



On the road to extinction? Population declines of the endangered white abalone, *Haliotis sorenseni*

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ABSTRACT

In 2001, the white abalone (*Haliotis sorenseni*) became the first marine invertebrate to be listed as endangered under the Endangered Species Act (ESA). Low densities and recruitment failure due to Allee effects were identified as being the major threats to the species' long-term viability. Visual transect surveys conducted using a remotely operated vehicle (ROV) since 2002 indicate a dramatic and continued decline in white abalone total abundance (~78% decrease) and density (33–100% decrease, depending on depth and year) between 2002 and 2010 at Tanner Bank, an area of historically high abundance (>1/m²). An increase in the size distribution over this same time period suggests individuals in the white abalone population are growing larger (and aging) with little or no indication of adequate recruitment success. The vast majority (between 77% and 89%, depending on the year) of white abalone were observed alone, which suggests that the likelihood of reproductive success within this population remains very low. The continuing decline 30 years after the last major commercial harvest demonstrates that the strategy of benign neglect, or allowing the population to recover without intervention, has clearly failed. We recommend immediate proactive conservation through population enhancement by out-planting healthy, captive-bred white abalone in areas where populations have reached or are approaching local extinction.

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1. Introduction

Abalone (*Haliotis* spp.) are long-lived, marine prosobranch mollusks that are the basis of valuable fisheries throughout the world (Shepard et al., 1992). Sexes are separate, and gametes are released freely into the ambient seawater during reproduction. Despite the fact that abalone are broadcast spawners, studies suggest that larvae are generally not widely dispersed (McShane, 1992; Prince et al., 1988; Tegner, 1992). There is evidence that juvenile abalone of multiple species may move tens of meters, but this tendency decreases with age (Cox, 1962; Tutschulte, 1976) and benthic adults exhibit relatively sedentary behavior (Morgan and Shepherd, 2006). Males and females must be in close proximity for successful fertilization to occur (Babcock and Keesing, 1999; Riffell et al., 2004; Shepherd et al., 1992), and dense aggregations occur in many populations (Vilchis et al., 2005). Because of the high market value of individuals and the life history of abalones, management of wild fisheries presents unique challenges. Abalone fishing is pursued by divers who inevitably maximize individual catch per effort. Thus, abalone aggregations are targeted during harvest.

These aggregations, however, are vital to successful reproduction and recruitment. At low densities, abalone populations suffer Allee effects (Allee, 1931). Depensatory population models, which account for Allee effects, are rarely if ever used in fishery management. Most over-fishing leads to commercial collapse and economic extinction (Hobday et al., 2001). However, in the case of abalone fisheries, it may lead to biological extinction.

White abalone (*Haliotis sorenseni*) were historically found between Point Conception, CA (USA) and Punta Abreojos, Baja California (Mexico). They are among the deepest occurring abalone species in California (5–50 m depth), with major concentrations having occurred between 25 and 30 m (Tegner, 1989). White abalone are estimated to live up to 35 years (Tutschulte and Connell, 1988), and their longevity has been validated to exceed 25 years using bomb radiocarbon dating (¹A. Andrews, NOAA Fisheries, Personal communication). Like other abalone species, the recruitment of white abalone may be episodic (McShane and Naylor, 1996). White abalone once supported a brief commercial fishery in North America. During a 10-year period from 1969 to 1978, 263 metric tons (roughly

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362,759 average-sized adults) were landed in California (prior to 1969, the species may have been landed but not separated from the pink abalone (*Haliotis corrugata*) landings data). By the mid-1980s, landings fell to near zero and the commercial fishery was closed in 1997 (Hobday et al., 2001). The white abalone fishery in Mexico appears to have collapsed in the 1960s (Shepherd et al., 1998). Despite fishery closures, white abalone abundance continued to decline through the 1990s and as a result, white abalone became the first marine invertebrate to be listed as endangered throughout its range under the Endangered Species Act (ESA) in 2001 (Anon, 2001). A formal status review concluded that the species' abundance was greatly reduced due to overharvesting during the 1970s and that remnant populations showed no sign of recovery following the closure of the fishery (Hobday and Tegner, 2000). It is believed that no significant recruitment has occurred since the 1960s (Davis et al., 1996; Hobday and Tegner, 2000) and that the substantial reduction in white abalone densities has contributed to this decrease in reproductive success through an Allee effect (Allee, 1931; Berec et al., 2007). Limited information on movement patterns suggests that the more sedentary behavior of white abalone compared to green and pink abalone make it unlikely that recovery of locally extirpated or depleted populations could occur through immigration or aggregation, respectively (Hobday and Tegner, 2000; Tutschulte, 1976).

Since the species' listing as federally endangered in 2001, surveys of remnant wild populations have substantiated the findings of the status review and indicated further population declines and decreased densities across all depths surveyed. Between 2002 and 2004, Butler et al. (2006) used multibeam sonar and visual surveys with a remotely operated vehicle (ROV) to calculate refined population estimates of white abalone at several locations in southern California where populations historically occurred, including Tanner, Cortes, and Farnsworth Banks, and San Clemente Island. In that study, white abalone densities within several sampling strata (three 10-m depth intervals between 30 and 60 m) were extrapolated over the entire amount of available rocky habitat at each location to calculate a total population estimate at each site. The highest densities of white abalone were observed in the intermediate (40–50 m) depth stratum at Tanner Bank (19.8 abalone/ha) and in the shallowest stratum (30–40 m) at Cortes Bank (12.3 abalone/ha). The total estimated population of white abalone at all three sites surveyed in 2002 was $22,122 \pm 10,520$ individuals. Subsequent surveys have focused on Tanner Bank because the highest abundance and density estimates were observed there ($12,818 \pm 3582$ individuals in 2002).

In this study, we reassessed the status of white abalone at Tanner Bank approximately 10 years after the initial listing as an endangered species in 2001. Here we present updated estimates of the density, abundance, size distribution, and average aggregation size of the white abalone population at Tanner Bank in 2002 and 2004 and compare those to newly derived estimates from visual transect surveys conducted in 2008 and 2010. We also discuss the implications that the demographic trends observed in this sub-population have on the likelihood of re-establishing the species with particular management approaches.

2. Methods

2.1. Survey design

Tanner Bank is a relatively deep (~30–70 m) offshore bank in southern California that provides habitat for an extant population of white abalone. Using an ROV, strip-transect surveys of white abalone habitat were conducted over hard-substrate between 30 and 60 m at Tanner Bank between June and October, 2008 and between October and December, 2010. The locations of these transects were

selected as areas similar to those surveyed by Butler et al. (2006) at Tanner Bank in 2002 and 2004. Effort was restricted to this depth range based on the previously described depth distribution of white abalone (Hobday and Tegner, 2000), which was later corroborated by Butler et al. (2006). In 2008 and 2010, 31 and 30 strip-transect surveys were conducted at Tanner Bank, respectively (Fig. 1).

The survey area was further stratified by depth to create three 10-m depth strata (e.g., 30–40, 40–50, and 50–60 m). Each transect was designed to sample within only one depth stratum. On occasion, however, transects would cross into the adjacent depth stratum due to the effects of prevailing wind and currents on the survey vessel and the ROV. In such cases, transects were post-stratified where they crossed the boundary of each 10-m depth stratum and considered as separate transects. Observations of white abalone were similarly assigned to each combination of transect–depth stratum to calculate density and population estimates following the methods of Butler et al. (2006) (see below). For both transect data and white abalone observations, depth was extracted from the same digital elevation model that was developed by Butler et al. (2006) and was used to determine the total amount of available white abalone habitat at Tanner Bank.

The ROV (Phantom DS4, Deep Ocean Engineering, Inc.) was equipped with a forward-looking color-video camera (Sony FCB-IX47C with 468×720 lines of resolution and an $18\times$ optical zoom) and a high-resolution still camera with $4\times$ zoom (Insite Pacific, Inc. Scorpio with Nikon Coolpix 995). High-resolution still images were used to verify sightings of white abalone that were often covered in crustose coralline algae and kelp, which sometimes made positive identification from video footage difficult, and to confirm species identification. The location of the ROV relative to the ship was estimated using an acoustic transponder. The geographic position of the ROV over the seabed (i.e., latitude and longitude) and speed over-ground was estimated in real-time using a combination of an ultra-short baseline (USBL) acoustic tracking system (TrackPoint II-Plus, ORE Offshore), a Doppler velocity log (Workhorse Navigator, Teledyne RDI), and integrated navigation software (WinFrog, Fugro Pelagos, Inc.). All other navigation data (e.g., sea-water depth, temperature, ROV heading, speed, and course over-ground) were synchronously logged at 1–2 s intervals using WinFrog. The ROV's speed over-ground was used to calculate the length of each transect (see below).

2.2. Effort analysis

Three high-intensity lasers were mounted parallel to the horizontal axis of the video camera: two parallel red lasers on either side of the video camera spaced 20 cm apart and one green laser that crosses the left parallel laser at 0.99 m and the right parallel laser at 2.72 m from the camera lens. The position of the green laser relative to the red lasers was used to calculate the distance from the camera lens to the seabed (i.e., slant range) and the parallel lasers provided a reference distance used to determine the field of view (FOV, or strip width) and the shell length of white abalone. Transect length (or distance, d in meters) was calculated as:

$$d = \sum_{i=1}^{n-1} (r_i \times t_i) \quad (1)$$

where r is the speed of the ROV (m/s) and t is the time (s) between speed measurements, i is the measurement number, and n is the total number of measurements. This method of estimating distance was calibrated over a submerged pipeline of known distance (1500 m) and was found to be accurate to ~1% (mean = 1519 m; SD = 18 m; $n = 3$ transects) (Stierhoff and Butler, unpublished data).

Field of view was calculated for each transect in 2008 and 2010 using the parallel reference lasers and an automated photogrammetric method. In general, the 20-cm parallel lasers were

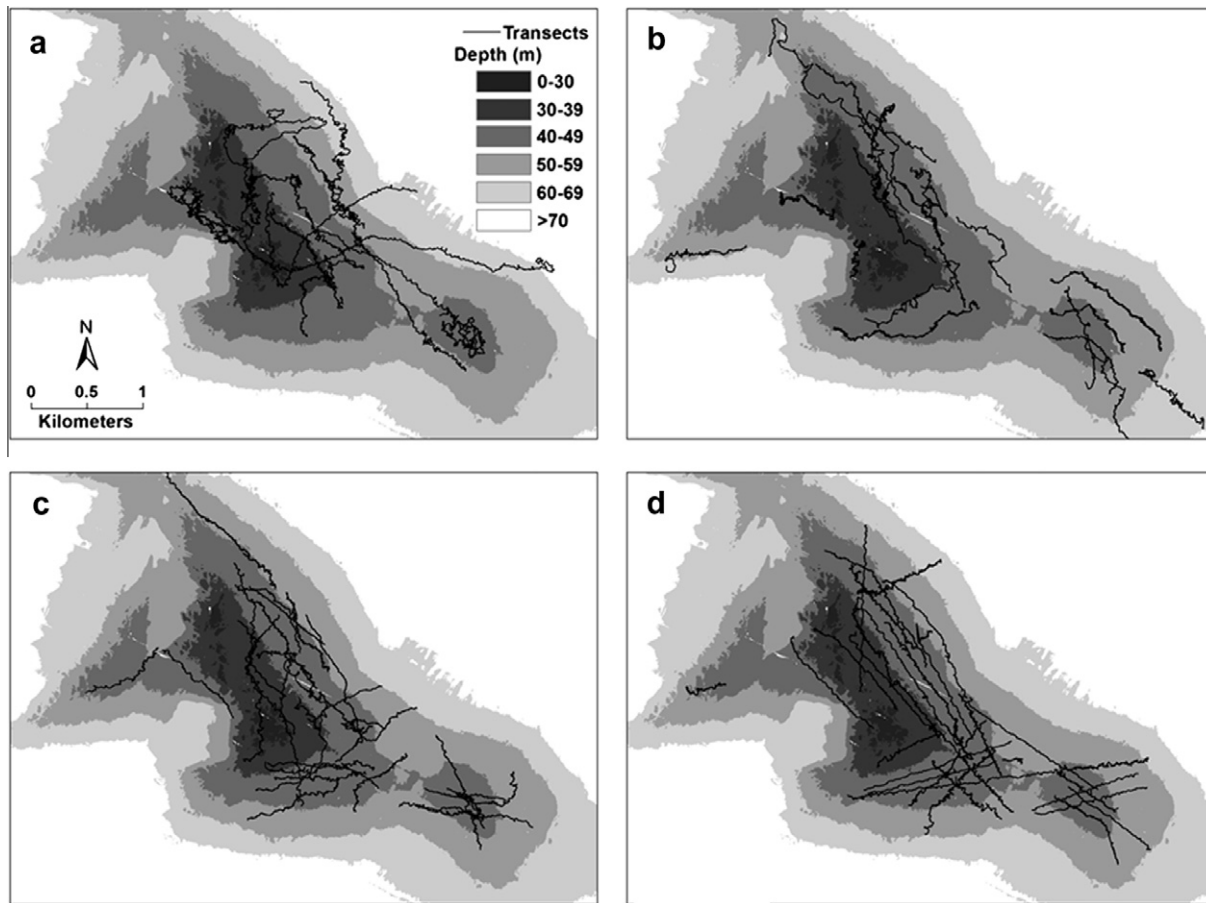


Fig. 1. Transects (black lines) at Tanner Bank in (a) 2002, (b) 2004, (c) 2008, and (d) 2010. The darkest gray stratum (0–30 m) near the center of the Bank was not sampled.

identified in video frames every 10 s using 3Beam© image analysis software (Kocak et al., 2002; Pinkard et al., 2005). The software provides estimates of the total width of the video frame (i.e., FOV, meters) from the number of pixels between the parallel lasers. Results from the automated laser identification algorithm were reviewed a second time by the analyst and manually corrected when false detections or incorrect laser positions were identified. For frames where the lasers were unable to be located (e.g., obscured by kelp or washed-out by the ROV lights) and for the distance traveled between each 10-s estimate of field of view, the field of view was calculated using linear interpolation. The total area searched (a) was calculated as:

$$a = \sum_{t=2}^n FOV_i \times d_i \quad (2)$$

where d is the distance (m) traveled between FOV estimates, i is the measurement number, t is the time (s) between FOV estimates, and n is the total number of measurements. The automated image analysis software was not available during the 2002 or 2004 surveys. In those surveys, area searched was calculated by multiplying the transect distance by the average FOV (2.0 m) as described in Butler et al. (2006). Otherwise, the configuration of the ROV system has not changed since surveys began in 2002.

2.3. Demographic analysis

The estimated population size (\hat{P}) within each depth strata was calculated using a weighted ratio estimator (Cochran, 1977):

$$\hat{P} = \frac{\hat{A}}{n} \sum_j \left(\frac{p_j}{a_j} \right) \quad (3)$$

where p is the number of individuals observed, a is amount of area searched, \hat{A} is the total amount of available hard substrate at Tanner Bank (see Butler et al. (2006) for details), j is the transect number, and n is the total number of transects. A weighted ratio estimator was used over a simple ratio estimator because the variance in white abalone observations increased relative to the area searched. The total population estimate in each year was calculated by summing \hat{P} over all depths.

Whenever possible, shell lengths of observed white abalone were measured from video frame grabs using image analysis software (ImageJ, National Institutes of Health) using the 20 cm parallel lasers as a reference distance. In some cases, the orientation of the abalone made accurate measurement impossible. Two-sample Kolmogorov–Smirnov (K–S) tests ($\alpha = 0.05$) were used to test for differences in the distribution of shell lengths between all year combinations.

In addition to counting individuals, group sizes were also recorded (group sizes ranged from 1 to 6 individuals in all years). For sightings in 2002 and 2004, Butler et al. (2006) calculated the linear distance between all individuals and considered abalone in groups when two or more individuals were within two meters of one another. In 2008 and 2010, ROV pilots searched the general vicinity around a sighting to determine whether a particular individual was alone or part of a larger group. Typically, groups were conspicuous and within the same video frame or still photograph. A group was still defined as two or more white abalone less than two meters apart. The weighted average across all groups was used to calculate average group size for each year. All statistical analyses were performed using (R Development Core Team, 2011).

Table 1

Sightings, density (\pm SEM, standard error of the mean), area searched, total available habitat, and population estimates (\pm SEM) for white abalone (*Haliotis sorenseni*) at Tanner Bank between 2002 and 2010. Total available habitat was determined using multibeam and sidescan sonar by Butler et al. (2006).

	Year	Sightings	Density		Area		Population	
			Average	\pm SEM	Searched	Total	Mean	\pm SEM
30–40	2002	32	9.84	\pm 3.82	2.41	245	2411	\pm 935
	2004	2	2.25	\pm 1.79	0.96		550	\pm 438
	2008	9	6.57	\pm 2.24	1.18		1610	\pm 548
	2010	9	4.24	\pm 3.05	1.31		1038	\pm 747
40–50	2002	142	24.06	\pm 6.31	4.33	425	10,224	\pm 2682
	2004	31	7.69	\pm 1.96	4.37		3266	\pm 835
	2008	60	15.15	\pm 4.37	4.63		6439	\pm 1857
	2010	30	5.50	\pm 1.53	4.89		2337	\pm 649
50–60	2002	20	3.90	\pm 2.53	2.47	689	2688	\pm 1744
	2004	3	1.02	\pm 0.59	2.01		706	\pm 406
	2008	2	1.07	\pm 0.74	1.37		736	\pm 511
	2010	0	0.00	\pm 0.00	1.55		0	\pm 0
All depths	2002	194			9.21	1359	15,323	\pm 5362
	2004	36			7.34		4523	\pm 1679
	2008	71			7.17		8785	\pm 2916
	2010	39			7.75		3375	\pm 1396

3. Results

3.1. Distance, field of view, and area searched

The total distance surveyed across all depths was nearly identical in 2002, 2008, and 2010 (46.0–47.8 km y^{-1}). In 2004, distance surveyed was \sim 20–30% lower (39.2 km) than in other years. The average field of view in 2008 and 2010 was 1.44 m (\pm 0.46 SD) and 1.59 m (\pm 0.56 SD), respectively, compared to the constant field of view of 2.0 m (\pm 0.85 SD) that was used to calculate area searched in 2002 and 2004. Despite similarities in total distance surveyed, the reduced field of view resulted in a nearly 25% decrease in area searched in 2008 and 2010 compared to 2002 (Table 1). The spatial distribution of effort was comparable between most years (Fig. 1), except in 2004 when sampling did not include many areas where white abalone were abundant in 2002.

3.2. Demographic changes in the white abalone population at Tanner Bank

A total of 340 white abalone were observed across all years of the survey. Despite nearly identical survey effort in 2008 and

2010, very few white abalone were observed (71 and 39 white abalone in 2008 and 2010, respectively) compared to 2002 (194 white abalone) (Table 1). In 2002, white abalone were distributed throughout the areas surveyed in the 40–50 m depth stratum and were also abundant in the 30–40 m depth stratum to the northeast of the central high-spot (Fig. 1a). In contrast, very few white abalone were observed throughout all depth strata in 2008 and 2010, and were conspicuously absent from the 30–40 m and 40–50 m depth strata to the north and northeast of the central high-spot (Fig. 1c and d).

The greatest abundance and density of white abalone were observed in the 40–50 m depth stratum in all years (Fig. 2). Density (Fig. 2a) and abundance (Fig. 2b) were intermediate in the 30–40 m stratum and lowest in the 50–60 m stratum. Compared to 2002, however, substantial decreases in density were observed in all depth strata between 2002 and 2010 (Fig. 2a). In the most densely populated depth stratum (40–50 m), densities declined by 38–77%. The decrease in density in all depth strata since 2002 has resulted in dramatic decreases in the overall population size within each depth stratum. When population estimates are summed over all depth strata, overall abundance decreased by approximately 78% (from 15,323 to 3375) since 2002 (Table 1).

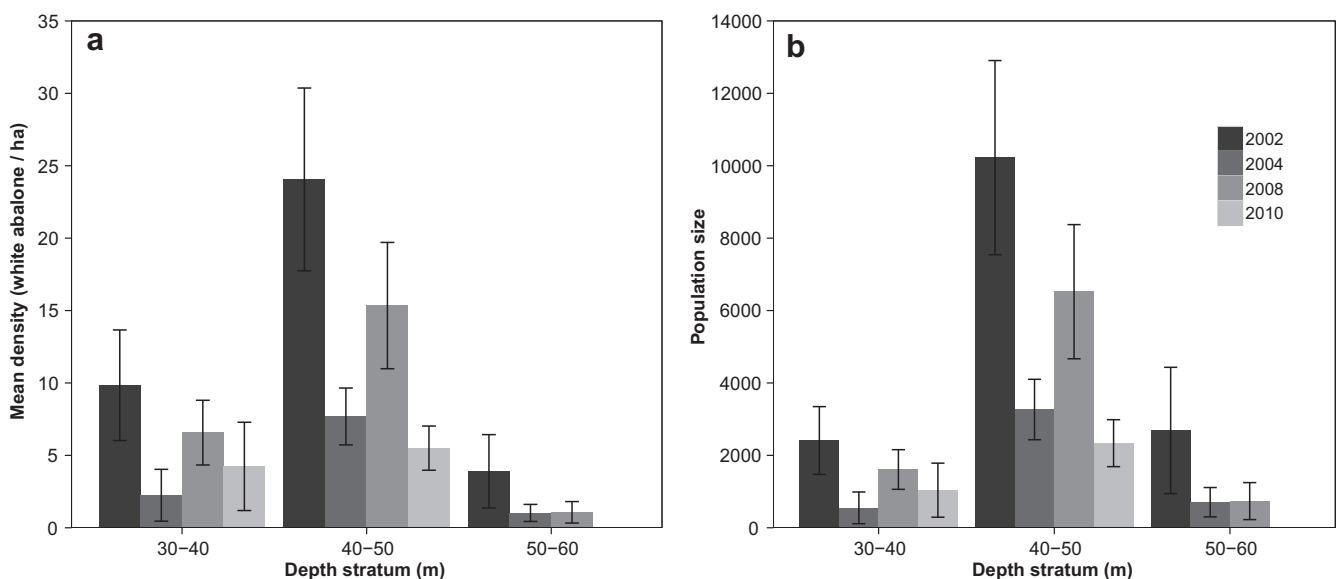


Fig. 2. Mean (a) density (\pm SEM) and (b) total abundance (\pm SEM) of white abalone (*Haliotis sorenseni*) by depth at Tanner Bank between 2002 and 2010.

Table 2

Two-sample Kolmogorov–Smirnov test statistics (D) for white abalone (*Haliotis sorenseni*) length distributions between 2002 and 2010. Bold values indicate statistically significant differences ($p < 0.01$).

	2002	2004	2008	2010
2002	–			
2004	0.155	–		
2008	0.342	0.378	–	
2010	0.349	0.410	0.088	–

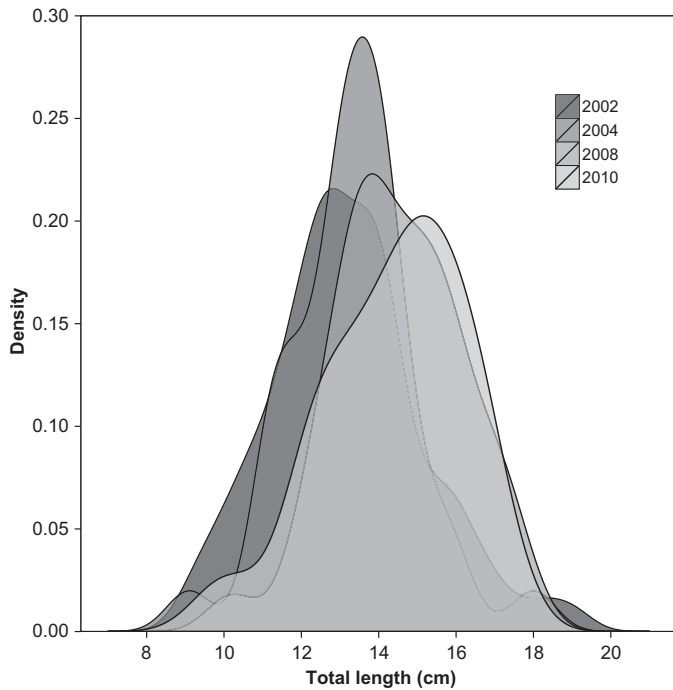


Fig. 3. Size (shell length) distribution of live white abalone (*Haliotis sorenseni*) observed at Tanner Bank in 2002 (mean = 13.20 cm, SD = 1.97, $n = 162$), 2004 (mean = 13.32 cm, SD = 1.63, $n = 35$), 2008 (mean = 14.53 cm, SD = 1.66, $n = 73$), and 2010 (mean = 14.38 cm, SD = 1.81, $n = 38$).

The size distribution of white abalone increased significantly between years (two-sample K–S test, Table 2). The average size (\pm SD) of individuals in the population increased from 13.2 ± 2.0 cm to 14.4 ± 1.8 cm between 2002 and 2010 (Fig. 3). In 2002, a large proportion of the abalone observed fell within the smallest size classes (9–12 cm), and a small proportion fell within the largest size class (18–19 cm). In 2008 and 2010, an even smaller proportion of animals included the smallest size classes, and neither year included the largest size class (Fig. 3). A growth rate of ~ 0.19 cm y^{-1} (assuming no recruitment and no mortality) was calculated from the change in mean shell length of white abalone observed from 2002 to 2010.

The vast majority of white abalone (77–89%) were observed as singletons (Table 3), with an average aggregation size across all years ranging from 1.06 to 1.15 aggregation $^{-1}$. Of all the aggregations observed, ~ 5 –8% of white abalone were observed in groups

Table 3

Percentages of white abalone (*Haliotis sorenseni*) observed in groups between 2002 and 2010. The number of groups within each group size is indicated in parentheses.

Group size	2002	2004	2008	2010
1	88.2% (172)	89.2% (33)	86.3% (63)	76.9% (30)
2	4.6% (9)	5.4% (2)	6.8% (5)	7.7% (3)
3	0.0% (0)	0.0% (0)	0.0% (0)	2.6% (1)
4	0.0% (0)	0.0% (0)	0.0% (0)	0.0% (0)
5	0.5% (1)	0.0% (0)	0.0% (0)	0.0% (0)
6	0.0% (0)	0.0% (0)	0.0% (0)	0.0% (0)

of two. One group of three white abalone was observed in 2010, and one group of five was observed in 2002. The sex of individuals within each group is unknown, so it is unclear whether any of the observed groups contained potential mates.

4. Discussion

A precipitous decline in both the density and total abundance of white abalone has been observed at Tanner Bank since focused monitoring efforts began in 2002. The white abalone recovery plan (National Marine Fisheries Service, 2008) identifies low population density as the primary threat to the recovery of the population. The maximum observed density of white abalone at Tanner Bank decreased from 24.1 ha $^{-1}$ in 2002 to 6.4 ha $^{-1}$ in 2010, both of which are well below the density of 2000 ha $^{-1}$, which has been suggested as the minimum density required to sustain viable white abalone populations (National Marine Fisheries Service, 2008). The overall population at Tanner Bank has declined from 12,818 to 3897 individuals over this same time frame. Given the recent development of the 3Beam© image processing software and more accurate estimates of area searched, the decline described here is likely to be conservative. For example, if white abalone densities were recalculated for 2002 and 2004 surveys using a ~ 1.45 m strip (the average strip width FOV during 2008 and 2010 surveys), the estimated population would have declined by $\sim 82\%$ (from 21,195–3897 individuals between 2002 and 2010).

The shift in the size distribution of white abalone since 2002 clearly indicates that individuals are getting larger and older, while little or no new recruitment has taken place in recent years. That is, the proportion of individuals in the smaller size classes has decreased, the proportion of individuals in the largest size classes has increased, and the average size has increased over this same time. The recovery plan recommends that the proportion of individuals in the 'large' size classes (>13 cm) should not exceed 0.15 in order to consider down-listing the species' status from endangered to threatened; however, the proportion of individuals in the large size class has increased from 0.31 to 0.66 since 2002. Growth rates of white abalone (~ 0.19 cm y^{-1}), as inferred by the difference in the average shell length since 2002, are within the range of growth rate estimates for white abalone held in the laboratory (between 0.099 and 0.25 cm y^{-1} for white abalone <10 cm and >10 cm, respectively) (Tutschulte and Connell, 1988). Many of the large individuals observed in 2002 were approaching reported values of their asymptotic length (21 cm), and were likely near the end of their maximum life expectancy of ~ 35 y (Tutschulte and Connell, 1988). It is possible that smaller, newly recruited white abalone, which are highly cryptic and inconspicuous, went undetected during these surveys. For example, no white abalone smaller than 9 cm were observed in any of the surveys at Tanner Bank since 2002. In any case, the size composition of this population is far from the robust distribution proscribed in the recovery plan. Even if a low level of recruitment of white abalone is occurring, the decrease in density throughout the study area suggests that mortality rates greatly exceed recruitment rates.

Aside from the slight increase in white abalone abundance between 2004 and 2008, overall abundance has decreased significantly between 2002 and 2010. The apparent increase in abundance between 2004 and 2008 is likely an artifact, however, that can be attributed to two factors: under-sampling during the 2004 survey and more precise estimates of area searched in the 2008 and 2010 surveys. In 2004, the amount of habitat surveyed was $\sim 20\%$ less than in 2002. Furthermore, the areas that were surveyed in 2004 did not include many of the areas of Tanner Bank where the greatest number of white abalone sightings occurred in 2002 (i.e., the 40–50 m depth stratum on the eastern portion

of the Bank). Second, the addition of the 3Beam© image analysis system resulted in a more precise and narrower field of view (~25% less than previous surveys) in 2008 and 2010. The effect of this decreased FOV would result in a smaller area searched for the same transect length and a greater density and overall abundance for the same number of white abalone observed.

The observed decline in white abalone density and small percentage of white abalone observed in groups strongly suggests that the lack of recovery is primarily the result of Allee effects acting on a population at a very low density. Although the percentage of individuals occurring in pairs or small aggregations has actually increased since 2002 (5.1% in 2002 to 10.3% in 2010), the actual number of aggregations observed decreased by about 60%. Furthermore, it is not known whether these animals were of different sex, and therefore constituted potential mating pairs. The small average aggregation sizes (1.06–1.15 aggregation⁻¹) observed in this population suggests that the probability of successful reproduction is likely very low. Reproduction may be further diminished by increasing distances between nearest neighbors as the population density declines (Button, 2008). The results from our study support accumulating evidence from others suggesting that low reproductive success of widely dispersed adult abalone populations coupled with short larval dispersal distances and limited movement of sedentary adults will limit the natural recovery of severely reduced populations (Gruenthal and Burton, 2008; Neuman et al., 2010; Tegner, 1992).

Although lack of recruitment due to Allee effects may be the major factor in white abalone population declines, illegal harvest and smuggling are also potential concerns. For example, frozen white abalone was recently confiscated entering Canada from the US (Art Demsky, Canada DFO, pers. comm.) and entering the US from Mexico (Michelle Zetwo, NOAA Enforcement, pers. comm.). This suggests that a second Allee effect, the anthropogenic effect of becoming more valuable as the species becomes rarer, may also contribute to the decline (Berec et al., 2007; Courchamp et al., 2006). This effect was evident as landings of white abalone were decreasing in the late 1970s until the early 1990s (Hobday et al., 2001), while the value of landed white abalone continued to increase (Hobday and Tegner, 2000). The present value of white abalone on the black market is unknown.

The question of level of risk and the time required to reverse risk factors is an important subject when selecting management strategies aimed at preventing extinction, as mandated by the ESA. The white abalone is an important example for conservation biologists and managers for a number of reasons. First, in all likelihood, this marine mollusk was decimated to the point where Allee effects prevented recovery in a period of just over a decade. This demonstrates that marine species, and in particular broadcast spawners, can be surprisingly vulnerable to extinction. Second, the time between reaching a point where recovery could not occur naturally likely predated listing under the ESA by a decade or two. Had monitoring begun in 1982 rather than 2002, the possibility that Allee effects could drive the species to extinction would have become apparent earlier, allowing the learning curve of captive breeding and out-planting to occur when abundance was higher, genetic diversity was higher, and the margin for error was consequently greater. Finally, this case makes it clear that thresholds for near-extinction (see Regan et al. (2009) for a full definition) will differ for different life-history strategies. The IUCN Red List of Threatened Species™ criteria use number of breeding adults as one metric for level of risk. In the case of white abalone on Tanner Bank, a more appropriate metric to assess extinction risk would be density rather than number of breeding adults, because it is the proximity of spawning individuals to one another that drives recruitment success (i.e., recruitment that will exceed the average death rate). Thus, while it is important to use default values for the number of individuals below which populations may be incapable

of recovery, there will always be a need to be flexible enough to accommodate species like the white abalone. It is not implausible that white abalone reached near-extinction when their abundance numbered in the tens of thousands and the number of breeding adults was in the thousands. The Allee effects for broadcast spawners even at that level resulted in deaths exceeding births, a condition certain to result in extinction. Absolute extinction will take at a minimum the lifespan of the species (30–50 years) and more likely double or triple that time, because some small level of recruitment possibly continues. Therefore, some time still remains to reverse the population decline.

From these results, it is clear that recovery of the white abalone population at Tanner Bank through an approach of benign neglect is not occurring, and is a trend that likely applies to other areas within its known historic distribution in the US. The status of white abalone in Mexican waters is largely unknown, but is likely to be at similarly low levels and also declining (Shepherd et al., 1998). Even if distant or isolated white abalone populations exist elsewhere, it is improbable that they would facilitate a large-scale reversal of long-term abundance trends naturally. Thus, active restoration actions are likely the only means to facilitate large-scale reversals of long-term abundance trends.

The field monitoring efforts presented here describe only one part of a concurrent, multi-faceted approach to recovering white abalone populations in southern CA as outlined in the white abalone recovery plan. Over the past 5 years, the National Marine Fisheries Service has also provided significant funding to regional stakeholders who are actively engaged in captive breeding activities with white abalone. The strong degree of spawning synchrony and higher fecundity of white abalone compared to pink or green (*Haliotis fulgens*) abalone (Tutschulte and Connell, 1981) suggest that captive breeding of white abalone is feasible. Although previous outplanting studies showed mixed results based on the survival rates of captive-reared individuals (for review see McCormick et al. (1994), National Marine Fisheries Service (2008) and Tegner and Butler (1989)), the percent survival indicates that size influences outplanting success, with larger initial sizes (>40 mm) yielding higher survival rates more often than not (De Waal and Cook, 2001; McCormick et al., 1994; Saito, 1984). Other management actions currently being implemented include the establishment of marine protected areas to ensure the protection of remaining populations and their habitats, a continued focus on enforcement to reduce the incidence of poaching, and public outreach and education to communicate the important role that abalone play in kelp forest ecosystems.

If spawning of captive brood stock proves successful, the outplanting of captive-reared juveniles would likely benefit from being placed in relatively shallow, nearshore locations for several reasons. Historically, white abalone populations were found in nearshore environments where their primary food source, drift kelp (*Macrocystis* and other laminarians), is more abundant (Tegner, 1989). Marine reserves like those that are currently being established in nearshore areas throughout southern CA, may be ideal locations to outplant captive-bred juveniles due to the positive effects of similar closed areas on the size structure and abundance of abalone populations in central CA (Micheli et al., 2008). Poaching remains a major concern for abalone fisheries and is quite possibly a serious impediment to population recovery. Based on high mortality rates, poaching was implicated in the disappearance of transplanted adult green abalone in areas where urchin fisheries still operated (Tegner, 1993). The ease of enforcement is an important consideration when selecting outplanting sites (Tegner, 1993), and outplanting sites could be selected to overlap with existing enforcement effort in these reserves. Lastly, the proximity of these sites to shore would facilitate frequent monitoring of outplanting sites and a more accurate assessment of survival rates.

5. Conclusions

Marine invertebrates were historically considered to be immune to extinction with the exception of species with small population sizes and limited habitat. The case of the white abalone illustrates that marine invertebrates, and particularly species with high commercial value, are unarguably vulnerable. Although all harvest was prohibited in 1997, white abalone populations continued to decline, and listing the species under ESA has not reversed that trend. Species like white abalone that suffer from acute Allee effects cannot recover without intervention. A variety of strategies have been recommended to promote the recovery of this species, including captive propagation for enhancement of wild populations. While progress is being made to develop methods for breeding and rearing healthy white abalone in captivity, to date the value of captive propagation and enhancement as a tool for restoring this imperiled species remains untested. Studies conducted with other species of abalone have reported wide-ranging survival rates of captive-reared animals outplanted to the wild (0–90%; for review see McCormick et al. (1994), National Marine Fisheries Service (2008), Stevick (2010) and Tegner and Butler (1989)). These studies have advanced our understanding of factors that control outplanting success, such as laboratory conditioning, size of outplanted animals, and delivery methods for transferring captive-reared animals to the wild. Using information gleaned from studies on other species of abalone and the enhancement strategy detailed in the white abalone recovery plan, active restoration through captive propagation and enhancement must remain a top priority to facilitate large-scale reversals of long-term abundance trends and prevent extinction.

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