

POPULATION STATUS ASSESSMENT AND RESTORATION MODELING OF WHITE ABALONE *HALIOTIS SORENSENI* IN CALIFORNIA

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ABSTRACT White abalone *Haliotis sorenseni* was listed as endangered in 2001 because of severe declines throughout southern California due to overfishing. Populations continue to decline despite the closure of the fishery in 1996. There has been little to no evidence of recruitment in southern California from population surveys and in artificial reefs targeting white abalone recruitment since the listing of the species. A 13-y time series of white abalone abundance in prime habitat, surveyed with a remote-operated vehicle, was used in a population viability analysis to quantify: (1) the population decline and (2) the time to reach a quasi-extinction threshold. The annual decline in the population is 12%, which is comparable to adult natural mortality rates for abalone species. The quasi-extinction threshold of 1,000 individuals is met within 15 y. These results confirm that the white abalone populations in southern California are at high risk of extinction, and highlight the importance of active stocking and restoration for the species. To inform restoration, a deterministic density-dependent size-based matrix model was developed to investigate different stocking scenarios, incorporating an innovative method for modeling low populations by setting the reproductive term as a function of adult density to mimic a reproductive Allee effect. A minimum density of 0.14 abalone/m² of stocked juveniles led to a maximum population growth rate (λ) of more than or equal to 1 for the model population within 10 y but that recovery was poor (mean $\lambda_{15-20} \leq 1.0$) over time if the level of juvenile stocking was less than 0.23 abalone/m² in the model population. The innovative approach of incorporating adult density into the reproductive term in the model quantitatively shows how low population densities can impact threatened and endangered species, and may be widely used for other species. These results can not only help guide stocking strategies but also allow for the quantitative evaluation of white abalone under the guidance of the IUCN Red List of Threatened Species, suggesting that white abalone should be considered Critically Endangered.

KEY WORDS: conservation, extinction, matrix model, recovery, Allee effect, Critically Endangered, IUCN

INTRODUCTION

Population surveys of white abalone *Haliotis sorenseni* in southern California show declining densities since 2002 (Stierhoff et al. 2012, 2014, unpublished data), despite the fishery closure in 1996 and the listing of the species on the U.S. Endangered Species List in 2001 (Federal Register 65 FR 2616 and 66 FR 29046). In the 2000 status review, Hobday and Tegner warned that existing white abalone were old (large) and that the population would disappear as a result of natural mortality without human intervention. In 2001, a rebuilding strategy for white abalone was developed that identified hatchery production and stocking of cultured white abalone as the primary restoration action recommended. The California and federal recovery plans for white abalone both call for active restoration of white abalone populations through captive-rearing and stocking efforts. The implementation of these plans is the focus of a broad partnership of government and academic institutions, as well as private and nonprofit organizations, called the White Abalone Recovery Consortium (Rogers-Bennett et al. 2016a).

A significant challenge to the white abalone populations, and to the recovery program is the influence of Allee effects on the population dynamics at low densities (Allee 1931, Hobday et al. 2001). The broadcast spawning reproduction of abalone requires males and females to be very near (<3 m) to each other to ensure high fertilization rates (Babcock & Keesing 1999).

Extremely low population densities (<1 abalone/ha) and large distances between spawning individuals have been observed for white abalone populations in southern California (Stierhoff et al. 2012), and is considered the primary factor responsible for the present day reproductive failure (Haaker et al. 1994, Davis et al. 1996, 1998, Behrens & Lafferty 2005). Juvenile white abalone (<80 mm) have not been observed in the wild or on artificial recruitment modules in the Channel Islands for nearly 15 years since 2001 (Rogers-Bennett et al. 2004), suggesting a lack of significant successful reproduction in the wild. To reestablish self-sustaining populations of white abalone, stocking efforts will need to release sufficiently large numbers of abalone to overcome the negative impacts of Allee effects to the population growth during the initial years after stocking.

Population models provide useful tools for assessing the restoration time frames, as well as identifying optimal stocking strategies and targets for juvenile production and monitoring. Simulation modeling allows comparison of multiple restoration scenarios to guide field trials. This approach is applied particularly before field trials for endangered species such as white abalone when captive juvenile production is limited. The goals of this study were 4-fold: (1) assess the risk of no restoration stocking action to the white abalone populations in southern California; (2) evaluate a minimum target stocking density, which may result in positive long-term population growth to inform juvenile production goals; (3) quantify the efficiency loss of spreading stocking effort over time; and (4) determine appropriate poststocking monitoring time frames for evaluating stocking effectiveness. A stochastic simulation model based on a standard exponential population model fit to the recent wild

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DOI: 10.2983/035.035.0304

survey data was used to assess quasi-extinction risk. A size-based matrix population model was also developed, incorporating density-dependent reproduction to represent low-density dynamics influenced by Allee effects, to simulate restoration stocking. The results of this work will inform the development of a restoration stocking program in southern California.

METHODS

Estimating Wild Population Dynamics

A deterministic exponential population model was fit to the abundance estimates at Tanner Bank from the surveys in 2000, 2004, 2008, 2010 (Stierhoff et al. 2012), and 2014 (Stierhoff et al. 2014, unpublished data). The model for population growth is $N_t = \lambda N_{t-1}$, where $\lambda = e^r$, and r is the intrinsic rate of population growth. When λ equals 1 ($r = 0$), the population is stable, so that birth rate equals the death rate in the population. When λ is less than 1, the population is declining. Assuming a closed population, the rate of decline ($1 - \lambda$) is equal to the death rate minus the birth rate. The estimated rate of decline was compared with mortality estimates for white abalone and close congeners ($M = 0.11-0.30/y$) (Ortiz Quintanilla 1973, Tutschulte 1976, Leaf et al. 2007, Rogers-Bennett et al. 2007, Button & Rogers-Bennett 2011) to evaluate the potential mean reproductive rate for this population during the survey period. In addition, the exponential model fit was compared with a linear model, using R^2 and Akaike information criterion (AIC) values (Akaike 1974).

Quasi-Extinction Risk

Quasi-extinction is the abundance below which the population is expected to become extinct. The quasi-extinction risk model uses the parameters estimated above to project the population forward in time to assess the probability of reaching a quasi-extinction threshold within a given time frame. Quasi-extinction was assumed to be 1,000 individuals. At this level, mean population densities would be less than 0.33 abalone/ha within the estimated appropriate habitat at three primary survey locations (3,386 ha; Butler et al. 2006).

Variable population growth was simulated for 50 y, and cumulative quasi-extinction risk over time was calculated. For each of 10,000 virtual populations, the population size at time t with randomized λ_t values was calculated for each year. The mean of λ was estimated from the exponential model fit to the data, and the variance (σ^2) was set equal to 0.005 to represent an optimistic environmental variability in population growth. Higher variance scenarios increase the probability of reaching the quasi-extinction threshold (Lande et al. 2003).

The most recent abundance estimates from three remote-operated vehicle (ROV) surveys were used to initialize the population model for evaluation of quasi-extinction risk. These three sites were chosen for surveys because of high historical abundances (Hobday et al. 2001, Butler et al. 2006). For Tanner Bank, the results from the 2014 ROV survey were used. For Cortes Bank and San Clemente Island, the 2014 abundances were estimated from past surveys (survey of Cortes Bank in 2002, San Clemente Island in 2012) by assuming the same population growth rate observed at Tanner Bank. Very few white abalone have been encountered outside these primary survey locations in the last decade, which lends support to the assumption that these three survey locations comprise the bulk

of the remaining population. Nevertheless, 10% was added to account for abalone that may reside outside of the survey locations. The results of this analysis present an optimistic view of quasi-extinction risk in southern California.

Matrix Population Model

A size-based matrix population model was constructed with 6 size classes, starting at the target stocking size of 25 mm. The lower bounds of the size classes are 25, 60, 95, 130, 152, and 175 mm. The break between size classes at 152 mm (the historical minimum legal size for the recreational fishery) was motivated by the goal of recovering the species to a level that may support a future fishery. Size categories in the matrix were selected to be comparable to previous modeling efforts for white abalone (Rogers-Bennett & Leaf 2006, Li & Jiao 2015). Each of the smallest three size classes is 35-mm wide to accommodate sparse data informing growth parameters (Rogers-Bennett & Leaf 2006), and the three largest size classes are narrower to reduce the variance in the fecundity estimates within a size class. Fecundity grows exponentially with size, so that wide size classes may represent a broad range of reproduction, particularly for individuals larger than 130 mm. Matrix models of long-lived species such as abalone are not normally considered sensitive to the reproductive terms (Crouse et al. 1987, Rogers-Bennett & Leaf 2006), so that size-classes may be chosen to optimize the growth or survival data inputs. For low population densities, influenced by reproductive Allee effects, the model results are however more sensitive to fecundity inputs (Catton & Rogers-Bennett 2013).

The basis of the matrix model is the growth transition matrix, which is populated using a semiempirical approach from a von Bertalanffy growth model fit to data from 21 individuals (Tutschulte 1976, Rogers-Bennett & Leaf 2006, Rogers-Bennett & Rogers 2006). Survival for each size class was based on estimates for pink abalone, a close congener in southern California kelp forests (Tutschulte 1976, Button & Rogers-Bennett 2011, Catton & Rogers-Bennett 2013). An estimate of 0.77/y for all size classes was used because there are no survival rate data for juveniles. These survival estimates represent an optimistic scenario for the stocked white abalone population, so that the results will provide insight into the minimum target stocking effort.

Fecundity for each size class (9,052 eggs/g) was calculated from the empirical relationship reported by Tutschulte and Connell (1981) for white abalone. The fecundity of the median size for each size class was calculated. In the historical wild population, the smallest reproductive individuals reported were ~88 mm though smaller individuals with mature gonads have been observed in the captive-rearing program at the Bodega Marine Laboratory (University of California, Davis) (K. Aquilino, personal communication). For the model population representing optimistic conditions, all size classes greater than 60 mm were considered reproductive.

To account for the influence of a reproductive Allee effect on the population dynamics at low densities, the fecundity terms in the matrix were modified according to the changing density of the reproductive stocked population through time. Egg survival to the first size class (P_0) was estimated so that the population growth rate of the model population would equal the observed growth rate from the ROV population surveys (2002 to 2014)

described above. This low-density P_0 estimate corresponds to an initial population density of 11.3 abalone/ha (weighted mean across depths) in the 2002 survey (Stierhoff et al. 2012). This low-density P_0 parameter was converted to a continuous density-dependent variable using a fertilization potential relationship derived from data on West Coast North American abalone populations of red (*Haliotis rufescens*), pink (*Haliotis corrugate*), and northern (*Haliotis kamtschatkana*) abalone (Button 2008, Catton & Rogers-Bennett 2013). The formula describing this relationship is a rational equation anchored at the origin:

$$\text{fert}(\rho) = \frac{p_1 \rho}{\rho + q_1}$$

where ρ is the mean population density (number of abalone/ha), $p_1 = 78.27$ [± 9.15 95% confidence interval (CI)], and $q_1 = 199.2$ (± 134.34 95% CI). The shape of this curve is asymptotic with a steep slope toward zero fertilization potential at low densities. A linear scaling equation on $\text{fert}(\rho)$ was applied to convert the fertilization potential relationship to a scaled density-dependent P_0 . The lower bound of the range to be scaled was the fertilization potential corresponding to 11.3 abalone/ha (4%) in accordance with the mean density estimated at Tanner Bank in 2002. The corresponding lower bound of the P_0 scale was back calculated from the matrix model, assuming a population growth rate equal to the mean λ estimated from the ROV survey data. The upper bound of the ranges to be scaled were set at levels attributed to equilibrium population states, where $\lambda = 1$. The P_0 value was back calculated from the matrix model and the value of $\text{fert}(\rho)$ resulting in equilibrium growth was assumed to occur at a population density corresponding to 60% fertilization potential (optimistic assumption). The density-dependent P_0 parameter is then multiplied to the size-specific reproductive potentials in the top row of the matrix.

Matrix Model Simulations

Matrix model simulations were run for 25 y, mimicking conditions at one of the locations currently being considered for future stocking. This location is an isolated small island with approximately 20 ha of suitable rocky reef kelp-forest habitat within the preferred depth range of white abalone. No adult white abalone have been observed in the vicinity for over a decade, so that stocked individuals at this location would comprise the entire population. As such, the growth of the stocked population is not expected to be aided by any reproductive contributions from outside populations (closed-population assumption). All stocked individuals were represented by the smallest size class at the time of stocking (25–60 mm). Although stocking will likely result in initial tight clusters of abalone, the model assumes that stocked individuals will migrate out of the immediate area to inhabit all available habitats at the site within 1 y (one time-step of the model). This assumption allows calculating the density of reproductive individuals in the population in 1 y as the total number of individuals in the largest five size classes (multiplied by two, to account for an equal number of males) divided by the total area of the stocking site.

The matrix model was used to investigate three questions for stocking planning: (1) how many years should monitoring occur to determine if the stocking densities were effective at producing

positive population growth, (2) what is the minimum stocking density that should be targeted that would result in a positive long-term growth rate ($\lambda > 1.0$) in the model population, and (3) given the potential limitations of juvenile production in captivity, what would be the effect of conducting multiple smaller stocking events over many years rather than one large effort? To assess poststocking monitoring needs, the shapes of the recovery curves were examined at different levels of stocking densities to determine the time at which the outcome of the models became apparent. To determine the minimum target stocking density, the model simulations were run by iteratively changing the initial stocking density and examining the 5-y geometric mean of λ after the model break-in period. Finally, to quantify the effect of conducting multiple smaller stocking events, the proportion of population recovery lost after 25 y was calculated for different numbers of stocking events compared with one strong stocking pulse in year 1.

RESULTS

Estimating Wild Population Dynamics

The exponential population model fit to the 2002 to 2014 ROV survey results at Tanner Bank yielded an estimated population growth rate of 0.88/y ($R^2 = 0.5520$; $df = 3$; $AIC = 84.1511$), suggesting a mean decline in abundance of 12% per year (Fig. 1). Because of the small number of surveys during the period ($n = 5$), the model fit produced wide 95% CI ($0.69 < \lambda < 1.12/y$). A linear model fit to the data did not result in a significantly improved fit ($R^2 = 0.4745$; $df = 3$; $AIC = 84.9486$), with a ΔAIC of -0.7975 . Bayesian analysis of the time series suggests a comparable rate of decline ($\lambda = 0.895/y$) and higher process variance (C. Boyd, personal communication) than $\sigma^2 = 0.005$ used in the quasi-extinction risk analysis. The IUCN Red List of Threatened Species directs the reporting of uncertainty in assessments of species considered for listing, but specifies that the risk tolerance of the assessment should be “precautionary and credible” (IUCN 2014). Faced with high uncertainty in the estimated population growth rate for an

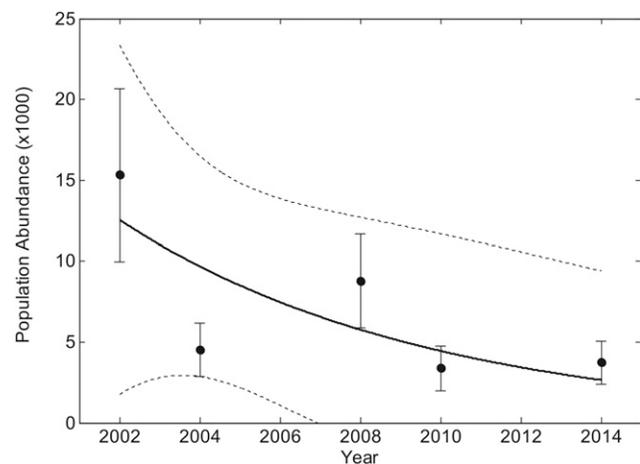


Figure 1. Exponential population model fit (solid line) to 5 years of population abundance estimates (black dots) from ROV surveys at Tanner Banks (data from: NOAA SWFSC). Dashed lines represent 95% CI of the model fit.

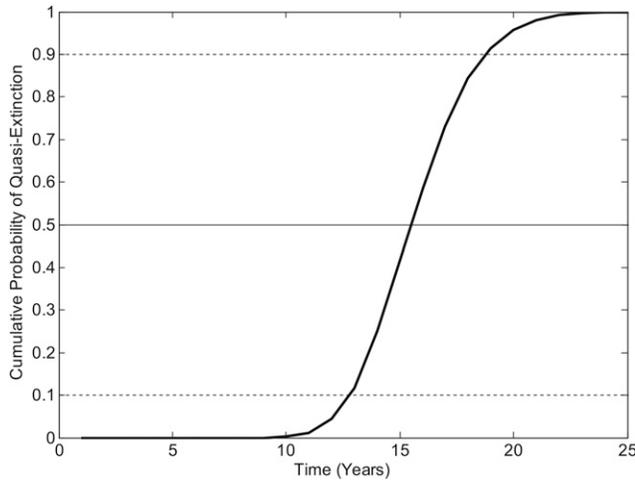


Figure 2. Cumulative probability of reaching quasi-extinction over time (solid line). Dashed and dotted lines are provided as reference lines for 0.1, 0.5, and 0.9 probability levels.

endangered species, the model mean result was adopted to apply to the remaining analyses to balance the risks of overestimating and underestimating the population growth rate.

The most recent surveys at each of the three sites confirm low densities, with all sites averaging fewer than 1 abalone/ha (Stierhoff et al. 2014, unpublished data). In 2014, an estimated 3,745 abalone resided within 1,359 ha of habitat near Tanner Bank (depth-weighted mean density: 0.002 abalone/ha). In 2012, an estimated 569 abalone resided within 892 ha of habitat near San Clemente Island (depth-weighted mean density = 0.62 abalone/ha). Assuming $\lambda = 0.88/y$, the population was estimated to have declined to 439 abalone in 2014. In 2002, an estimated 7,366 abalone resided within 1,138 ha of habitat near Cortes Bank. Assuming $\lambda = 0.88/y$, the population was estimated to have declined to 2,019 abalone in 2014. The quasi-extinction risk model was initialized with an abundance of 6,823 abalone, equaling the sum of these 2014 estimates and 10% more for abalone outside of the three survey sites.

Quasi-Extinction Risk

All randomized simulations of the stochastic population dynamics reached quasi-extinction within 28 y (by 2042) (Fig. 2). The mode of the time to quasi-extinction was 15 y (by 2029). Ninety percent of the simulations reached quasi-extinction with 13–19 y (by 2027–2033).

Matrix Model

The matrix model, including the unadjusted median-size fecundity estimates for each size class, is shown in Table 1. The P_0 value yielding $\lambda = 0.88/y$ was $4.730 \times 10^{-8}/y$ and the value yielding stable population growth was $2.165 \times 10^{-7}/y$. The density-dependent equation for calculating P_0 from estimated fertilization potentials is as follows:

$$P_0(\text{fert}) = 4.73 \times 10^{-8} \left(1 - \frac{\text{fert} - 4.1}{55.9} \right) + 2.165 \times 10^{-7} \left(\frac{\text{fert} - 4.1}{55.9} \right)$$

where “fert” is the density-dependent fertilization potential as calculated above.

The estimated net reproductive rate (R_0) for the white abalone population at Tanner Bank in 2002, based on the model population, was 0.28 abalone per abalone lifetime. The generation time (number of years for the population to increase by R_0) is estimated to be 10 y (Caswell 2001).

Model Simulations

For all of the simulations, the stocked model population exhibited an initial steep decline in abundance due to mortality before reproduction (Fig. 3). Populations experienced a maximum growth rate within 8–9 y poststocking (Fig. 4), resulting in a short-term increasing abundance for populations stocked at densities greater than or equal to $0.15/m^2$. For simulations with insufficient initial stocking densities, abundances slowly declined as stocked individuals grew to larger reproductive sizes. Populations with sufficient initial stocking densities to yield positive long-term growth rates experienced a short-term boost to population growth rates within 8–9 y, followed by a period of lower but slowly increasing growth rates. Based on these results, poststocking population monitoring may not be effective at determining the recovery trajectory for at least 10 y.

A minimum target stocking density was determined based on the model simulations that yielded a mean growth rate more than or equal to $1.0/y$ during years 15–20. This period was chosen because it was less variable than the dynamics of the first 15 y. Although a model population with initial stocking density between 0.14 and 0.22 abalone/ m^2 experienced positive growth rates within the first 10 y, this positive growth was not sustained (Fig. 4). The minimum initial stocking density that resulted in long-term positive growth was 0.23 abalone/ m^2 ($\lambda_{15-20} = 1.00/y$).

TABLE 1.
Population matrix model including fecundity estimates.

Size class (mm)	25–59.9	60–94.9	95–129.9	130–151.9	152–175.9	>175
25–59.9	0.33	$1.81 \times 10^5*$	$8.13 \times 10^5*$	$2.02 \times 10^6*$	$3.66 \times 10^6*$	$6.36 \times 10^6*$
60–94.9	0.44	0.41	0	0	0	0
95–129.9	0	0.36	0.49	0	0	0
130–151.9	0	0	0.28	0.40	0	0
152–175.9	0	0	0	0.37	0.50	0
>175	0	0	0	0	0.27	0.77

* Before scaling by P_0 .

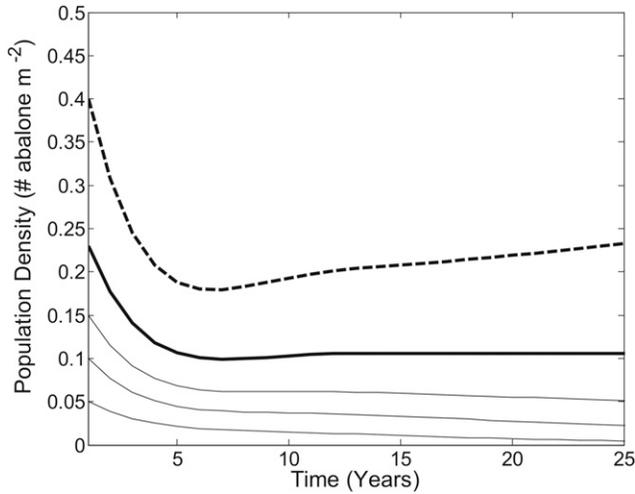


Figure 3. Model simulation results: changes in population density through time with different initial stocking densities ranging from 0.05 to 0.40 abalone/m². Models above the thick black line had positive long-term growth. The dashed black line indicates the model used in further analysis (Fig. 5).

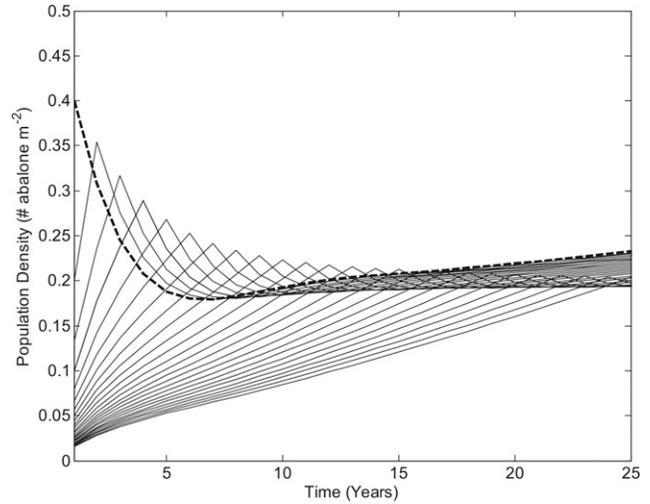


Figure 5. Model simulation results: comparison of the population densities resulting from different numbers of stocking events. Each line represents stocking of the same total number of abalone, but over differing numbers of consecutive years. The dashed line is the result from one pulse of stocking at the beginning of the simulation.

A minimum initial stocking density of 0.40 abalone/m² resulted in $\lambda_{15-20} = 1.01/y$ for the model population. This model simulation exhibiting stronger long-term growth was used to examine the effectiveness of multiple smaller stocking events for establishing a population.

The number of juveniles needed to stock a 20-ha area at 0.40 abalone/m² is 80,000. The simulations with multiple stocking events resulted in decreased population abundances when compared with results from one stocking pulse during year 1 (Fig. 5). For the model with five stocking events of 16,000 juveniles, the population size at year 25 was 5% lower, and a 10% reduction was reached for 14 equal-sized

annual stocking events. This estimated reduction in stocking efficiency is dependent on mortality assumptions of the smallest size classes. As juvenile mortality increases, long-term stocking inefficiency also increases because more of the stock is lost before reproductive contributions to the population dynamics.

DISCUSSION

Population Status Assessment

The white abalone abundance at Tanner Bank is considered the highest-density population in southern California, yet ROV surveys have estimated a 76% reduction in abundance in 12 y (2002 to 2014) at this site. The wild population decline near the rate of natural mortality (0.12/y) supports observations of insignificant reproduction in nearby areas within the last 15 y. The observed decline exceeds the IUCN Red List Criterion C1 for Critically Endangered status, which requires an observed, estimated, or projected decline of more than or equal to 25% in 3 y or one generation (whichever is longer) (IUCN 2014) for populations with fewer than 250 reproductive individuals. The generation time of the Tanner Bank population was estimated to be 10 y, based on the matrix model analysis, which is within the time frame of the observed declines. This estimate of generation time is comparable to the IUCN Red List definition, which uses the average age of current broodstock in the population. Based on the large sizes of white abalone in the population ($\mu_{2014} = 150$ mm; Stierhoff et al. 2014, unpublished data), the average age of the reproductive adults may be greater than 9 y.

Furthermore, the total population abundance in southern California in 2014 was estimated to be 2% of baseline abundances calculated from historic fisheries data during the 1970s (Rogers-Bennett et al. 2002). From the initial ROV surveys (2002 to 2004) at the three primary survey locations, the total estimated population abundances declined by more

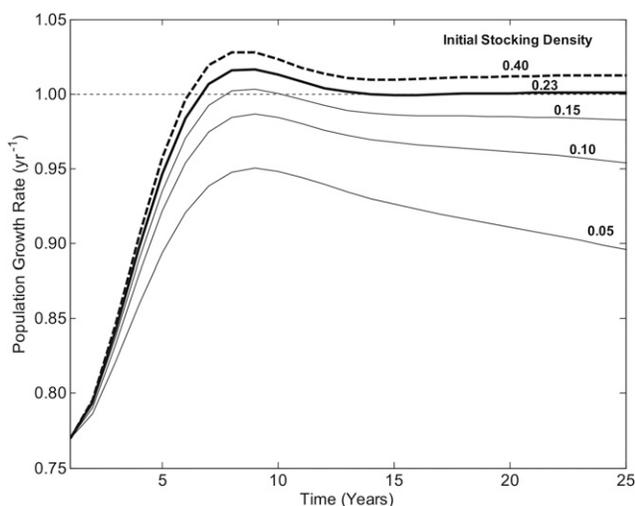


Figure 4. Model simulation results: changes in population growth rate through time with different initial stocking densities ranging from 0.05 to 0.40 abalone/m². Models above the thick black line had positive long-term growth. The dashed black line indicates the model used in further analysis (Fig. 5). The dotted horizontal line is provided as a reference line for stable population growth.

than 93% within a few years of listing on the U.S. Endangered Species List (Butler et al. 2006, Stierhoff et al. 2012). This decline exceeds the IUCN Red List Criterion A2a (population size reduction) for Critically Endangered status based on more than or equal to 80% reduction in abundance within three generations (~ 30 y), where the causes of the reduction may not have ceased.

The result of the stochastic quasi-extinction risk model based on the decline observed at Tanner Bank represents an optimistic outcome. From this analysis, the wild populations may be expected to reach quasi-extinction levels ($<1,000$ abalone in total) within 15 y, by the year 2029. These results suggest that populations may not persist beyond one or two more generations of white abalone. While the IUCN Red List Criterion E (Quantitative Analysis) requires more than or equal to 50% probability of extinction within three generations to qualify for Critically Endangered status, a 100% probability of quasi-extinction was estimated within that time frame. This result underscores the imperative need for rapid restoration actions to reestablish self-sustaining populations in southern California.

Restoration Modeling

The restoration stocking simulation model results provided valuable insight informing juvenile production goals, minimum stocking densities, and expectations for monitoring time frames. The “minimum” stocking density identified from the model population, which led to long-term positive population growth, was 0.23 abalone/m² within the total available habitat within the stocking site. This result is based on a deterministic (non-stochastic) model with optimistic vital rate parameters, and should be considered a low-target stocking density. This result may be used to guide the development of juvenile production goals and increasing production capacity to exceed the minimum target. Currently, juvenile production is an order of magnitude lower than necessary to meet this minimum target (Rogers-Bennett et al. 2016a).

Although the matrix model simulations indicate that one large pulse of stocked juveniles maximizes long-term population abundance, there are many reasons why conducting multiple smaller stocking efforts may be more desirable. Spreading stocking effort across multiple years may increase chances of avoiding stocking only during years with poor conditions (e.g., El Niño). Releasing large numbers of abalone into one small area may also limit natural resource availability (e.g., crevice habitat and food), potentially dampening vital rates and impacting stocking efficiency (Shepherd et al. 2000, Beal & Kraus 2002). Furthermore, the addition of large numbers of abalone to an area may lead to increasing predator populations (e.g., octopus), which would also dampen survival rates of newly stocked individuals. Therefore, annual juvenile production levels that are lower than the total target specified by the model may be acceptable if production can continue for the number of years required to meet the target. Conducting multiple smaller annual stocking events that collectively release the same large number of juveniles may provide a viable solution with limited loss of efficiency. If the multiple stocking approach is used, then efforts should be made to minimize mortality for the smaller size classes to maximize stocking efficiency through time.

Monitoring stocking effectiveness provides essential information on performance measures for meeting the stocking goal of reestablishing a self-sustaining population. Monitoring short-term changes in abundance, however, may not clearly indicate population recovery until 15 y poststocking. Short-term assessments may mistakenly identify early increases in population growth as representing recovery. Furthermore, there may be slight changes in population abundance for many years following an initial drop in abundance after stocking. If the total stocking density is too low, it may be difficult to detect recovery for decades. It is recommended that long-term monitoring programs (>15 y) of stocking locations should be developed that not only report estimates of abundance over many years, but also growth and survival estimates using tag-recapture methods that may be used to improve matrix model parameters. It is also recommended that genetic techniques should be used for local larval production and newly settled individuals detected in the vicinity of the stocking site (Rogers-Bennett et al. 2016b). This information will be vital for quantifying the reproductive dynamics of the stocked population.

Data from monitoring future stocking efforts can inform and improve the population models developed for this work. Experimental stocking including tag-recapture data can improve model parameter estimates and help to inform spatial dynamics of the stocked population so that poststocking dispersal rate may be included in future modeling efforts. Model parameters may also be adjusted to fit the poststocking size-frequency and abundance data obtained through long-term monitoring. Additional point estimates linking λ and density (particularly 1,000–3,000 abalone/ha) would also improve the scaling of P_0 , though these analyses require many years of monitoring the same population. These potential improvements to the matrix model would be useful for fine-tuning the results to fit the dynamics of the stocked population, which may adjust the estimated minimum stocking density target. These improvements would not lead to significant changes in the conclusions of the model, specifically that large numbers of stocked individuals will be needed and that recovery from overfishing will take decades.

ACKNOWLEDGMENTS

This work is the result of a collaborative project between the California Department of Fish and Wildlife (CDFW), the National Oceanic and Atmospheric Administration, the University of California Davis. We thank the White Abalone Recovery Consortium for all their efforts large and small to conduct and support the restoration of the endangered white abalone in California. This work was funded in part by a federal NOAA Section 6 grant NA10NMF4720024 to CDFW and its partner facilities and in part by NOAA Protected Resources awards: NFFR5300-9-11649, NA12NMF4690236, and NA14NMF4550168 to G. Cherr. This work was also supported by the CDFW Marine Region. None of this work would have been possible without the support from the UC Davis Bodega Marine Lab and UC Davis that holds the federal white abalone permit no. 14344. We thank C. Boyd, C. Mundy, and two anonymous reviewers whose feedback improved the manuscript, with a special thanks to Dr. C. Shuman and T. Barnes for support through CDFW Marine Region. This publication is a contribution of the Bodega Marine Laboratory, University of California, Davis, CA.

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