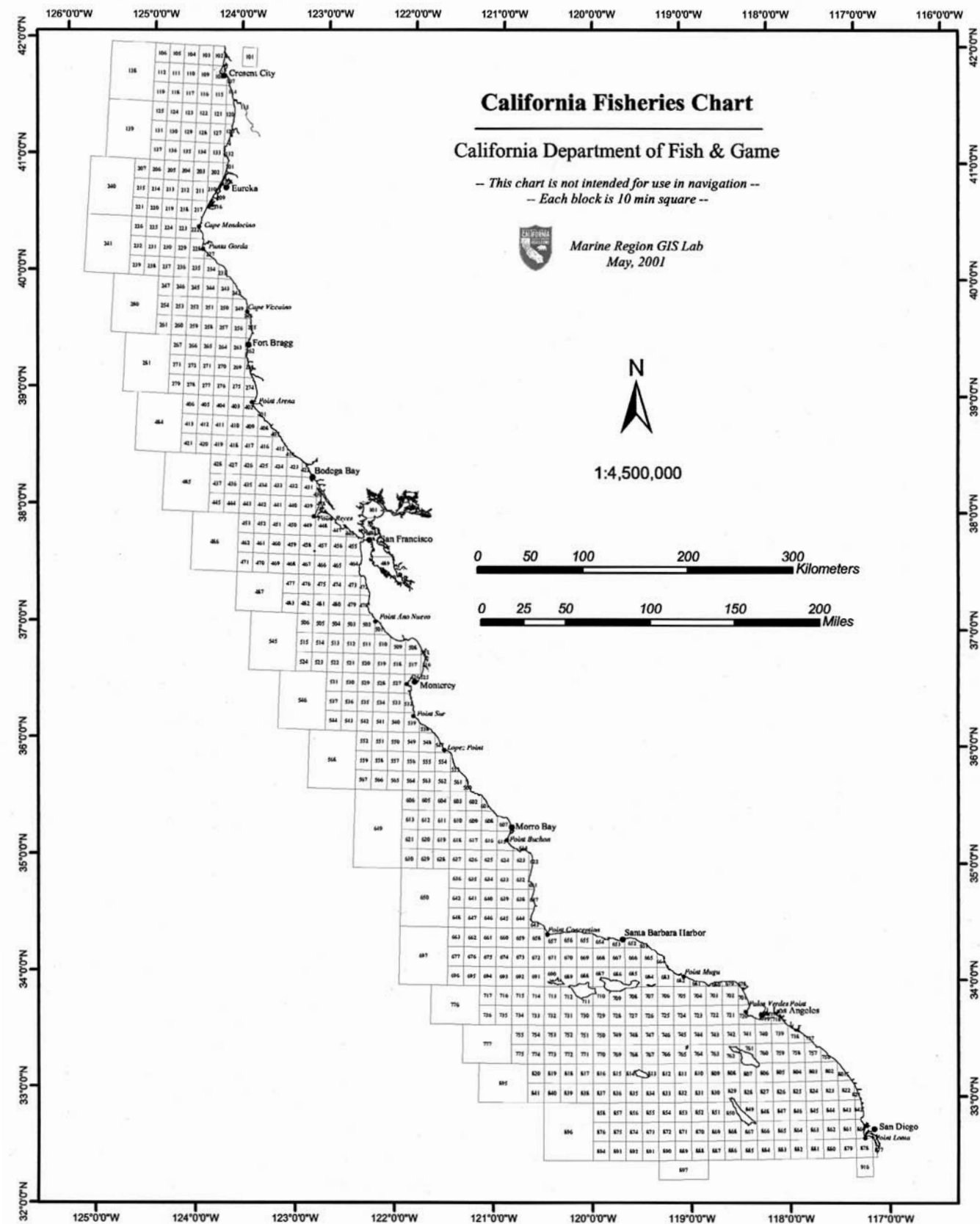Figure 1. Map of California showing fishery landing blocks.

TABLE 2
**Abundance and Density Estimates for White Abalone
in California, 1970s to the Present**

Study/year	Abundance estimate	Density[a] (abalone per ha)
Tutschulte, 1967	644,464[b]	857
Tutschulte, 1971-73	1,729,600[c]	2,300
Current study, 1969-78	360,476	479
Davis et al. 1980-81	15,792	21
Davis et al. 1992-93	1,256	1.67
Haaker 1996-97	880	1.17
Hobday et al. 2001	2,053	2.73

[a]Deep (25–65m) rocky reef habitat for white abalone in California is esti-
mated at 752 ha (Davis et al. 1998); recent side-scan sonar estimates of deep
habitat are six times as large (R. Kvitek, pers. comm.).
[b]Based on three white abalone within a 5×7 m quadrat.
[c]Based on seven white abalone within three 10 m^2 quadrats at Santa Catalina
Island.

Combining this abundance estimate with previously published estimates of habitat area (752 ha) (Davis et al. 1998; Hobday et al. 2001) suggests that population density in California in 1969 was approximately 479 animals per hectare. Most white abalone (271,051 abalone) over the ten-year period (approximately 75%) were taken from San Clemente Island. This island has an estimated total shelf area of 5,557 ha[6] within the 25–65 m depth range (Rogers-Bennett et al. 2002). If we assume that 3% of this area is suitable rocky substrate (Davis et al. 1998), then white abalone habitat would comprise 167 ha (Rogers-Bennett et al. 2002), and the density of abalone at San Clemente Island in 1969 would have been 1,623 abalone per hectare. In contrast, if all of the habitat at this depth is suitable white abalone habitat (5,557 ha), then the density falls to 49 abalone per hectare in 1969.

For white abalone we are able to compare our baseline estimate (479 white abalone per hectare) with other estimates derived from published data. The earliest study during the 1970s (Tutschulte 1976) estimated abundance at 2,300 animals per hectare, almost five times greater than our estimate derived from fishery data (tab. 2). One possible explanation for the discrepancy is that Tutschulte's fishery-independent estimate was based on a limited sample of three quadrats (10 m^2) at Santa Catalina Island in which seven white abalone were found (Tutschulte 1976; Hobday et al. 2001).

Modern Estimates

Modern estimates of white abalone abundance suggest that populations have declined dramatically since the 1960s. In the late 1990s, submersible surveys found 157 white abalone and estimate that there are now 21 white abalone per hectare (Davis et al. 1996, 1998).

[6]This is four times larger than previous estimates of white abalone habitat at San
Clemente Island (40 ha) (Davis et al. 1998).

Fishery-independent population estimates have been made using small submarines in southern California (Davis et al. 1996; Davis et al. 1998; Haaker et al. 1998). These estimates suggest that less than 3,000 white abalone exist throughout their range in southern California and Mexico (Hobday et al. 2001). Despite our limited knowledge of modern abundances, today's estimates are less than 1% of our baseline estimate generated from fishery landings (1969–78) and less than 0.1 % of Tutschulte's (1976) estimate.

PINK ABALONE

An estimate of baseline pink abalone population abundance using landings data during the peak of the fishery, 1950–59, is 9.3 million animals (tab. 1). There are no records of recreational pink abalone fishing during this period. We assumed that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Pink abalone are estimated to reach the minimum legal size of 159 mm (6.25 in.) in 16 years (Tutschulte 1976; Tutschulte and Connell 1988).

There are currently no estimates of subtidal rocky habitat for pink abalone in southern California, but kelp canopy occurs primarily over rocky reefs of intermediate depth, suitable habitat for pink abalone; we therefore used kelp canopy area as a highly conservative proxy for pink abalone habitat. We examined aerial photographs of kelp surface canopy taken in the spring and summer of 1967 and found approximately 14,000 ha of kelp coverage in southern California from Point Arguello south to the Mexican border (8,500 ha) and at the offshore islands (5,500 ha) (kelp data provided by CDFG). Using this crude method of estimating habitat area, we estimated that pink abalone density in the 1950s would have been at most 664 animals per hectare. This estimate would be greatly reduced if pink abalone habitat estimates were revised upward. One additional caveat is that local densities may have been much higher, as earlier qualitative records suggest (see sections on early abalone exploitation).

Modern Estimates

To estimate current densities of pink abalone we used data from fishery-independent surveys conducted in 2001 by the Kelp Forest Monitoring Program. Divers found no pink abalone at 15 of the 16 sites surveyed at five northern Channel Islands (fig. 2). Pink abalone were found only at Landing Cove within the Anacapa Island Ecological Reserve, at a density of 42 animals per hectare. Using this density and averaging it with densities at two other locations at Anacapa Island, both of which lacked pink abalone, we calculated an average density for the entire island of 14 animals per hectare.
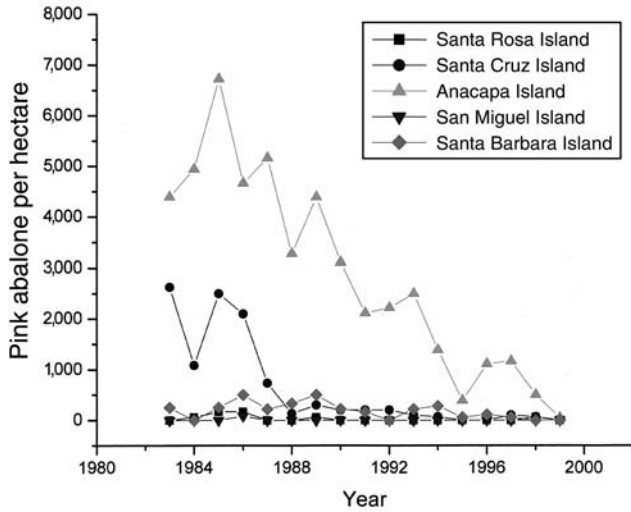
Figure 2. Density of pink abalone at subtidal Kelp Forest Monitoring Program survey sites at northern Channel Islands.

Figure 3. Density of black abalone at intertidal survey sites in southern California.

To estimate the size of potential habitat for pink aba-lone at Anacapa Island we used two different methods. First, we examined aerial photographs of kelp canopy coverage taken in October 1989 by ECO Scan.[7] These showed approximately 27 ha of kelp canopy around Anacapa Island. Using the abalone density data discussed above, we estimated a modern abundance of 378 pink abalone in the northern Channel Islands for 2001. No data were available for other islands or mainland locations.

The second method of estimating potential habitat at Anacapa Island was developed by the U.S. Geological Survey GIS program for southern California habitats. The subtidal rocky areas along the northern side of Anacapa island have been mapped, and it is estimated that 115 ha of subtidal rocky substrate occur at 10–50 m depth (Cochrane et al., in press); extrapolating from this, we estimate that 230 ha of suitable habitat occurs around the entire island. This area is ten times the habitat area we estimated based on kelp surface area (27 ha). It yields a modern abundance estimate of 3,220 pink abalone at the northern Channel Islands. Regardless of the method one chooses to estimate suitable pink abalone habitat area, however, modern estimates of abundance are less than 0.01% of the estimated 9.3 million pink abalone that occurred in the 1950s.

BLACK ABALONE

A conservative estimate of the baseline abundance of black abalone, using landings data from the peak of the fishery, 1972–81, is 3.54 million animals (tab. 1). Black abalone was the last species of abalone to be exploited; landings peaked in 1973. We assumed that no new in-dividuals were added to the population during the ten-
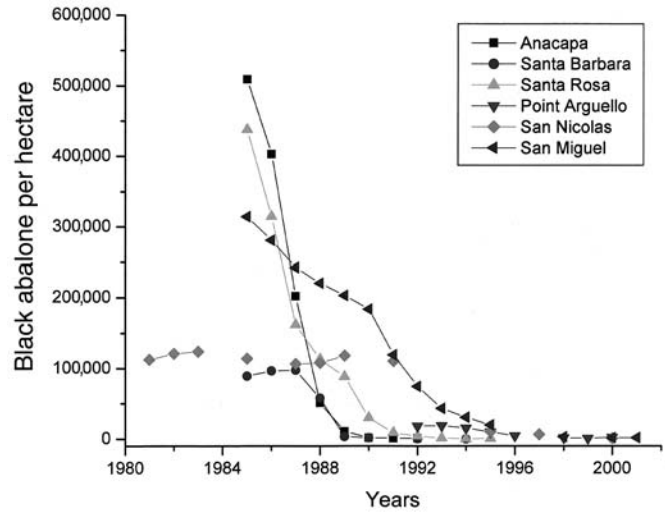
year peak of the fishery for this species. Black abalone are slow-growing animals, and mean asymptotic length (152 mm) appears to be smaller than minimum legal size for sites at San Miguel Island and Point Arguello in the late 1980s (Haaker et al. 1995).

Modern Estimates

Based on three data sets from population surveys in the intertidal zone at five islands and one mainland site, populations have severely declined since the late 1980s (fig. 3). Using fishery-independent surveys of black abalone abundance we find that three of the six areas now have no black abalone. In the three areas with black abalone surveyed in 2000, densities have dropped more than 99%, from hundreds of thousands per hectare prior to 1985 to 2,500 per hectare at Point Arguello, 1,706 per hectare at San Miguel Island,[8] and 953 per hectare at San Nicolas Island[9] (fig. 3).

GREEN ABALONE

A conservative estimate of baseline green abalone abundance, using landings data during the peak of the fishery, 1966–75, is 1.5 million animals (tab. 1). We as-sumed that during the ten-year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Green abalone appear to be the slowest growing of the five commercially exploited southern abalone species and are estimated to reach the minimum legal size of 178 mm (7 in.) in 20 years (Tutschulte 1976; Tutschulte and Connell 1988; Shepherd et al. 1991).

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[7]ECO Scan Resources Data, Box 1046, Freedom, CA 95019, (831)728-3289.

[8]CDFG, unpubl. data.

[9]CDFG, unpubl. data; and G. VanBlaricom, unpubl. data.

Modern Estimates

There are few estimates of current green abalone abundance. In the early 1970s abundance estimates were made by divers conducting timed swims at Santa Catalina and San Clemente Islands; however, no density information was provided. Abundance at each of four sites at Santa Catalina Island in 1974 averaged 130 green abalone per hour; at San Clemente Island in 1973 abundance averaged 126 green abalone per hour.[10] In comparison, timed swims in 1995 at Santa Catalina Island at four sites yielded 26 green abalone during 1,172 min of search time (1.33 per hour), and in 1997 at San Clemente Island only 2 green abalone were found during 458 min of search time (0.26 per hour). Using these data we were unable to determine estimates of abundance for comparison with our estimated baseline abundance for this species, but clearly abundances have declined dramatically. Modern density surveys of green abalone are desperately needed.

THREADED ABALONE

A conservative estimate of baseline population abundance for threaded abalone, using landings data during the peak of the fishery, 1971–80, is 21,000 animals (tab. 1). Within this ten-year period 99.6% of all the threaded abalone taken by the fishery had been landed. After 1980 only 66 threaded abalone were landed We assume that during the ten year period (1) the majority of the population was "sampled" by the fishery and (2) no new individuals were added to the population. Threaded abalone landings were not recorded in the recreational landings database. Threaded abalone, like white abalone, is a deepwater species. The distribution of threaded abalone extends farther north than white abalone and not as far south (Geiger 1999), so habitat estimates generated for white abalone cannot be used for threaded abalone. At present, there are no reliable estimates of threaded abalone habitat that can be used to estimate population density.

Modern Estimates

Few fishery-independent estimates of threaded abalone exist. This species appears to have been rare even in the 1970s. A survey conducted in 1974 found that of 1,877 abalone quantified during more than nine hours of search time at Santa Catalina and San Nicolas Islands, only one was a threaded abalone (tab. 3).[11]

In 2001 the Kelp Forest Monitoring Program found five threaded abalone for the first time since their surveys began in 1972: four inside abalone-recruitment

TABLE 3
Abundance of Threaded Abalone from Fishery-independent Abalone Surveys in 1974 at Two Channel Islands in Southern California

Survey site	Abalone Species					
	Red	Pink	Green	Black	White	Threaded
San Nicolas Island[a]	760	214	0	0	5	1
Santa Catalina Island[b]	0	352	453	89	3	0

[a]Surveys at San Nicolas Island ranged in depth from 5 to 21 m during 6.6 hr of search time.
[b]Surveys at Santa Catalina Island ranged in depth from 2 to 14 m during 3.9 hr of search time.

modules and one on rocky substrate.[12] Divers found another 11 threaded abalone at a site near Santa Barbara on the mainland. All ranged in size from 50 to 82 mm. We are not aware of any other fishery-independent data for this subspecies. The data suggest that this subspecies may now number in the hundreds and may be at least as rare as white abalone, if not more so.

FLAT AND PINTO ABALONE

Commercial data on flat and pinto abalone are limited and may not accurately reflect the take by the fishery. The total number of flat abalone reported in the commercial abalone landings database is 130 animals, all taken from 1973 to 1994. The bulk of this information is likely reporting error, since only 0.6% of the landings are reported from blocks north of Point Conception. Reports of pinto abalone in commercial landings also appear to be spurious since of the 549 abalone taken from 1973 to 1996 only 3% are reported from blocks north of Point Conception. Furthermore, there are some flat and pinto abalone landings reported from blocks far offshore at depths deeper than abalone exist. These species are not recorded in the southern recreational landings database. Flat and pinto abalone are small in size compared with red abalone and rarely reach 179 mm shell length. Flat abalone have always been considered rare (McMillen and Phillips 1974). For these reasons neither pinto nor flat abalone were targeted by the recreational fishery in northern California. Therefore, we do not use fishery-dependent landing information to determine historical baseline abundances for these species.

Northern California

We compiled fishery-independent information for flat and pinto abalone to estimate baseline abundances in northern California. Fishery-independent estimates of abalone density were made in 1971 and 1975 in northern California (tab. 4). Surveys in 1971 quantified abalone abundance along transects of known size, resulting in

[10]CDFG, unpubl data.

[11]Burge, R. 1974. Abalone-lobster investigations. 74-KB-15 and 74-M-3. Unpublished cruise report, Calif. Dept. Fish Game, Long Beach, Calif., 6 p.

[12]D. Kushner, pers. comm.

estimates of density at three fished sites in northern California: Fort Ross State Park (FRSP) in Sonoma County and Point Arena (PA) and Van Damme State Park (VDSP) in Mendocino County. Abalone surveys in 1971 were conducted using differing protocols. The first survey examined abalone density within 38 subtidal transects (each 4 m × 30 m), covering an area of 4,560 m². The second survey examined abalone density using 2 m × 30 m transects and 30 m² arcs, covering an area of 2,070 m². The third survey in 1975 enumerated abalone abundances and species composition during timed swims (but did not report density) at seven areas in northern California that encompassed both fished (including FRSP and VDSP) and reserve sites.

No direct estimates of abalone habitat exist for northern California, although subtidal maps are currently being generated.[13] To arrive at a conservative estimate of abalone habitat area we used the abundance of kelp canopy as determined from aerial photographs taken flying over the land-sea interface in 1989. We estimated a minimum of 1,480 ha of rocky subtidal habitat along the north coast including Marin, Sonoma, Mendocino, and Humboldt Counties.

We used the 1971 estimate of flat and pinto abalone density in northern California to generate early estimates of population size (the 1975 surveys did not estimate density). Population size estimates were generated using Jolly-Seber methods; we input estimates of total habitat area, probability of type I error (alpha = 0.05), and sampling with replacement parameters into the empirical calculation.

Our baseline estimate of abundance for flat abalone in northern California (1,480 ha of habitat) in 1971 using Jolly-Seber estimates is 71,000 (upper 95% confidence interval: 133,000; lower 95% confidence interval: 10,000). Our baseline abundance estimate for pinto abalone in 1971 is 156,000 (upper 95% confidence interval: 341,000; lower 95% confidence interval: 29,000). The population estimates based on data from 1971 have extremely large confidence intervals. The patchy nature of the abundance data, with only a few patches occupied by flat and pinto abalone, along with the limited sampling in 1971, contributed to this wide confidence interval.

Modern Estimates

We compared these early surveys with our modern estimates (1999–2001) of abundance and density from five sites: Bodega Marine Life Refuge and Cabrillo Marine Reserve, Fort Ross State Park, Salt Point State Park in Sonoma County, and Van Damme State Park in Mendocino County. We used transects of two sizes: large emergent transects 2 m × 30 m (60 m²) and small inva-

TABLE 4
Abundance of Flat, Pinto, and Red Abalone
by Depth in Northern California

Survey year and type	Species	Abundance (no. of animals)		
		< 8.5 m depth (shallow)	> 8.5 m depth (deep)	Total (all depths)
1971[a]				
Emergent	Flat	17	5	22
	Pinto	7	41	48
	Red	701	32	733
1971-72[b]				
Emergent	Flat	5	16	21
	Pinto	11	56	67
	Red	327	85	412
1975[c]				
Timed swim	Flat		149	23
	Pinto	101	105	206
	Red	9,598	1,086	10,684
1999-2001[d]				
Emergent	Flat	9	2	11
	Pinto	1	8	9
	Red	3,849	1,241	5,090
Invasive	Flat	3	2	5
	Pinto	0	2	2
	Red	761	313	1,074

[a]Surveys covered an area of 4,560 m² along 38 transects (30 m × 4 m) at two sites (CDFG, unpubl. data).
[b]Surveys covered an area of 2,070 m² at one site, Point Arena, in northern California (Gotshall et al. 1974).
[c]Surveys during 33 timed swims covered an area of approximately 5,406 m² at seven study sites (Schultz and Burge, unpubl. data).
[d]Both large emergent transects (30 m × 2 m) and small invasive transects (5 m × 2 m) were surveyed. Investigators surveyed a total of 163 emergent and 120 invasive transects, examining 10,980 m² of area at the same five sites in northern California as were examined in 1975 and 1971 (Rogers-Bennett et al., current study).

sive transects 2 m × 5 m (10 m²). A total of 163 large and 120 small transects were surveyed (roughly 32 and 24 per site, respectively). Surveyors searched smaller transects invasively, moving cobbles, rocks, and corallines and turning over red sea urchins (*Strongylocentrotus franciscanus*) to look for small abalone (tab. 4).

Density estimates suggest that populations of flat abalone, which were not targeted by the fishery have remained consistent over time in northern California from the baseline estimate of 71,000 animals in 1971 to the present estimate of 83,845 animals (upper 95% confidence interval: 99,000; lower 95% confidence interval: 69,000). In contrast, pinto abalone populations appear to be declining in northern California, dropping nearly ten-fold from a baseline abundance of 156,000 in 1971 to 18,000 in 1999–2001 (upper 95% confidence interval: 22,000; lower 95% confidence interval: 13,000). Modern estimates have narrower confidence intervals because abalone were more evenly distributed and more transects were sampled.

DISCUSSION

Our estimates of baseline abundance for all species of abalone examined indicate that populations were larger

in the past than they are today (tab. 1). In the case of white abalone, modern dive surveys estimate densities of 21 animals per hectare (Davis et al. 1996) and submersible surveys in 1996–97 and 1999 yield fewer than 3 animals per hectare (Haaker 1998); this is in marked contrast to our estimates of 479 animals per hectare in 1969. These findings suggest that white abalone now occur at less than 5% of their previous density (tab. 2). If we examine densities at San Clemente Island where 75% of the white abalone catch was taken, we find that densities have dropped from a high of 1,623 per hectare in 1969. Clearly at such low densities, Allee effects will be of concern for population recovery of this free-spawning invertebrate (Hobday and Tegner 2001).

The present distribution of white abalone at deep depths may be problematic for recovery. Remnant populations of adult white abalone remain only at the deepest portions (at depths > 33 m) of their former distribution, whereas divers report that they previously occurred at shallower depths.[14] Moreover, laboratory work indicates that larval development is arrested at temperatures below 12°C (Leighton 1972), which is common at depths (beyond 30 m) where adult broodstock have recently been collected.[15] In the laboratory, no larval settlement was observed at 10°C, whereas only 57–66% settled at 12°C after 15 days, and those larvae did not survive beyond day 30 (Leighton 1972). Furthermore, no signs of recruitment had been observed for two decades until 2000, when two juvenile white abalone were observed at Yellow Banks, Santa Cruz Island, at a depth of 10 m, and again in 2001, when one juvenile was observed at this location.[16] Although this is an indication that some recruitment is occurring at shallower depths, this is far less than the percentage of juveniles (15%) in samples (N = 20) collected in the early 1970s (Tutschulte 1976). Clearly, these few juveniles will not sustain the population. Today, a captive-rearing program is underway at the Channel Islands Marine Resources Institute with 8 wild adults and 18,000 hatchery-raised abalone. Withering syndrome reduced the number of hatchery-raised abalone from 100,000 to 18,000 in 2002.[17]

Pink abalone were once landed in quantities as large as 1.2 million per year during the peak of this fishery (1952) but are now absent from many survey areas in the northern Channel Islands. Fishery-independent declines of pink abalone preceded the fishery collapse (Davis et al. 1992) as did fluctuations in recruitment and recruitment failure (Davis 1995), suggesting that warning signs were present in the early 1990s. In 2000, diver sur-

veys found pink abalone at only 1 site, inside the Anacapa Island Ecological Reserve (42 per hectare), of the 16 sites surveyed around five islands (fig. 2). This protected site, despite having fewer pink abalone than the nearby fished site when the fishery-independent surveys began in 1983, had significantly more abalone, of a greater mean size yielding higher estimates of egg production, than the nearby fished site by the end of the surveys (Rogers-Bennett et al. 2002). Abalone inside protected areas have been shown to have greater reproductive potential than those in fished areas (Wallace 1999; Rogers-Bennett et al. 2002), as has been observed with fin-fishes (Roberts and Polunin 1991; Paddack and Estes 2000). Once abalone abundances fall too low, however, populations may not recover, as was demonstrated by the failure of abalone restoration efforts using a fishery closure from the Palos Verdes Peninsula to Dana Point in southern California (Tegner 1993, 2000).

Restoration experiments aggregating 600 pink abalone broodstock were begun in 1995 in Channel Islands National Park. Preliminary results suggest that recruitment occurred in 1998 and that adult densities still exceed 2,000 animals per hectare; however, the population is declining at about 15% a year, presumably due to attrition through old age (Davis 2000). Time will tell the fate of this aggregation experiment.

Black abalone densities have been reduced by 99% (fig. 3) as a result of the combined impacts of fishing and Withering Syndrome (Haaker et al. 1992; Davis et al. 1992; Altstatt et al 1996; Moore et al. 2000). Mass mortalities associated with Withering Syndrome were first observed in 1986 at Anacapa Island; the disease spread north to central California (Steinbeck et al. 1992; Altstatt et al. 1996) and then to other offshore islands (VanBlaricom et al. 1993) and to other species. Increases in sea water temperature have been shown in the laboratory to exacerbate mortality from this disease (Friedman et al. 1997; also see Moore et al., this volume). At Anacapa, Santa Barbara, and Santa Rosa Islands, populations at intertidal sampling sites fell to zero in the mid-1990s, and at San Miguel Island, the coldest of the Channel Islands, densities at three sites average 0.18 animals per square meter in 2001.[18]

Today, survivors of the disease are at exceptionally low densities at sites that once supported 27–74 abalone per square meter (Richards and Davis 1993). It is unknown whether survivors are resistant to the disease, and if so whether this resistance can be passed on to produce disease-resistant progeny. Artificial spawning efforts with black abalone have been unsuccessful to date.[19] Re-population without intervention seems unlikely since

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[14]B. Owen, pers. comm.

[15]L. Rogers-Bennett, pers. observ.

[16]D. Kushner, pers. comm.

[17]T. McCormick, pers. comm.

[18]Kelp Forest Monitoring Program data.

[19]C. Friedman, pers. comm.

TABLE 5
Abundance of Flat, Pinto, and Red Abalone Observed in Northern California

		Number of abalone			Percentage of total	
Survey period	Investigators	Flat	Pinto	Total[a]	Flat	Pinto
1971	CDFG et al.	22	48	803	3%	6%
1971–72	Gotshall et al.	21	67	500	4%	13%
1975	Schultz and Burge	172	206	10,963	2%	2%
1996–97	Rogers-Bennett and Pearse[b]	57	0	2,162	3%	0
1999–2001	Current study	16	11	6,191	< 1%	< 1%

[a]Flat, pinto, and red abalone combined.
[b]Study conducted at shallow depths more suitable for flat abalone than for pinto abalone.

dispersal distance appears to be short, as indicated by the genetic differentiation of neighboring populations of black abalone in central California (Hamm and Burton 2000). Aggregating resistant broodstock in the wild may facilitate spawning success, yet this could also facilitate the spread of the disease by increasing adult density. A status report on black abalone has recently been funded by the NMFS and will likely be completed in 2003.

Green abalone populations have been greatly reduced from a baseline estimate of 1.5 million; however, there are few current sources of data to compare with this baseline estimate. We know that early in the 1900s green abalone near Avalon on Catalina Island were stacked 4–5 deep in the intertidal zone but were absent just 13 years later (Edwards 1913). These observations along with current low densities and the species shallow-water distribution suggest that this species is particularly susceptible to overfishing. A captive-breeding program has begun for green abalone in southern California (Lapota et al. 2000).

Threaded abalone, which appear to have been even more rare than white abalone, were also occasionally landed in the fishery. The baseline abundance of this species is estimated to have been 21,000 animals in 1971. Had this been known prior to the 1970s, the species could have been excluded from the fishery. In fishery-independent surveys as early as 1974 only one threaded abalone was seen out of 1,876 abalone observed (tab. 3), indicating that this subspecies was rare even in the 1970s.[20] The fishery removed 21,000 threaded abalone from 1969 to 1995, apparently the bulk of the population in southern California. In 2002 only 16 threaded abalone were documented in California, all at depths greater than 20 m.[21] Captive breeding may be the only option for recovery of this subspecies since populations appear to be at such low numbers. Since invertebrate conservation is often species driven, the decisions by taxonomists to "lump or split " (Murphy 1991) threaded

abalone from pinto abalone will be relevant to the conservation status of threaded abalone.

In northern California, pinto and flat abalone both occur at low densities (< 50 per hectare), and recent surveys indicate that they comprise less than 1% of the total abalone population (tab. 5). Populations of flat abalone have remained low in northern California but do not appear to have declined from 1972 levels. In contrast, flat abalone populations in central California have fallen dramatically from 31% to 6% of the population in just 30 years, raising concerns about their persistence in this region.[22] Pinto abalone in northern California have fallen from 13% of the total abalone population in the early 1970s to less than 1% today (tab. 5). Population estimates in northern California suggest that densities of pinto abalone have fallen ten-fold in 30 years. Previous reports suggest that pinto abalone were also found in southern California in the northern Channel Islands, but they have not been observed there for the past two decades.[23] Similarly, pinto abalone have not been observed in central California for at least 30 years (tab. 5). Pinto abalone in northern California may have declined due to light fishing pressure. It was not until 1999 that pinto and flat abalone were effectively excluded from the recreational fishery in northern California as a result of an increase in the minimum legal size limit from 102 mm (4 in.) for flats and pintos to 178 mm (7 in.) for all species.

Pinto abalone, though rare in northern California, also occur in portions of Oregon, Washington, British Columbia, and Alaska. Surveys conducted in British Columbia in the late 1990s estimate densities ranging from 200 to 2,900 pinto abalone, with a mean density of close to 1,000 per hectare (Campbell 2000b; Lucas et al. 2000). The fishery in all these areas is now closed, and restoration programs including stocking have been proposed (Campbell 2000a),[24] an indication that declines in this species are widespread.

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[20]Burge, R. 1974. Abalone-lobster investigations. 74-KB-15 and 74-M-3. Unpublished cruise report, Calif. Dept. Fish Game, Long Beach, Calif., 6 p.

[21]D. Kushner, pers. comm.

[22]L. Rogers-Bennett, unpubl data.

[23]D. Parker, pers. comm.

[24]M. Banks, pers. comm.

IMPLICATIONS FOR RESTORATION
OF ABALONE STOCKS

A network of marine reserves, or no-take areas, has been recommended for a number of fisheries to protect against their collapse and aid in restoration (Roberts and Polunin 1991; Rogers-Bennett et al. 1995; Roberts 1997; Lauck et al. 1998). Scientists advocated establishing a network of abalone reserves in California as early as 1913: "It would be very advantageous to establish a number of protected reservations, similar to those at Monterey Bay and at Venice, at regular intervals [a network] along the coast" (Edwards 1913). A network of reserves was never established. Today, the California Fish and Game Commission is considering establishing a network of no-take reserves along the California coast under the Marine Life Protection Act (AB 993). Already, the commission has approved reserves in the Channel Islands.

Positive multispecies interactions (Bertness and Leonard 1997) can be maintained inside marine reserves (Rogers-Bennett and Pearse 2001). Juvenile abalone, for example, have been observed in close association with the spine canopy of adult red sea urchins (Ebert 1968; Tegner and Dayton 1977). Established marine reserves in northern California with red sea urchins present had significantly more juvenile red abalone and rare flat abalone than fished sites (Rogers-Bennett and Pearse 2001). Sea urchins appear to be vital for the survival of small wild abalone in the 5–20 mm size class (Rogers-Bennett and Pearse 2001; Day and Branch 2002) and hatchery-reared abalone stocked in the ocean (Kojima 1981; Rogers-Bennett and Pearse 1998). This suggests that marine protected areas where red sea urchins are not fished may be essential habitat for abalone and could play a crucial role in restoration efforts. Furthermore, molluscs, such as abalone, may be a good indicator group when selecting marine reserves that could benefit multiple species (Gladstone 2002). Areas that at one time had high numbers of abalone may indicate productive subtidal sites that could be set aside as no-take reserves for multiple species (Rogers-Bennett et al. 2002).

Benthic invertebrates such as abalone, sea urchins, queen conch, and scallops must occur in dense patches to successfully reproduce, suggesting that Allee effects (or depensation) are important (Tegner et al. 1996; Hobday et al. 2001; Levitan et al. 1992; Stoner and Ray-Culp 2000; Stokesbury and Himmelman 1993). Aggregation size and distance between neighbors, in addition to abundance, play important roles in the population dynamics of abalone (Shepherd et al. 2001). Experiments have shown that fertilization may be limiting in populations of *H. laevigata* when distances separating spawning individuals are greater than 2 m (Babcock and Keesing 1999). Studies estimate that if 11% of the remaining white abalone are close enough to a conspecific for successful fertilization, then only 73 pairs of the remaining 3,000 animals have the potential to reproduce successfully (Hobday et al. 2001). Minimum viable population density for *H. laevigata* has been estimated at 2,000 animals per hectare, below which recruitment collapses (Shepard and Brown 1993). More work must be done to set appropriate density goals for abalone restoration in California since reliable estimates of habitat area are lacking in most subtidal areas.

Collapsed populations of abalone worldwide are in need of restoration. In California, restoring abalone (other than those species currently federally listed) will be guided by the state's Abalone Recovery and Management Plan (CDFG Code 5522), which is now under review (Dec. 2002). This study helps to define the challenges of restoring populations to 20% or 40% of baseline. Furthermore, restoration efforts will need to consider the potential impacts of climate change (Tegner et al. 2001), sea otter expansion (Wendell 1994), and illegal take. Restoration will need to be completed prior to the re-opening of abalone fisheries, but restoration to what level? In 1903 a Japanese hard-hat diver in the Mendocino area in northern California could collect an average of 2,300 red abalone in 6 hr (360 min) (Lundy 1997); almost 100 years later (in 2000) only 406 red abalone were found in the same area in 326 min.[25] In 1953 biologists concluded that "too few abalones" were found in northern California in comparison to central and southern California (Cox 1962). These examples reinforce the concern that our perception of abundance, so critical to restoration efforts in southern California and management in northern California, may have become the victim of shifting baselines. The challenge for managers in this and other fisheries will be to set restoration and management goals at baselines that do not rely solely on the limited perspective of modern data but instead take into account historical abundances. The reintroduction of long-lived and high-value species such as abalone in nearshore ecosystems along the northeastern Pacific may be required if they are to get "back to the future" (Pitcher 2001).

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[25]L. Rogers-Bennett, unpubl. data.

LITERATURE CITED

Altstatt, J. M., R. F. Ambrose, J. M. Engle, P. L. Haaker, K. D. Lafferty, and P. T. Raimondi. 1996. Recent declines of black abalone *Haliotis cracherodii* on the mainland coast of central California. Mar. Ecol. Prog. Ser. 142:185–192.

Anderson, P. K. 1995. Competition, predation, and the evolution and extinction of Steller's sea cow, *Hydrodamalis gigas*. Mar. Mamm. Sci. 11:391–394.

Babcock, R., and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. Can. J. Fish. Aquat. Sci. 56:1668–1678.

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

Bonnot, P. 1930. Abalones in California. Calif. Fish Game 16:15–23.

Carlton, J. T., J. B. Geller, M. L. Reaka-Kudla, and E. A. Norse. 1999. Historical extinctions in the sea. Annu. Rev. Ecol. Syst. 30:515–538.

Campbell, A., ed. 2000a. Workshop on rebuilding abalone stocks in British Columbia. Can. Spec. Publ. Fish Aquat. Sci. 130:150.

Campbell, A., 2000b. Review of northern abalone, *Haliotis kamtschatkana*, stock status in British Columbia. Can. Spec. Publ. Fish Aquat. Sci. 130: 41–50.

Casey, J. M., and R. A. Myers. 1998. Near extinction of a large widely distributed fish. Science 281:690–692.

Cincin-Sain, B., J. E. Moore, and A. J. Wyner. 1977. Management approaches for marine fisheries: the case of the California abalone. Sea Grant Pub. 54, University of California Sea Grant College Program, 223 p.

Cochrane, G. R., R. D. Vetter, N. M. Nasby, C. A. Taylor, and R. Cosgrove. In press. Benthic habitats in four marine-reserve locations surrounding the Santa Barbara Basin. Final report, part II. California Sea Grant-Marine Ecological Reserves Research Program 4-M-N: Egg and larval fish production from marine ecological reserves, 12 p.

Coastal Ecology Group. 1985. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates—black, green, and red abalones. Fish and Wildlife Service Biol. Rept., 82:8–19.

Cox, K. W. 1960. Review of the abalone of California. Calif.. Fish Game. 46:381–406.

Cox, K. W. 1962. California abalones, Family Haliotidae. Calif. Dept. Fish Game, Fish Bull. 118:1–133.

Croker, R. S. 1931. Abalones. *In* The commercial fish catch of California for the year 1929. Calif. Dept. Fish Game, Fish Bull. 30:58–72.

Davis, G. E. 2000. Refugia-based strategies to restore and sustain abalone *Haliotis* spp. populations in southern California. Can. Spec. Publ. Fish Aquat. Sci. 130:133–138.

Davis, G. E. 1995. Recruitment of juvenile abalone (*Haliotis* spp.) measured in artificial habitats. Mar. Freshw. Res. 46:549–554.

Davis, G. E., P. L. Haaker, P. L., and D. V. Richards. 1996. Status and trends of white abalone at the California Channel Islands. Trans. Amer. Fish. Soc. 125:42–48.

Davis, G. E., D. V. Richards, P. L. Haaker, and D. O. Parker. 1992. Abalone population declines and fishery management in southern California. *In* Abalone of the world: biology, fisheries, and culture, S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo, eds. Oxford: Fishing News Books, Blackwell Science Ltd., pp. 237–249.

Davis, G. E., P. L. Haaker, and D. V. Richards. 1998. The perilous condition of the white abalone, *Haliotis sorenseni*. J. Shellfish Res. 17:871–875.

Day, E., and G. M. Branch. 2002. Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). Ecol. Mono. 72:133–149.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Applic. 8:309–322.

Dugan, J. E., and G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Can. J. Fish. Aquat. Sci. 50:2029–2042.

Ebert, E. E. 1968. A food habits study of the southern sea otter, *Enhydra lutris nereis*. Calif. Fish Game 54:33–42.

Ebert, T. A. 1999. Plants and Animal Populations: Methods in Demography. San Diego, Calif.: Academic Press, 312 p. Edwards, C. L. 1913. The abalone industry in California. Calif. Dept. Fish Game, Fish Bull. 1:5–15.

Erlandson, J. M., D. J. Kennett, B. L. Ingram, D. A. Guthrie, D. P. Morris, M. A. Tveskov, G. J. West, and P. L. Walker. 1996. An archaeological and paleontological chronology for Daisey Cave (CA-SMI-261), San Miguel Island, California. Radiocarbon 38:355–373.

Estes, D. 1977. Kondo Mahaharu and the best of all fishermen. J. San Diego History, 23(2): 1–19.

Friedman, C. S., M. Thomson, C. Chun, P. L. Haaker, and R. P. Hedrick. 1997. Withering syndrome of the black abalone *Haliotis crachrodii* (Leach): water temperature, food availability, and parasites as possible causes. J. Shellfish Res. 16:403–411.

Geiger, D. L. 1999. Distribution and biogeography of the recent Haliotidae (Gastropoda: Vetigastropoda) world-wide. Bollett. Malacol. 35:5–12.

Gladstone, W. 2002. The potential value of indicator groups in the selection of marine reserves. Biol. Conserv. 104:211–220.

Gotshall, D. W., R. N. Lea, L. L. Laurent, T. L. Hoban, and G. D. Farrens. 1974. Mendocino Power Plant site ecological study. Final Report. PG & E Coop. Res. Agree S-1902. Calif. Dept. Fish Game, Marine Resources, Admin. Rept. 74–7.

Haaker, P. L. 1998. White abalone—off the deep end forever? Outdoor Calif. Jan.–Feb., pp. 17–20.

Haaker, P. L., D. O. Parker, H. Togstad, D. V. Richards, G. E. Davis, and C. S. Friedman. 1992. Mass mortality and withering syndrome in black abalone, *Haliotis cracherodii*, in California. *In* Abalone of the World, S. A. Shephard, M. J. Tegner, and S. A. Guzmán del Proo, eds. Oxford: Blackwell Scientific, pp. 214–224.

Haaker, P. L., D. O. Parker, and C. S. Y. Chun. 1995. Growth of black abalone, *Haliotis cracherodii* Leach, at San Miguel Island and Point Arguello, California. J. Shellfish Res. 14:519–525.

Haaker, P. L., D. O. Parker, K. C. Barsky, and C. S. Y. Chun. 1998. Growth of red abalone, *Haliotis rufescens* (Swainson), at Johnsons Lee, Santa Rosa Island, California. J. Shellfish Res. 17:747–753.

Hamm, D. E., and R. S. Burton. 2000. Population genetics of black abalone, *Haliotis cracherodii*, along the central California coast. J. Exp. Mar. Biol. Ecol. 254:235–247.

Heath, H. 1925. The abalone question. Calif. Fish Game 11:138–139.

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

Hobday, A. J., M. J. Tegner, and P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. Rev. Fish Biol. Fish. 10:493–514.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs 16: S23–S32.

Jackson, J. B. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

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

Kojima, H. 1981. Mortality of young Japanese black abalone *Haliotis discus discus* after transplantation. Bull. Jap. Soc. Sci. Fish. 47:151–159.

Karpov, K. A. 1997. Relative abundance and size composition of subtidal abalone (*Haliotis* sp.), sea urchin (*Strongylocentrotus* sp.) and abundance of sea stars off Fitzgerald Marine Reserve, California, September 1993. Calif. Dept. Fish Game, Mar. Res., Admin. Rept. 1–16.

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. J. Shellfish Res. 17:863–870.

Karpov, K. A., P. L. Haaker, I. K. Taniguchi, and L. Rogers–Bennett. 2000. Serial depletion and the collapse of the California abalone fishery. *In* Workshop on rebuilding abalone stocks in British Columbia, A. Campbell, ed. Canadian Spec. Publ., Fish. and Aquat. Sci. 130:11–24.

Lapota, D., G. Rosen, J. Chock, and C. H. Liu. 2000. Red and green abalone seed growout for reseeding activities off Point Loma, California. J. Shellfish Res. 19:431–438.

Lauck, T., C. Clark, M. Mangel, and G. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecol. Applic. 8:S72–S78.

Leighton, D. L. 1972. Laboratory observations on the early growth of abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. Fish. Bull., U.S. 70:373–381.

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

Lowry, L., and J. S. Pearse. 1973. Abalones and sea urchins in an area inhabited by sea otters. Mar. Biol. 23:213–19.

Lucas, B. G., A. Campbell, and D. Brouwer. 2000. Survey of the northern abalone, *Haliotis kamtschatkana*, populations in Lotbiniere Bay, British Columbia, March 2000. Can. Manu. Rep. Fish. Aquat. Sci. 2545:1–10.

Lundy, A. L. "Scrap." 1997. The California Abalone Industry—A Pictorial History. Flagstaff, Arizona: Best Publishing Co.

McEvoy, A. F. 1977. In places men reject—Chinese fishermen at San Diego, 1870–1893. J. San Diego History 23:12–24.

McMillen, R., and J. Phillips. 1974. In search of the elusive *Haliotis walallensis*. Conchologists Amer. Bull. 1:2.

McLean, J. H. 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol. Bull. 122:95–114.

Moore, J. D., T. T. Robbins, and C. S. Friedman. 2000. The role of a Rickettsia-like prokaryote in withering syndrome in California red abalone, *Haliotis rufescens*. J. Shellfish Res. 19:525–526.

Murphy, D. D. 1991. Invertebrate Conservation. In Balancing on the brink of extinction: the endangered species act and lessons for the future, K. A. Kohm, ed. Washington, D.C.: Island Press, pp. 181–198.

Orr, P. C. 1960. Radiocarbon dates from Santa Rosa Island. 2 Ibid. Bull. 3:9. Paddack, M. J., and J. E. Estes. 2000. Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. Ecol. Applic. 10:855–870.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. TREE 10:430.

Pinkas, L. 1974. California Marine Fish Landings for 1972. Calif. Dept. Fish Game, Fish. Bull. 161:1–53.

Pitcher, T. J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. Ecol. Apps. 11:601–617.

Redford, K. H. 1992. The empty forest. Biosci. 42:412–422.

Richards, D. R., and G. E. Davis. 1993. Early warnings of modern population collapse in black abalone *Haliotis cracherodii*, Leach, 1814, at the California Channel Islands. J. Shellfish Res. 12:189–194.

Roberts, C. M. 1997. Ecological advice for the global fisheries crisis. TREE 12:35–38.

Roberts, C. M., and J. P. Hawkins. 1999. Extinction risk in the sea. TREE 14:241–246.

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

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

———. 2001. Indirect benefits of marine protected areas for juvenile abalone. Conserv. Biol. 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. Ecol. Applic. 5:1171–1180.

Rogers-Bennett, L., Haaker P. L., Karpov, K. A. and D. J. Kushner. 2002. Using spatially explicit data to evaluate marine protected areas for abalone in southern California. Conserv. Biol. 16:1308–1317.

Rothschild, B. J., J. S. Ault, P. Goulletquer, and M. Heral. 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar Ecol. Prog. Ser. 111:29–39.

Safina, C. 1998. Song for the Blue Ocean. New York: Holt. 458 p.

Shepherd, S. A., and L. D. Brown. 1993. What is an abalone stock: implications for the role of refugia in conservation. Can. J. Fish. Aquat. Sci. 50:2001–2009.

Shepherd, S. A., K. R. Rodda, and K. M. Vargas. 2001. A chronicle of collapse in two abalone stocks with proposals for precautionary management. J. Shellfish Res. 20:843–856.

Shepherd, S. A., S. A. Guzman del Proo, J. Turrubiates, J. Belmar, J. L. Baker, and P. R. Sluczanowski. 1991. Growth, size at sexual maturity, and egg-per-recruit analysis of the abalone *Haliotis fulgens* in Baja California. Veliger 34:324–330.

Steinbeck, J. R., J. M. Groff, C. S. Friedman, T. McDowell, and R. P. Hedrick. 1992. Investigations into a mortality among populations of the California black abalone, *Haliotis cracherodii*, on the central coast of California, USA. *In* Abalone of the World, S. A. Shephard, M. J. Tegner, and S. A. Guzmán del Proo, eds. Oxford: Blackwell Scientific, pp. 203–213.

Stokesbury, K., D. E. Himmelman, and J. H. Himmelman. 1993. Spatial distribution of the giant scallop *Placopecten magellanicus* in unharvested beds in the Baie des Chaleurs, Quebec. Mar. Ecol. Prog. Ser. 96:159–168.

Stoner, A. W., and M. Ray-Culp. 2000. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. Mar. Ecol. Prog. Ser. 202:297–302.

Taniguchi, I. K., and L. Rogers-Bennett. 2001. Wavy turban snail. *In* California's living marine resources: a status report, W. S. Leet, C. M. Dewess, and R. E. Larson Klingbeil, eds. CDFG, Univ. of Calif. Agr. Nat. Res. Publ. SG01-11, pp. 140–141.

Tarr, R. 2000. The South African abalone (*Haliotis midae*) fishery: a decade of challenge and change. Workshop on Rebuilding Abalone Stocks in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 130:32–40.

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

———. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? Can. J. Fish. Aquat. Sci. 50:2010–2018.

———. 2000. Abalone (*Haliotis* spp.) enhancement in California: what we've learned and where we go from here. *In* Workshop on rebuilding abalone stocks in British Columbia, A. Campbell ed. Can. Spec. Publ. Fish. Aquat. Sci. 130:61–71.

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

———. 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar. Sci. 57:579–589.

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

Tegner, M. J., P. L. Haaker, K. L. Riser, and L. Ignacio Vilchis. 2001. Climate variability, kelp forests, and the southern California red abalone fishery. J. Shellfish Res. 20:755–763.

Tutschulte, T. C. 1976. The comparative ecology of three sympatric abalones. Ph.D. diss. Univ. of Calif., San Diego.

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

VanBlaricom, G. R., J. L. Ruediger, C. S. Friedman, D. D. Woodard, and R. P. Hedrick. 1993. Discovery of withering syndrome among black abalone *Haliotis cracherodii*, Leach, 1814, populations at San Nicolas Island, California. J. Shellfish Res. 12:185–188.

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

Walters, C., and J-J. MacGuire. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. 6:125–137.

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

Woodby, D., R. Larson, and J. Rumble. 2000. Decline of the Alaska abalone (*Haliotis* spp.) fishery and prospects for rebuilding the stock. *In* Workshop on Rebuilding Abalone Stocks in British Columbia, A. Campbell, ed. Can. Spec. Publ. Fish. Aquat. Sci. 130:25–31.

Yamaguchi, G. 1975. Estimating growth parameters from growth rate data. Problems with marine sedentary invertebrates. Oecologia 20:321–332.