



# Evaluation of stocking strategies for endangered white abalone using a hierarchical demographic model



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## ABSTRACT

Evaluation of stocking strategies for endangered white abalone (*Haliotis sorenseni*) has been challenging due to limited data. The present study demonstrated an application of hierarchical demographic model for investigating population dynamics of white abalone and evaluating efficacy of hypothetical restoration strategies. The model represented demographic parameters as multi-level hierarchies, which accounted for uncertainty in parameter estimation due to limited data, and accounted for individual/sub-population variability in demographic traits in response to spatiotemporal heterogeneity. The model also accounted for the Allee effect (i.e., density-dependent fertilization success) observed in white abalone populations. In the calculation of fertilization success, we applied region-specific density estimates from three regions (Tanner Bank, Cortes Bank and San Clemente Island). Elasticity analyses showed that survival affected growth rate more than fertility, and fertility and survival of large-size individuals (>130 mm) had the most influence on growth rate; the mean elasticity to fertility decreased while the one to survival increased as the population became less abundant. Evaluation of stocking strategies suggested that restoration efforts directed at larger-size individuals may be more effective in increasing population density than efforts focusing on juveniles; the degree of increase depended on both initial population density and initial size structure. However, stocking large-size individuals led to a decrease in the intermediate-size class (90–130 mm) proportion in most cases. Efficacy of increasing intermediate-size class proportion heavily depended on initial population density. We suggest that restoration efforts may need to consider the region-specific density-dependence effect, and to balance stocking efficacy and laboratory expenses/time consumption.

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## 1. Introduction

White abalone (*Haliotis sorenseni*) is the first marine invertebrate protected under the Endangered Species Act (Hobday and Tegner, 2000). It is native to sand-surrounding rock or boulder habitat at depths of 20–60 m along the west coast of California and the northwest coast of Mexico (Tutschulte, 1976; Davis et al., 1996; Hobday and Tegner, 2000). It is a species with long life span (40 years, Cox, 1960), slow movement, external fertilization, and highly variable recruitment rates (Cox, 1960; Hobday and Tegner, 2000). The white abalone fishery in California began in 1968, peaked in 1972 and collapsed by 1978, driven by intensive exploitation and other factors such as environmental changes, diseases,

hybridization, accidental mortality, and predation and competition (Hobday and Tegner, 2000). The abundance of white abalone has declined by greater than 99%, compared to the estimated pre-exploitation abundance (Hobday and Tegner, 2000). The most recent survey between 2002 and 2010 at Tanner Bank revealed dramatic and continued decline in both abundance and density, along with an increased proportion of large individuals and vast majority being singletons (Stierhoff et al., 2012). At low density, white abalone populations may suffer from the Allee effect (Allee, 1931) because external fertilization success requires high densities of sperms and eggs provided by aggregation of remnant individuals (Hobday and Tegner, 2000).

As the deepest-living and the latest harvested species among all abalone species along the west coast, the white abalone has been poorly studied (Hobday and Tegner, 2000). As concerns about its extinction arise, researchers and fishery managers have been taking actions to collect more information and to develop recovery plans for restoring the white abalone population. However, limited biological and ecological data complicate the assessment of its current

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status and extinction risk. Natural recovery without intervention seems unlikely to occur for white abalone (Stierhoff et al., 2012), and thus evaluation of different restoration strategies, particularly under different stocking protocols will be essential. However, such assessment has been deficient relative to work on other endangered species. Rogers-Bennett and Leaf (2006) developed a deterministic demographic matrix model for white abalone and evaluated the impacts of recovery actions and potential threats on population growth, but did not account for uncertainty due to limited data, Allee effect or spatial heterogeneity. Thus, an analysis that fully utilizes available information and accounts for uncertainty in parameter estimation due to limited data would better inform conservation of white abalone.

Demographic models are commonly used to understand population dynamics and to evaluate management tactics for threatened and endangered species (Beissinger and Westphal, 1998; Caswell, 2001). This type of models requires demographic information about the species. By representing demographic parameters as multi-level hierarchies, the hierarchical approach can incorporate demographic and environmental stochasticity (Gelman et al., 2004; Jiao et al., 2009). In the hierarchical model, each of the parameters that govern the probability distribution in the lower-level hierarchy is further determined by a probability distribution governed by parameters in the higher-level hierarchy (hereafter, termed “hyper parameters”) (Gelman et al., 2004). Hierarchical models are preferred in cases where we have limited data or knowledge about the species, or we believe that the species has strong variability in population dynamics across individuals, sub-populations, regions and years (Jiao et al., 2009), which is likely the case of white abalone. Ignorance of this spatiotemporal variation in parameter values might lead to incomplete understanding of the population dynamics of the species and misleading management recommendations (Jiao et al., 2009).

Fertilization success of white abalone is seriously hindered by low density due to the Allee effect (Clavier, 1992; Babcock and Keesing, 1999; Hobday and Tegner, 2000; Stierhoff et al., 2012), and its density is very likely to show spatial heterogeneity due to its limited movement (Davis et al., 1998; Hobday and Tegner, 2000). The most recent survey using multibeam sonar mapping techniques revealed a significant difference in densities among two offshore banks (Tanner Bank and Cortes Bank) and one island (San Clemente Island) off California coast (Butler et al., 2006). Additionally, its historic commercial catch data have shown spatial heterogeneity (Karpov et al., 2000). After fertilization, the planktonic larvae of abalone disperse to suitable habitat for settlement. Larval dispersal has been shown to be very limited for several Australian abalone species (Prince et al., 1987; McShane et al., 1988) and green abalone in California (Tegner and Butler, 1985a), but no information about larval dispersal distance exists for white abalone (Hobday and Tegner, 2000).

The purpose of this study was to: (1) develop a region-specific hierarchical demographic model for white abalone; (2) conduct sensitivity and elasticity analyses to identify critical size classes and demographic parameters for population growth; (3) evaluate efficacy of hypothetical restoration strategies to aid in management of white abalone and to prioritize recovery efforts.

## 2. Materials and methods

### 2.1. Hierarchical size-structured demographic model

We assumed a pre-breeding population for white abalone and applied the matrix model (Caswell, 2001) because it has long been used to forward project population dynamics, to estimate the population growth and the stable age or size structure and to conduct

population viability analysis (Caswell, 2001). We constructed the matrix model based on size structure instead of age structure due to the difficulty and uncertainty in aging white abalone and the distinct demographic characteristics across size classes. The size-structured matrix model comprises two components, the projection matrix and the initial population structure:

$$N_{y+1} = AN_y,$$

where  $N_y = \{N_{y,1}, N_{y,2}, \dots, N_{y,v}\}$  is a vector of size-specific population abundance at size class one to size class  $v$  in year  $y$ , in which  $v$  indexes the largest size class that we predetermined. In this study, we used four size classes, and thus,  $v=4$  and the matrix  $A$  represents the projection matrix with a size of  $4 \times 4$ :

$$A = \begin{bmatrix} s_1 p_{1 \rightarrow 1} + e_1 & e_2 & e_3 & e_4 \\ s_1 p_{1 \rightarrow 2} & s_2 p_{2 \rightarrow 2} & 0 & 0 \\ s_1 p_{1 \rightarrow 3} & s_2 p_{2 \rightarrow 3} & s_3 p_{3 \rightarrow 3} & 0 \\ s_1 p_{1 \rightarrow 4} & s_2 p_{2 \rightarrow 4} & s_3 p_{3 \rightarrow 4} & s_4 p_{4 \rightarrow 4} \end{bmatrix},$$

where  $e_i$ ,  $i = 1, 2, 3, 4$ , is the size-specific fertility every year,  $i$  indexes the  $i$ th size class,  $s_i$  is the probability of individuals surviving from one year to the next,  $p_{i \rightarrow i}$  is the probability of individuals staying within size class  $i$  and  $p_{i \rightarrow j}$  is the probability of individuals growing from size class  $i$  to another size class  $j$  after one year. Values for  $s$  and  $p$  range from 0 to 1 and  $\sum_{j=1}^v p_{i \rightarrow j} = 1$ . Negative growth was not

permitted in this study, and thus we had  $j \geq i$  and the growth transition probabilities were standardized by dividing the probability of growing from a given size class to each size class by the summation of these probabilities of growing from a given class to all the size classes. The last size class was a plus group with the probability of staying in the same size being one (i.e.,  $p_{4 \rightarrow 4} = 1$ ). Values for  $e$  are positive by definition.

The size-specific population abundance can be forward projected by using the projection matrix, and will eventually become stationary. This forward projection yields the growth rate  $\lambda$ , the stable size structure and the reproductive values, which are the dominant eigenvalues, the corresponding right and left eigenvectors of the projection matrix, respectively (Caswell, 2001). In a non-hierarchical model, the projection matrix is further governed by parameters while in a hierarchical model, both parameters and hyperparameters determine values in the projection matrix (Caswell, 2001; Jiao et al., 2009).

Size classes were constructed using biologically meaningful sizes. We constructed four size classes with unequal interval width. The first size class encompassed growth from the size at one year (25 mm) to the size before becoming incryptic (75 mm, Cox, 1960), and thus abalones within this size class stay cryptic. The first size class did not start with the size at settlement (0.1 mm) because of the assumption of prebreeding populations (i.e., censuses are conducted just prior to the breeding period, and thus all individuals are at least one year old). Tutschulte (1976) estimated growth from a sample of 20 white abalones collected during search dives and a sample of 21 white abalones grown in the laboratory. The size at one year (25 mm) was determined from these analyses. The second size class ranged from 75.1 mm to 90 mm where white abalones stay incryptic before reaching maturity (Tutschulte, 1976). The third size class ranged from 90.1 mm to 130 mm, representing individuals reaching maturity and intermediate size (Davis et al., 1996; Hobday and Tegner, 2000). The Final White Abalone Recovery Plan (The Recovery Plan, NMFS, 2008) defines the intermediate-size individuals to be those within size class 90–130 mm, and sets conservation goals targeting this size class. Thus, we constructed this size class for evaluating hypothetical restoration strategies. The

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