Abstract—Multibeam sonar mapping techniques provide detailed benthic habitat information that can be combined with the data on species-specific habitat preferences to provide highly accurate calculations of populations in a particular area. The amount of suitable habitat available for the endangered white abalone (*Haliotis sorenseni*) was quantified to aid in obtaining an accurate estimate of the number of remaining individuals at two offshore banks and one island site off the coast of southern California. Habitat was mapped by using multibeam sonar survey techniques and categorized by using rugosity and topographic position analysis. Abalone densities were evaluated by using a remotely operated vehicle and video transect methods. The total amount of suitable habitat at these three sites was far greater than that previously estimated. Therefore, although present estimates of white abalone densities are several orders of magnitude lower than historic estimates, the total population is likely larger than previously reported because of the additional amount of habitat surveyed in this study.

The use of multibeam sonar mapping techniques to refine population estimates of the endangered white abalone (*Haliotis sorenseni*)

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Accurate classification of habitat is important for examinations of the distribution and abundance of marine organisms. The potential complexity of species-habitat relationships is such that the use of a single parameter when trying to link species to specific areas has become obsolete. Multiple physical oceanographic parameters that link species to their habitat have proven to be useful, although they are not applicable to all types of marine organisms (Freeman and Rogers, 2003). The use of high-resolution multibeam sonar maps for classifying habitat has become a critical step in the process of estimating the distribution and abundance of marine animals that are known to be associated with particular habitat types. Because an increasing number of marine resources are in states of decline, information on the amount of habitat of specific types and qualities becomes crucial to making predictions for the purposes of fisheries management, and to aid in decisions concerning potential locations of marine protected areas (Kvitek et al.[1]; Iampietro et al., in press). For species in states of decline, protection of known critical habitat may be the only approach available to enhance survival of the species. Detailed habitat mapping provides a large amount of information on the benthic makeup of an area in a relatively short amount of time, and further processing of data with GIS (geographic information system) can produce accurate estimates of actual areas categorized by various physical parameters. These pieces of information, coupled with field surveys to obtain information on animal or plant habitat associations,

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[1] Kvitek, R., P. Iampietro, C. Bretz, K. Thomas, S. Zurita, B. Jones, and E. Morris. 2004. Hydrographic data acquisition in support of MLPA and MLMA Implementation. California Department of Fish and Game Final Report P0170015, p. 1–74. Foundation of California State University Monterey Bay, 100 Campus Center, Seaside, CA 93955.

can allow for detailed and accurate estimates of abundance of marine organisms.

The white abalone (*Haliotis sorenseni*) is one of six abalone species (red, green, pink, pinto, black, and white) that have been exploited commercially on the west coast of North America. The species ranged historically from Morro Bay, California, USA, to Punta Rompiente, Baja California, Mexico (Geiger, 1999). Serial depletion of stocks of congeneric, relatively shallow-dwelling abalone species led to the exploitation of white abalone, the deepest living abalone species in the North Pacific (Karpov et al., 2000). During a ten-year period from 1969 to 1978, approximately 360,000 white abalone were harvested (Hobday et al., 2001). After 1978, the mandatory reporting of white abalone landings was no longer required, and although abalone fishing effort has remained high, there are (at present) no data on the numbers taken (Tegner, 1989).

In surveys conducted in the late 1990s in suitable habitat, very low numbers of white abalone were reported (Davis et al., 1996, 1998; Haaker et al.[2]; Hobday et al., 2001). Densities at many localities were less than 1 abalone/ha, and the entire population of white abalone was estimated at less than 3000 individuals (Hobday et al., 2001). Reproductive efforts of the remaining adults are believed to have been seriously hindered by potential Allee effects (Allee, 1931) because of low densities. Concern for the survival of the species prompted a status review and the white abalone was listed as an endangered species by the Department of Commerce on 29 May 2001 (Federal Register, 2001).

Postexploitation estimates of abundance and available white abalone habitat need revision because the spatial coverage of sampling in the 1980s and 1990s was limited in the case of determining abundance estimates and virtually nonexistent in the case of determining habitat classification (Lafferty et al., 2004). Accurate estimates of density and the amount of suitable habitat are critical for making informed decisions regarding how to prioritize recovery actions and where to focus population enhancement efforts. In addition, identification of the specific locations of white abalone in the wild will help both to focus efforts to protect areas where the species remain and to locate potential brood stocks for captive breeding. Information on the recruitment potential of the remaining individuals cannot be directly assessed, but an examination of the temporal trends in size distributions may be helpful in addressing questions of population viability and sustainability. The present study was conducted with recovery efforts in mind, and therefore included intensive sampling of offshore banks and islands where white abalone abundance was high historically. We used a combination of advanced mapping technology (multibeam sonar and

side-scan sonar) and a remotely operated vehicle (ROV) to quantify the total amount of available habitat at each location, in order to examine the size distributions of surviving populations, and to derive new estimates of white abalone abundance.

Materials and methods

Habitat mapping

Habitat was surveyed during three cruises on the NOAA ship RV *David Starr Jordan* at Tanner Bank (July 2002 and September 2004), Cortes Bank (July 2003), and San Clemente Island (August 2004) with multibeam (all years, Fig.1) and side-scan sonar techniques (2002 only). The multibeam sonar system, which was installed on the RV *David Starr Jordan* for the Tanner Bank 2002 and Cortes Bank 2003 cruises, included a Reson 8101 multibeam sonar (Reson Inc. Goleta, CA) supplemented with a side-scan sonar option, and was used in conjunction with a Triton-Elics Isis System (Triton Elics International, Portland, OR) for data logging and sonar control. The San Clemente Island 2004 habitat survey was conducted by using the same sonar system aboard a smaller vessel, the RV *VenTresca*, in conjunction with ROV operations conducted aboard the RV *David Starr Jordan*. Delphmap and BathyPro software (Triton Elics International, Inc., Portland, OR) were used to create real-time side-scan mosaics and to generate digital elevation models. The pitch and roll motion of the vessel used for mapping was corrected for using a TSS HDMS (heading and dynamic motion sensor) (pitch, roll and heading accuracy ±0.02°; heave accuracy ±5% or 5 cm). Hypack Max software (Hypack, Inc., Middletown, CT) was used for survey planning and navigation. Positioning information was provided by a Trimble 4700 GPS receiver and NavBeacon for receiving U.S. Coast Guard RTCM (radio technical commission for maritime communications) corrections. Sound velocity profile data were collected with an Applied Microsystems (Sydney, British Columbia, and CA) SVPlus sound velocimeter. Multibeam data were processed with CARIS HIPS software (CARIS USA, Ellicott City, MD), and all final GIS products were derived from shoal-biased data.

Microhabitat analysis

Habitat type and algal cover were examined for surveys conducted at Tanner Bank in 2002. Habitat was characterized by broad type (e.g., bank, seamount), modifiers (e.g., faulted, eroded), microhabitat (e.g., sand, boulders), seafloor slope (by degree), seafloor complexity (5 levels), and algal cover (species identification and four levels of coverage), after Greene et al. (1999; Table 1).

Abalone surveys

Abalone surveys were conducted with a Phantom HD 2 + 2 (2002 and 2003) and a Phantom DS4 (2004)

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[2] Haaker, P. L., D. V. Richards, and I. Tanaguchi. 2000. White abalone program October 9–25, 1999, cruise report, p. 1–17. California Department of Fish and Game, 330 Golden Shore Suite 50, Long Beach, CA 90802.

Table 1

Habitat analysis variable descriptions (Greene et al., 1999). Only those classifications that were used frequently enough to influence the PCA write out are listed (a total of 12 were included in the analysis). For algal levels, coverage was defined by the following within the video-captured field of view: absent = <10%, rare = 10–35%, present = 35–75%, and highly abundant = 75–100%.

Variable abbreviation	Variable type	Levels
Mhab 1–4	Macro/Microhabitat	1=boulders; 2=deformed (faulted or folded); 3=deformed (faulted or folded) + boulders; 4=deformed (faulted or folded) + sand
Slope 1 and 2	Seafloor slope	1=flat (0 to 1 degree); 2=sloping (1 to 30 degrees)
Com 1 and 2	Seafloor complexity	1=very low complexity; 2=low complexity
Br 1–4	All brown algae	1=absent; 2=rare; 3=present; 4=highly abundant
L 1–4	*Laminaria farlowii*	1=absent; 2=rare; 3=present; 4=highly abundant
A 1–4	*Agarum fimbriatum*	1=absent; 2=rare; 3=present; 4=highly abundant
E 1–4	*Eisenia arborea*	1=absent; 2=rare; 3=present; 4=highly abundant
D 1–4	*Dictyotaceae* spp.	1=absent; 2=rare; 3=present; 4=highly abundant

remotely operated vehicle (ROV) equipped with a forward-looking 12:1 zoom color video camera (all surveys) and a high resolution Nikon Coolpix digital still camera (2004 surveys only, Insite Pacific Inc., Solana Beach, CA). We recorded video footage continuously on digital tapes and overlaid footage with temperature, depth, heading, and time information from an on-screen display. Two pairs of lasers were mounted near the front of the ROV in parallel: one pair to measure abalone upon sighting (10.0 cm apart), and one pair to estimate the search field of view (60 cm apart). Upon sighting an abalone, the ROV pilot maneuvered the vehicle into position to zoom in on and photograph the animal for species confirmation, ensuring that the narrow pair of lasers passed over the abalone so that a size estimate could be obtained. Empty abalone shells were also noted and identified.

The ROV was tracked by using a directional hydrophone mounted on the ship and a transponder mounted on the ROV. Positional data and all other navigational and physical data associated with the ROV dives (e.g., heading, depth, and water temperature) were recorded every two seconds. Because of the great depth range that white abalone inhabit, it was not logistically feasible to compare ROV transect observations with diver transect observations. It is possible that we missed abalone residing on the back sides of rocks as the ROV passed over.

Sampling design and site selection

Multibeam and side-scan surveys were conducted the preceding night at sites that were to be surveyed with the ROV during the next day. Transect locations were chosen randomly initially, but after preliminary surveys at Tanner Bank revealed a narrow depth range of abalone occurrence from 30 to 60 m and a habitat restriction to rock reef or the sand-and-rock reef interface, only areas of suitable habitat (depths ranging from 30 to 60 m [±5 m]) were surveyed. In general, we attempted to run transects for approximately two hours, and to a length of 1 km, although actual lengths were calculated after the dive. Several of the early surveys included transects of greater lengths of time and distances. Georeferenced bathymetry maps were interfaced with the ROV navigational software for all dives, allowing for the ship, and in effect the ROV, to remain within a particular depth stratum and within suitable habitat.

Postdive processing

Videotapes and still photos were reviewed to confirm species identification, measure sizes, search for additional abalone, record search effort, examine microhabitat, and determine the search field of view. Other abalone species that were encountered were noted (red and pink). We used strip transect techniques to estimate densities, and therefore the field of view was measured for abalone sightings from the first survey (Tanner Bank, 2002), and the average (2 m [±0.85 SD], n=171) was used as the strip width for the entirety of each transect in the study.

Data analysis

For habitat classification a statistical approach called textural analysis (described in Cochrane and Lafferty, 2002) was used to identify complex rock areas at Tanner Bank as documented by side-scan sonar (Fig. 1, A and B). We estimated the total area of available white abalone habitat on each bank by calculating the amount of rocky substrate in depth intervals, as determined by multibeam sonar surveys. A combination of rugosity and topographic position analysis (TPI) were used
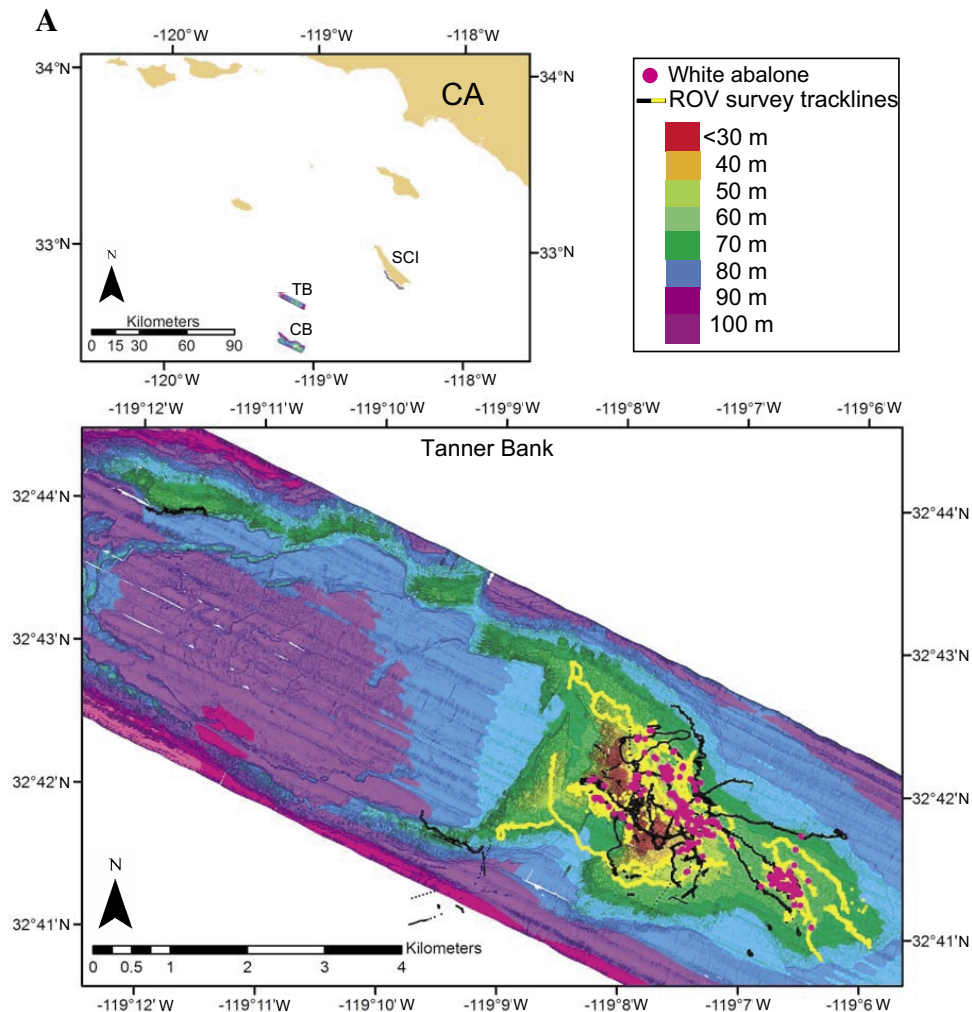
Figure 1

(**A**) High-resolution bathymetry of Tanner Bank and map of the southern California coast. Black lines represent ROV transect track lines in 2002 and yellow lines represent track lines in 2004. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend). CA=California; SCI=San Clemente Island; TB=Tanner Bank; CB=Cortes Bank. (**B**) High-resolution bathymetry of Cortes Bank and San Clemente Island. Black lines represent ROV transect track lines. Pink dots on track lines represent white abalone (*Haliotis sorenseni*) sightings. Depth strata are distinguished by color (see legend).

for multibeam habitat classification (Kvitek et al.[3]). A rugosity measure was used to evaluate the "texture" of the seafloor by quantifying the surface area to planar area. Rugosity calculations were done with ArcView 3.2 (ESRI, Redlands, CA) by using the "Surface Area and Ratios from Elevation Grid , vers 1.2." (Jenness, 2002).

Rugosity measures ranged from 1 to 4, and higher values indicated more texture (i.e., rocky terrain). TPI was calculated in ArcGIS, vers. 8.3 by a multistep process. For each cell the focal mean of the digital elevation model (DEM) was calculated to compute an average depth value used to obtain a measure of relative elevation. Relative elevations were classified into six TPI classes to allow for visual representation of elevations. Bottom types were noted during ROV surveys and compared to bottom types determined by sonar data, and in all cases results were confirmed.

Principal component analysis (PCA) was used to examine potential relationships between habitat type and
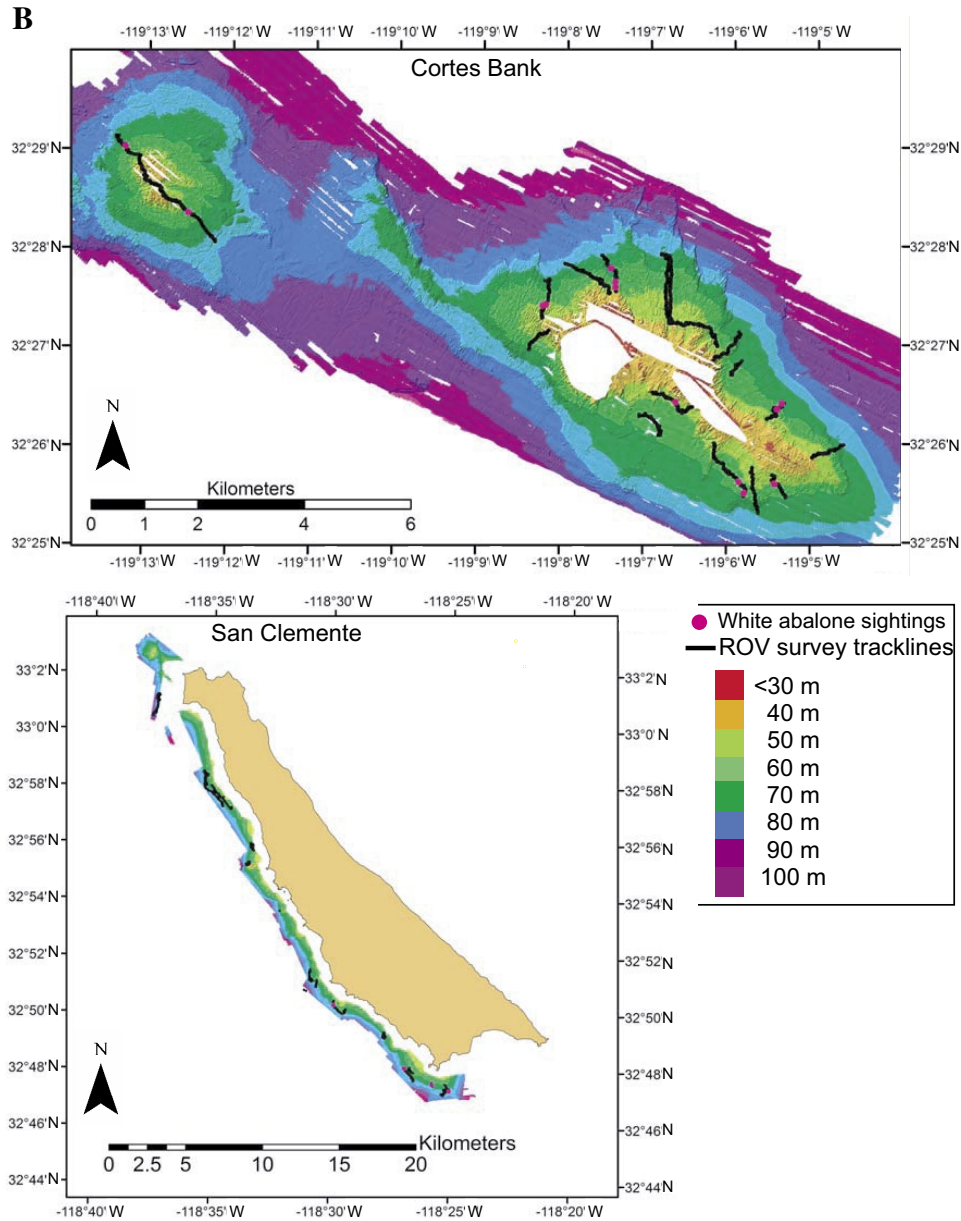
[3] Kvitek, R. G., P. J. Iampietro, and E. Summers-Morris. 2003. Integrated spatial data model tools set for the auto-classification and delineation of species-specific habitat maps from high-resolution, digital hydrographic data. Report prepared for NOAA National Ocean Service (NOS), p 1–74. NOAA Coastal Services Center, 2234 South Hobson Ave., Charleston, SC 29405.
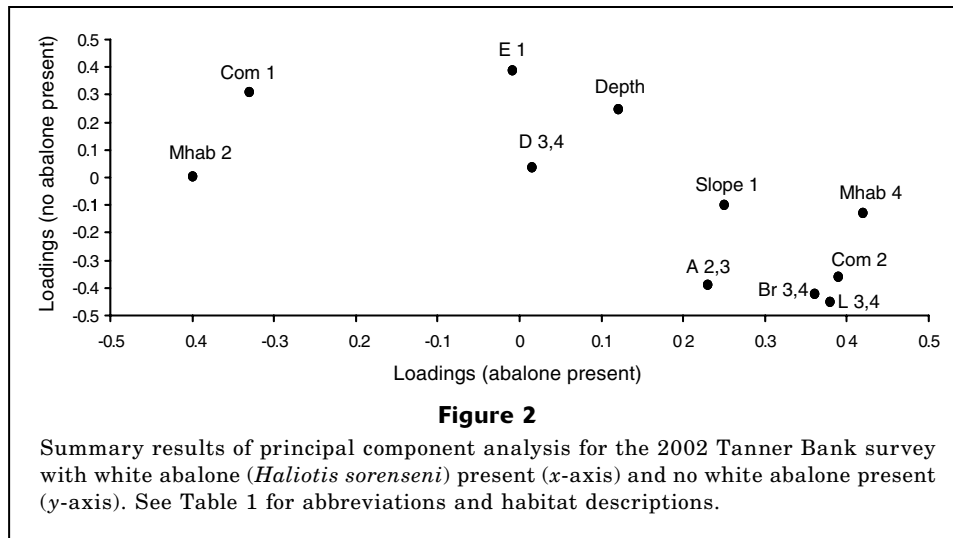
Figure 1 (continued)

algal cover in segments containing abalone, and those where abalone were absent for the Tanner Bank 2002 survey. For the purposes of PCA, transects were divided into 100-m segments. All PCA coefficients were plotted initially to examine relationships between abalone presence and absence and defined variables. Coefficients from the most influential variables were then plotted to examine these relationships more closely.

Transects varied in length from 0.4 to 6 km, although most transects were close to 1 km in length. To estimate abalone densities we attempted to search within a particular 10 m depth interval during each transect. When this was not possible, transects were poststrati-

fied by depth interval (10 m), because results of preliminary surveys provided evidence of the prevalence of white abalone within particular depth ranges. For the few cases (2) where poststratification yielded a search area of less than 100 m^2, the data for these areas were excluded from the analysis because densities would be artificially inflated. We calculated density per unit of area for each transect and stratified transects by three depth intervals (30–40 m, 40–50 m, and 50–60 m) to test for differences among depths and sites using Kruskal-Wallis nonparametric techniques on ranked data (Systat vers. 11, Systat Software Inc., Point Richmond, CA). The mean depth of abalone occurrence was tested

Figure 2

Summary results of principal component analysis for the 2002 Tanner Bank survey with white abalone (*Haliotis sorenseni*) present (*x*-axis) and no white abalone present (*y*-axis). See Table 1 for abbreviations and habitat descriptions.

for differences among sites with a one-way ANOVA. Depth and size distributions were compared among sites with a Kolmogorov-Smirnov (K-S) test. To estimate population sizes at each site, densities were applied to depth-area polygons derived from multibeam sonar bathymetry.

To examine the fine-scale spatial distribution of white abalone on the banks we determined and plotted linear distances between individuals along transects and recorded the number of groups (individuals within 2 m of another abalone) versus individuals (no other abalone within 2 m). Additionally, the distances between all individuals at each site were calculated, and for each abalone the distance to the nearest subsequent abalone sighting was determined. This was not a traditional nearest neighbor analysis, because transects were not designed for such an analysis. To test the degree of dispersion of the population on a broader scale, the cumulative number of white abalone observed within 250-m^2 segments of transect between 40 and 50 m depth (the depth range with the highest abalone densities) at Tanner Bank in 2002 were fitted to a negative binomial distribution (Elliott, 1977). The Tanner Bank 2002 surveys were appropriate for this analysis because of the high number of abalone sightings there.

Results

Habitat

The amount of rocky habitat between 30 and 60 m depth at Tanner Bank, Cortes Bank, and the west side of San Clemente Island was 1359, 1139 and 889 ha, respectively (Fig. 1). Side-scan sonar data indicated that the majority of the sea floor shallower than 60 m at all sites is hard substrate (Fig. 1). High-resolution bathymetry from multibeam sonar revealed a complex structure on the offshore banks. Tanner Bank and Cortez Bank are

uplifted anticlines that have been eroded by wave action from the northwest during past periods of lower sea level (Vedder et al., 1986). Erosion of more recent geologic units has exposed erosion-resistant marine sedimentary and volcanic rocks that through differential erosion have developed layering and fracture features favorable to abalone. San Clemente Island is on the uplifted southern side of the San Clemente fault (Vedder et al., 1986), and is composed of erosion-resistant volcanic rocks of the same age as those at Tanner and Cortez Banks.

Microhabitat analysis

At Tanner Bank in 2002, white abalone were generally found in association with two species of brown algae (*Laminaria farlowii* and *Agarum fimbriatum* [88% of white abalone sightings included one or both species]), a foliose red alga (*Rhodymenia* spp. [45% of sightings]), geniculate coralline algae (*Calliarthron* spp.) and *Corallina* spp. [79% of sightings]), and encrusting coralline algae (*Lithothamnion* spp. [100% of sightings]). The brown alga *Dictyotaceae* spp. was present in 9% of white abalone sightings (mostly in deeper waters), and *Eisenia arborea* in 6% of sightings (mostly in shallower waters).
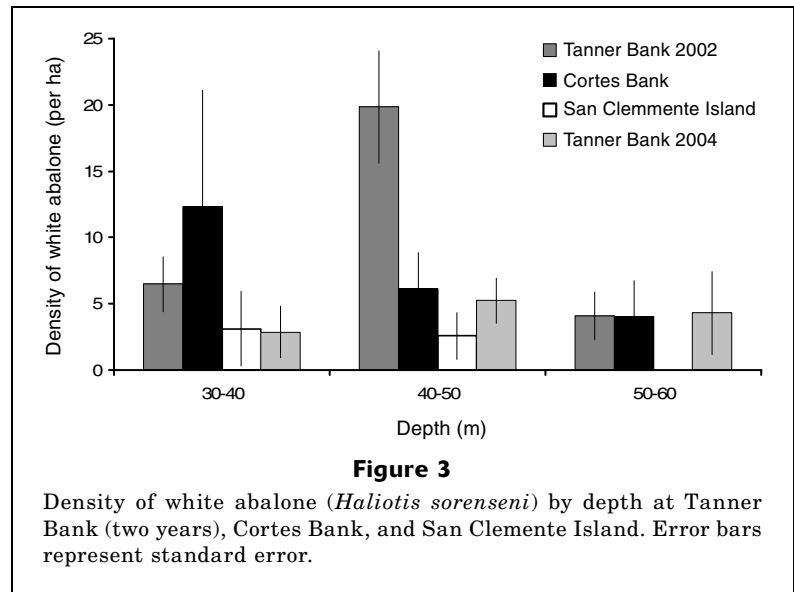
A PCA examination of these data revealed a strong positive relationship between the presence of white abalone and several factors; the strongest loadings occurred with depth, microhabitat type (Mhab 4 (deformed with sand)), the magnitude of seafloor slope (slope 1, flat), moderate seafloor complexity (Com 2 (low)), and the relative abundance (common or abundant) of brown algae A (*Agarum fimbriatum*), L (*Laminaria* spp.), and Br (brown algae spp. in general); (Fig. 2, Table 1). In contrast, a strong negative relationship existed between zero white abalone density and habitat characteristics; the strongest negative relationships occurred with the frequent presence of various algal species (same as above). There were strong positive relationships

between zero white abalone density and the presence of *Eisenia arborea*, and zero white abalone density and low seafloor complexity (com 1 [very low]).

Although detailed habitat analyses were not completed for the 2003 Cortes Bank survey, we noted the presence of the brown algae *Pterygophora californica* and *Cystoseira* spp. (both absent at Tanner Bank in 2002), and the apparent absence of *Dictyotaceae* spp. in deeper waters.

Abalone abundance, depth, and size distribution

A total of 258 individual white abalone were identified in all surveys, and the highest numbers were seen at Tanner Bank in 2002 (19.8 abalone/ha, Fig. 3, Table 2). Densities ranged from 0.0 abalone/ha (San Clemente Island, 50–60 m depth range) to 19.8 abalone/ha (Tanner Bank 2002, 40–50 m depth range, Fig. 3, Table 2). Very few individuals of other haliotids (5 pink and 3 red) were identified. Search effort was focused on the 30–60 m depth range after preliminary results at Tanner Bank indicated that white abalone inhabit this depth range, but surveys were conducted at shallower and deeper depths at each site to confirm these findings. No abalone were found shallower than 32 m or deeper than 61 m at any site, and therefore the results of these surveys were not included in the analysis. Overall densities differed significantly between surveys (n=162, Kruskal-Wallis test, test statistic=23.76, P<0.0001). Densities within

Figure 3

Density of white abalone (*Haliotis sorenseni*) by depth at Tanner Bank (two years), Cortes Bank, and San Clemente Island. Error bars represent standard error.

surveys grouped by 10 m depth bins only differed significantly by depth for the Tanner Bank 2002 survey (n= 33, Kruskal-Wallis test, test statistic=10.45, P<0.01, Fig. 3). The total number of abalone shells ranged from 44 (San Clemente Island) to 154 (Cortes Bank). The depth distribution of white abalone for all surveys combined reveals that white abalone were stratified by depth overall, although search effort was focused on the middle depth ranges (Figs. 3 and 4). The depth distribution of empty shells was similar to that of live white abalone (31–61 m), although there were several (<10) shells found
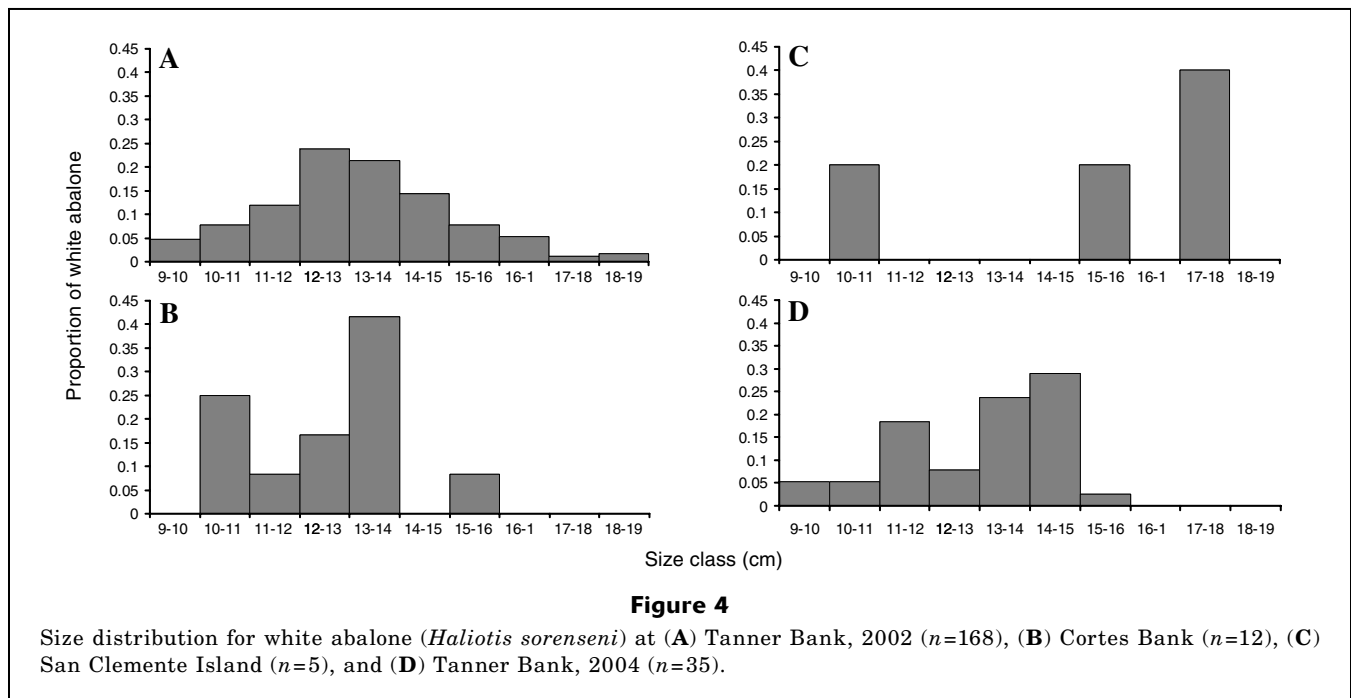

Figure 4

Size distribution for white abalone (*Haliotis sorenseni*) at (**A**) Tanner Bank, 2002 (n=168), (**B**) Cortes Bank (n=12), (**C**) San Clemente Island (n=5), and (**D**) Tanner Bank, 2004 (n=35).

Table 2

Density of white abalone (*Haliotis sorenseni*), area surveyed by the ROV, habitat area and population estimates by depth strata for Tanner Bank, Cortes Bank, and San Clemente Island.

		Tanner Bank		
Depth (m)	Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
30–40	2002: 6.5 ±2.1	2002: 3.5	245	2002: 1592.5 ±514.5
	2004: 2.9 ±1.9	2004: 0.93		2004: 710.5 ±465.5
40–50	2002: 19.8 ± 4.3	2002: 5.0	425	2002: 8415.0 ±1827.5
	2004: 5.2 ± 1.7	2004: 3.9		2004: 2210.0 ±722.5
50–60	2002: 4.08 ±1.8	2002: 2.3	689	2002: 2811.1 ±1240.2
	2004: 4.3 ±3.1	2004: 1.7		2004: 2962:7 ±2135.9
Total	2002: 13.0 ±3.5	2002: 10.8	1619	2002: 12,818.6 ±3582.2
	2004: 6.1 ±1.5	2004: 6.5		2004: 5883.2 ±3323.9

at relatively shallow (<25 m) and one shell found at a relatively deep depth (72 m).

The sizes of white abalone at all sites ranged from 9.0 to 19.0 cm (Fig. 4). No small abalone were observed, although turban snails smaller than 6 cm were detected by using ROV sampling methods. Size distributions differed significantly for comparisons made between Tanner Bank 2002 and Cortes Bank, and Tanner Bank 2002 and San Clemente Island (K-S test, P<0.01, Fig. 4). There was an apparent shift in size distributions between years at Tanner Bank; fewer large animals were found in 2004 than in 2002, although the overall size distributions did not differ significantly between years (K-S test, P=0.19, Fig. 4). The size distribution at Cortes Bank included animals in the mid size range, and no abalone in the smallest or largest size ranges. Densities at San Clemente Island were too low to show any real pattern in size distribution (Fig. 4). The mean size of abalone ranged from 12.4 cm to 13.7 cm and did not differ significantly between surveys (ANOVA, P>0.05).

Site-specific white abalone population estimates were based on the amount of available habitat quantified from the results of multibeam sonar surveys and white abalone density estimates determined from data from ROV surveys. The total population of white abalone on Tanner Bank based on 2002 density measurements was estimated at 12,819 ±3582 (SE), whereas the total population estimate based on 2004 density measurements was 5883 ±3324. The total population on Cortes Bank was estimated at 7366 ±5340 (SE), and that at San Clemente Island was estimated at 1938 ±1598 (SE; Table 2).

White abalone reproductive potential

Eighty-nine percent of white abalone at all sites were observed as singletons, and only 6% were observed in groups. Group sizes ranged from two to five individuals and the largest group was observed at Tanner Bank in 2002. There were no sightings of abalone in groups at Tanner Bank in 2004. White abalone were not found frequently in groups during any of the surveys, and the observed number of individuals within 250-m^2 subsamples within the 40–50 m depth range at Tanner Bank in 2002 did not differ from values predicted by the negative binomial distribution (chi-square=4.9, P=0.67).

The results of an analysis of distances between sightings indicated that less than 25% of individual abalone were located within 5 m of one another for all surveys. The majority of individuals (60%) were over 20 m away from another sighted abalone. The survey with the highest proportion of abalone located within a distance of 20 m of another individual was that at Tanner Bank in 2002. In regard to potential mating pairs, out of a possible 19,503 combinations of mating pairs, only 202 were within 30 m from one another at Tanner Bank in 2002, 4 out of 231 pairs at Cortes Bank, 3 out of 12 pairs at San Clemente Island, and 10 out of 861 pairs at Tanner Bank in 2004.

Discussion

Few areas in U.S. waters have been adequately mapped to reveal detailed bathymetry or substrate characteristics. Consequently, our knowledge of the amount of habitat available for benthic marine organisms is so inadequate that one can only speculate about overall population sizes. White abalone populations in southern California are no exception; all previous estimates of the amount of suitable habitat available for white abalone have been based on the assumption made by Thompson et al. (1993) that 3% of the sea floor between 25 m and 65 m was rocky substrate (Davis et al., 1998;

	Cortes Bank				San Clemente Island		
Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population		Density (/ha ±SE)	Area surveyed (ha)	Habitat area (ha)	Population
12.3 ±8.8	2.6	232	2853.6 ±2041.6		3.1 ±2.8	0.8	392	1215.2 ±1097.6
6.1 ±2.8	1.5	423	2580.3 ± 1184.4		2.6 ±1.8	2.4	278	722.8 ±500.4
4.0 ±2.7	0.7	483	1932 ±2114.1		0	0.7	219	0
8.0 ±3.1	4.8	1138	7365.9 ±5340.1		1.5 ±0.2	3.9	889	1938 ±1598

Hobday and Tegner, 2000; Hobday et al., 2001). Using this assumption, the total amount of white abalone habitat in southern California was estimated to be only 752 ha (Davis et al., 1998; Hobday et al., 2001). The results of surveys from the present study at only three sites (Tanner and Cortes Banks and San Clemente Island) revealed 3646 ha of rocky substrate between 30 and 60 m, which is much higher than estimates based on the 3% rocky habitat assumption. Thus, the total available habitat area for white abalone and other benthic dwelling organisms in southern California is likely far greater than previously reported.

The definition of available white abalone habitat, however, may need further refinement if white abalone exhibit a preference for a certain type of rocky substrate. Cochrane et al. (2005) suggested that white abalone prefer the edges of reefs at the sand-rock interface rather than the areas in the middle of the reef. Although there is some qualitative evidence supporting this idea, there have been no conclusive studies on specific habitat preferences. The only conclusion that can be drawn in relation to habitat preference from the present study is that white abalone are not typically found in areas with no rock (i.e., sand only). Even if white abalone were found only at the sand-rock interface, our estimates of available habitat would still far exceed past estimates. Although the time and effort involved in mapping habitat may lead to the temptation to make broad generalizations to estimate habitat types and amounts, the results of this study have shown that specific habitat mapping is necessary to accurately identify the amounts of each type of habitat existing in a particular area.

The depth distribution of white abalone at these three sites was grouped into three depth bins (30–40 m, 40–50 m, and 50–60 m) and was less stratified than predicted according to preliminary surveys at Tanner Bank. The number of abalone was highest in the middle depth bin (40–50 m) at Tanner Bank during 2002 and 2004, but only significantly so in 2002. The highest number of abalone observed at Cortes Bank was in the shallowest depth bin (30–40 m). Too few abalone were sighted at San Clemente Island and they were not included in the analysis. These results indicate that there are not clear, broad trends in depth distribution that can be applied to all sites, although the deepest depth bin did yield the fewest abalone sightings at all sites. It is also possible that the only realistic trends observed were those at Tanner Bank in 2002 because of the relatively large number of animals observed at this site.

The white abalone population in California has been estimated to number less than 3000 (Davis et al., 1998; Hobday and Tegner, 2000; Hobday et al., 2001). In this study a total of between 15,187 and 22,123 white abalone was estimated at two offshore banks and one island location. Our population estimate is greater for two reasons: 1) the multibeam sonar maps revealed more habitat than was previously known to exist, and 2) search effort, and therefore the calculation of density, was dependent on suitable habitat, i.e., densities were not artificially deflated by including portions of surveys conducted in inappropriate habitat (e.g., sand).

The highest densities (19.8 abalone/ha between 40 and 50 m) were observed at Tanner Bank in 2002. Previous surveys at Tanner Bank underestimated habitat area and included the entire search area without regard to depth or habitat to determine density. A re-examination of data from surveys conducted by the Delta submersible in 1999 at Tanner Bank (Haaker et al.[2]) yielded an overall density of 15.7 abalone/ha. This value varies only slightly from our overall density esti-

mate of 13.0 abalone/ha. Densities were lower overall in our surveys conducted at Tanner Bank in 2004, and the most significant differences were apparent in the 40–50 m depth range. These lower densities in surveys conducted only two years after initial surveys are noteworthy and worrisome, especially because Tanner Bank is a site where the population was thought to be relatively stable.

The density of white abalone prior to commercial and recreational exploitation is poorly known, and the few reported estimates are the subject of considerable speculation. Tutschulte (1976) reported an estimate of white abalone density of 2300 abalone/ha, based on three 10-m^2 quadrats. Because of the small sample size and lack of replicate sites, caution should be used when applying this estimate to all of California. However, it is important to note that one cluster of five white abalone was observed in the present study, which would lead to a local density close to that reported by Tutschulte (1976). It is also of interest to note that Shepherd et al. (2001) suggested that once populations of *Haliotis laevigata* reached densities below 0.25 abalone/m^2 (2500 abalone/ha) management action should be taken, and therefore estimates of 0.23 abalone/m^2 reported by Tutschulte (1976) were not extremely high.

More recently Rogers-Bennett et al. (2002) used historical landings data and the habitat area estimated by Davis et al. (1998) and Hobday et al. (2001) in an attempt to reconstruct past population densities. Applying the 3% rocky habitat criteria referred to above (Discussion section, paragraph 1) (Thompson et al., 1993), Rogers-Bennett et al. (2002) calculated a density of 479 abalone/ha for all of California and a density of 1623 abalone/ha for San Clemente Island, where 75% of the landings were reported. These densities are lower than those reported by Tutschulte (2300 abalone/ha; 1976), but the more recent estimate is also too high because the proportion of rocky habitat is greater than 3%, as observed in the present study. The maximum density observed in the present study (19.8 abalone/ha) is only an order of magnitude less than Rogers-Bennett et al.'s (2002) calculation of historic density for all of California (479 abalone/ha), but is two orders of magnitude less than the estimates by Tutschulte (2300 abalone/ha, 1976). Regardless of the problem of inflated density estimates, the densities observed in the present study at San Clemente Island were less than 5 abalone/ha at all depths, which is astoundingly lower than the 1623 abalone/ha calculated by Rogers-Bennett et al. (2002).

Whether the existing white abalone populations are viewed as viable depends largely on the validity of estimates of past population distributions and densities and on establishing confidence in current density estimates. Total abundance of individuals becomes irrelevant if these animals are distributed such that densities within a particular area are below the critical level necessary for successful reproduction. The relatively deep range of *H. sorenseni* is outside the range of dense macroalgal

growth, and therefore we can assume that the ROV does an adequate job in identifying animals within its field of view (2 m). Based on the assumption that we are actually sighting nearly all of the animals that are within the search range, our data indicate that the majority of individuals at these sites are greater than 5 m (linear distance) from any other individuals along and between transects, and that many are over 30 m away from a potential mate. These distances well exceed what has been shown to be a critical minimum distance (≤2 m) for successful spawning and fertilization in other species of abalone (e.g., *Haliotis laevigata*; Shepherd and Brown, 1993; Babcock and Keesing, 1999; Shepherd et al., 2001). The large distances between individuals coupled with density estimates that are several orders of magnitude lower than those necessary for a viable population (Shepherd et al., 2001) would indicate that white abalone populations are currently in a dire state.

Despite generally large distances between individuals, an analysis of dispersion within the population surveyed at Tanner Bank in 2002 showed a large proportion of individual sightings within 30 m of another sighting. Additionally, there was a high degree of contagion between individuals in 250-m^2 subsamples at depths of 40–50 m. It may be true that white abalone at this site are aggregated on a larger scale, indicating that certain habitats within their most prevalent depth range (40–50 m) may promote higher survival of white abalone. However, ultimately, if animals are not packed densely enough at smaller scales, successful spawning and fertilization will not occur. This study highlights the importance of establishing accurate density estimates at appropriate scales for guiding assessments of population viability and future enhancement protocols.

The mean sizes of white abalone observed in the present study varied little between sites and were comparable to those observed during 1999 submersible surveys at Tanner Bank and Cortes Bank (Behrens and Lafferty, 2005). The size distribution of white abalone did differ slightly between the two banks and island location. More notable was an apparent shift in the size distributions of animals observed at Tanner Bank in 2002 versus those observed in 2004. Unlike in 2002, there were no large individuals observed in 2004, indicating a possible die-off of older individuals and a lack of new, younger individuals to fill this size class. No white abalone smaller than 9.0 cm (approximately three years old; Tutschulte, 1976) were observed at any of the sites. If this were a self-sustaining population, smaller individuals indicating recruitment from several preceding year classes would be present, although the likelihood of sighting abalone recruits and juveniles younger than three years is not very high. Juvenile white abalone shells are mottled red in color and settlement occurs on pink crustose coraline algae-covered rocks, thus making them very cryptic during the first few years of life. Even during historic periods when white abalone density was much higher than cur-

rent levels, juveniles were observed on extremely rare occasions (Owen[4]). Thus, the absence of small individuals during ROV observations does not rule out recent recruitment to this population. Consequently, although recruitment in the last three years may be undetectable, recruitment from the last three decades should be evident in our surveys.

Conclusions

The use of detailed sonar mapping techniques has proven to be an invaluable method to estimate amounts of different habitat types for the purposes of quantifying marine organisms within their specific habitat. Specifically, white abalone restoration efforts would be greatly enhanced by more surveys incorporating high-resolution bathymetric maps that would serve to better define the characteristics of suitable white abalone habitat. Our concept of what a viable white abalone population is would benefit from more accurate density estimates for other areas within the historic range and from a better understanding of how white abalone are distributed within populations.

The ultimate goals of recovery and eventual removal of white abalone from the Endangered Species List depends upon establishing confidence in the demographic parameters that define a viable white abalone population. It has become apparent that conducting studies such as this one, with continuing efforts to improve sample standardization techniques over time, is critical to achieving recovery goals.

Acknowledgments

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