ELASTICITY ANALYSES OF SIZE-BASED RED AND WHITE ABALONE MATRIX MODELS: MANAGEMENT AND CONSERVATION

Laura Rogers-Bennett[1,3] and Robert T. Leaf[2]

[1]*California Department of Fish and Game, University of California-Davis, Bodega Marine Laboratory, 2099 Westside Rd., Bodega Bay, California 94923-0247 USA*
[2]*Moss Landing Marine Laboratories, California State University, Moss Landing, California 95039-9647 USA*

Abstract. Prospective elasticity analyses have been used to aid in the management of fished species and the conservation of endangered species. Elasticities were examined for deterministic size-based matrix models of red abalone, *Haliotis rufescens*, and white abalone, *H. sorenseni*, to evaluate which size classes influenced population growth (λ) the most. In the red abalone matrix, growth transitions were determined from a tag recapture study and grouped into nine size classes. In the white abalone matrix, abalone growth was determined from a laboratory study and grouped into five size classes. Survivorship was estimated from tag recapture data for red abalone using a Jolly-Seber model with size as a covariate and used for both red and white abalone. Reproduction estimates for both models used averages of the number of mature eggs produced by female red and white abalone in each size class from four-year reproduction studies. Population growth rate (λ) was set to 1.0, and the first-year survival (larval survival through to the first size class) was estimated by iteration. Survival elasticities were higher than fecundity elasticities in both the red and white matrix models. The sizes classes with the greatest survival elasticities, and therefore the most influence on population growth in the model, were the sublegal red abalone (150–178 mm) and the largest white abalone size class (140–175 mm). For red abalone, the existing minimum legal size (178 mm) protects the size class the model suggests is critical to population growth. Implementation of education programs for novice divers coupled with renewed enforcement may serve to minimize incidental mortality of the critical size class. For white abalone, conservation efforts directed at restoring adults may have more of an impact on population growth than efforts focusing on juveniles. Our work is an example of how prospective elasticity analyses of size-structured matrix models can be used to quantitatively evaluate research priorities, fishery management strategies, and conservation options.

Key words: deterministic matrix models; endangered species; growth transitions; marine conservation; population growth; prospective elasticity analysis; sustainability.

INTRODUCTION

Matrix models have been shown to be powerful tools for addressing management and conservation issues (Crouse et al. 1987, Lande 1988, Heppell et al. 1994). Quantitative vital rate information can be incorporated into matrix models to explore the consequences of various management and conservation options (Caswell et al. 1998, Ebert 1999, Morris et al. 1999). Perturbations of these models, by simulation, can systematically compare which rates influence the intrinsic rate of population growth the most (Benton and Grant 1999 and references therein). This type of "forward looking" or prospective sensitivity analysis (Caswell 2000) has been used with far-reaching consequences. Perturbation analyses of loggerhead sea turtle matrix models lead to a redirection of conservation efforts away from "headstarting" hatchlings (enhancing the survival of

eggs in nests) toward the use of turtle exclusion devices in fishing nets (reducing adult mortality) (Crouse et al. 1987, Crowder et al. 1994, Heppell and Crowder 1996).

Abalone are long-lived, slow-growing species with a poor track record for fisheries sustainability worldwide (Campbell 2000, Karpov et al. 2000, Shepherd et al. 2001). Organisms with these life history traits may fit into a suite of species that respond to perturbations in a predictable way with low fertility elasticities and high juvenile or adult survival elasticities (Heppell et al. 2000, Sæther and Bakke 2000, Gerber and Heppell 2004). To help guide management and conservation of abalone populations it is important to examine the relative importance of juvenile and adult elasticites. What we learn about the population dynamics of abalone may aid us in working with lesser known long-lived marine invertebrates which are being fished at an increasing pace in California (Rogers-Bennett 2001).

Elasticity analysis can be used to support decisions regarding the management of red abalone, *Haliotis rufescens* (see Plate 1), and the conservation of the en-

PLATE 1.   Large red abalone are susceptible to multiple sources of mortality, including fishing, predation, disease, wave dislodgement, and boring clams and sponges that compromise the integrity of the shell. Photo credit: L. Rogers-Bennett.

dangered white abalone, *H. sorenseni*, in California. The recreational red abalone fishery in northern California is now the only abalone fishery open in the state. Recreational and commercial abalone fisheries in southern California have been closed since 1997 (California Senate Bill 463). Failure to manage individual species masked serial depletion of the species complex by the fishery (Dugan and Davis 1993, Karpov et al. 2000). Predatory sea otters also expanded their range south toward Point Conception (Wendell 1994, Vogel 2000). In addition, the warm water regime in the 1980s and 1990s may have been unfavorable for red abalone productivity (Hobday and Tegner 2002) as confirmed by the lack of juveniles signaling recruitment collapse in southern California (Rogers-Bennett et al. 2004*a*). In contrast, estimates of landings from the recreational free-diving fishery for red abalone in the north appear to be stable (California Department of Fish and Game, *unpublished data*). Concerns however, about the continued sustainability of the northern red abalone fishery precipitated reductions in the daily and yearly bag limits in 2001 leading the California Department of Fish and Game Commission to decrease the total allowable catch by an estimated 20%. To date, there have been few quantitative evaluations of the efficacy of the current size limits and the other management strategies in the fishery (but see Tegner et al. 1989). Assessments

have been hindered by a lack of vital rate information for red abalone in northern California.

Quantitative analyses of white abalone populations are also lacking as little is known about their vital rates (Hobday et al. 2001). White abalone are a deep-water species and today only remnant populations exist at depths below 40 m on remote offshore banks in southern California (Lafferty et al. 2004; J. Butler, *personal communication*). White abalone were highly prized by the fishery and, in just five years (1971–1976), populations were reduced to <10% of their prefishing biomass (Hobday et al. 2001, Rogers-Bennett et al. 2002). The absence of evidence for successful recruitment in areas which once produced >80% of the total fishery landings has increased the concern for the recovery of white abalone (National Marine Fisheries Service, White Abalone Recovery Team, *personal communication*). Quantitative evaluations are needed to aid the White Abalone Recovery Team (NOAA Fisheries) in drafting a recovery plan that addresses restoration options and potential threats (M. Neuman, *personal communication*).

We determined vital rate information for red and white abalone to construct deterministic size-based matrix models (Lefkovitch 1965) for elasticity analyses (Caswell 1978, de Kroon et al. 1986). We determined which size classes of abalone had the greatest influence
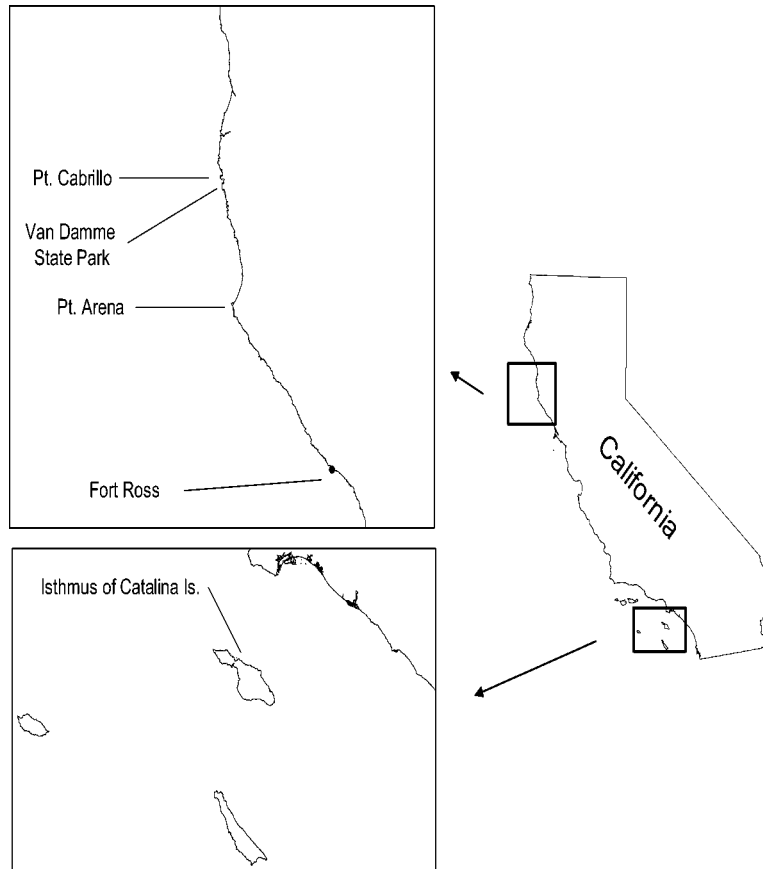
FIG. 1. Map showing red abalone tag and recapture sites in northern California and white abalone reproduction site in southern California, USA.

on the intrinsic rate of population increase in the models. For red abalone in northern California, we used demographic data from a large tag recapture study to generate growth transition probabilities and survival probabilities as well as a four-year reproduction study quantifying egg abundance to estimate size-specific fecundities. For white abalone, we used growth data from a one-year laboratory growth experiment in conjunction with estimates of survival from a congener and a four-year reproduction study (Tutschulte 1976). Since survival in the plankton through to the first year is unknown for abalone (and many other invertebrates), we set population growth to 1.0 (dominant eigenvalue of the matrix) and solved for first-year survival by iteration (Vaughn and Saila 1976). For red abalone, we determined if the size classes that have the most influence (greatest elasticities) on population growth rate in the model are being protected by the current fishery management regulations. For white abalone, we determined which of the size classes have the most influence on population growth in the model to examine restoration options and assess population threats. Matrix perturbations simulating management and conservation impacts were used to examine how combinations of

changes in vital rates changed population growth (Morris and Doak 2003).

METHODS

Red abalone mark and recapture field study

Red abalone were tagged at five sites in northern California (Fig. 1). This tagging program was initiated in 1971 and recaptures were conducted at approximately annual frequencies. Red abalone were collected by divers, brought to the boat, measured for maximum shell length (SL), and tagged with individually labeled stainless steel disc tags. Tags were attached with stainless wires inserted into the first two open respiratory pores and then twist tied. Red abalone tagged at the five sites ranged in size from 50 to 222 mm SL (Table 1). Growth data from a total of 845 abalone recaptured at one-year intervals plus or minus 30 days (335 to 395 days) were used in our analysis of growth transition rates (S. Shultz and J. DeMartini, *unpublished data*). Growth was normalized for all individuals to one year by determining the daily growth rate and then standardizing to 365 days.

Growth information for abalone <100 mm shell length was supplemented using data from this study

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TABLE 1. Tag recapture information for red abalone in northern California.

Site	No. tagged	No. recaptured	No. years sampled	Size range at first tagging (mm)
North Pt. Cabrillo	837	137	7	42–227
South Pt. Cabrillo	1774	58	3	42–224
Van Damme	704	92	3	48–219
Pt. Arena	1227	252	3	71–218
Fort Ross	1415	306	3	50–185
Stocking	50 000	42	1	5–30
Total	55 957	887		

and another tag and recapture study. Since tagged abalone in the 50–100 mm size class were rare, we relaxed the one-year criterion and used abalone that had been at large for at least six months and then normalized to one year growth (using the monthly growth average and then multiplying by 12 months). We used 27 abalone, ranging in size at the time of tagging from 53 to 92 mm, from South Cabrillo Cove.

Growth information for juvenile abalone (<50 mm) was used from a second tag recapture study. Stocking tagged juveniles took place in October 1995 at five sites in northern California and juveniles were recaptured one year later (Fig. 1). Growth data were obtained from red abalone ranging in size at the time of stocking from 5 to 29 mm (Rogers-Bennett and Pearse 1998). Positive identification of recaptured juveniles one year later was made for 42 abalone (Table 1). The pale blue/green coloration allowed for the measurement of shell length at the time of stocking (initial) and the difference between the initial and the final shell length (blue plus red shell) gave a measure of growth during the year.

Growth transitions

A matrix of growth transitions was constructed from the probabilities of individuals staying the same size or changing size classes using the observed changes in lengths of tagged abalone recaptured after one year (Caswell 2001). The results yielded a matrix in which diagonal elements represent the probability of staying within a size class after one year and the elements in the subdiagonal (below the diagonal elements) are the probability of growing into (transferring to) the larger size class. Elements below this represent the probability of skipping a size class.

Annual survival probability

Survivorship was estimated using tag recapture data from the North Point Cabrillo Cove site, a no-fishing reserve. At this site, 837 abalone were tagged (Table 1) and 746 were recaptured at approximately annual intervals (339 to 398 days) from March 1971 to April 1977. Annual tagging and recapture surveys were restricted to periods ranging from 2 to 38 days each year during spring. Tagged red abalone recaptured between

sampling periods were excluded from analysis. Tag recapture histories were converted to a vector format of tagged (ones) and untagged (zeros) following Lebreton et al. (1992).

We analyzed the recapture history data at North Point Cabrillo Cove using the ''recaptures-only'' protocol in program MARK (White and Burnham 1999). Four candidate models were specified for analysis in which survival (Φ) and recapture probability (p) were either constant (.) or time dependent (t). Maximum shell length at tagging was incorporated as a covariate to the probability of annual survivorship in each model using a ''logit link'' function (White and Burnham 1999). Parametric resampling was used to assess global model dispersion, $\hat{c}$, of the time dependent model Φ_t, p_t. If the global model deviance/mean of resampled model deviance was >1, then $\hat{c}$ was adjusted for all models with this new estimate. We used quasi-likelihood criterion, $QAIC_c$ (Burnham and Anderson 1998) to rank candidate models.

Fecundity

Red abalone fecundity was determined from animals collected at Van Damme State Park and the Point Arena Abalone Derby in northern California. Abalone were collected at Van Damme over four years from April 2000 to August 2003 and ranged in size from 29 to 224 mm in shell length ($N = 393$). Large abalone were collected at the Derby in August 2000 and 2001 ranging in size from 212 to 260 mm ($N = 32$). Of these 425 animals, 154 were fecund females over 100 mm, the size at maturity (Rogers-Bennett et al. 2004b). Abalone were detached from the shell, weighed, and dissected to estimate the gonad volume and obtain gonad tissue samples. Gonad volumes were estimated assuming that the gonad was cone wrapped around an inner cone of digestive gland. The volume of gonad was equal to the gonad/digestive gland complex minus the digestive gland cone (as per Tutschulte [1976]).

To estimate the number of mature eggs in each ovary, slide preparations were used to quantify egg number (see the methods in Rogers-Bennett et al. [2004b]). The number of eggs enumerated on each slide was then multiplied by the width of the tissue section and the ovary volume to obtain the number of eggs spawned in one year for each female. Fecundity was defined as the number of mature eggs present in the ovary (f_x). Mature oocytes averaged 170–190 μm in diameter, were circular in shape, and detached from the trabeculae ready to be spawned.

The relationship between female size and mature egg number was modeled using a three-parameter Gaussian curve (Rogers-Bennett et al. 2004b). This curve was used to estimate the number of mature eggs produced per year by a female in the middle of each size category in the matrix model. The relationship between shell length (X) and egg number (Y) was modeled by the curve in the following form:

$$Y = Ae^{-(X-\mu)^2/2\sigma^2}$$

where A is defined as the maximum productivity (A = 2 850 000 eggs per female, SE = 1 079 000 eggs), μ is defined as the size at maximum productivity (μ = 215 mm), and σ (the standard deviation) describes the width of the distribution of maximum productivity vs. size (σ = 38 mm). This model has r^2 = 0.354.

Growth transition matrix

Size categories were selected using biologically meaningful sizes while taking into account both sampling and distribution error (Vandermeer 1978, Moloney 1986, Caswell 2001). The boundaries of the first size class were set such that they encompassed growth in the first year from 0.1 mm, the size at settlement, to the size at one year, approximately 25 mm. We use a break at 100 mm, as this is the size at first reproduction (Rogers-Bennett et al. 2004b). We then set 25 mm as the size class interval, but deviated slightly at the larger sizes adjusting the size category from 175 to 178 mm to allow for a break at the minimum legal size for red abalone. The sample sizes of the growth data would not support smaller size class widths such as 20 mm since no animals remained in the second and third size classes and no animals remained or advanced in the largest size class.

Sampling errors arise when too few animals are sampled within a size class. Distribution errors arise when the model treats all animals within a size class equally, if in fact, some are at the start of the size class (left boundary) and some are closer to the end (right boundary) of the size class at the beginning of the year. To minimize distribution errors, size classes should be as narrow as allowed by sampling error. We used the Maloney-Vandermeer algorithm (Caswell 2001) to contribute more information to our size class determinations in an effort to minimize both the sampling and the distribution errors. The results from these procedures did little to influence our size class interval decision since sampling error and distribution errors were minimized at a very large size such that the matrix would have had only a few size classes. Furthermore, the sampling and distribution errors reflect only one of the vital rates growth and did little to account for potential errors in the other two vital rates (Caswell 2001).

Size-based red abalone matrix

A deterministic size-based projection matrix was constructed as vital rates are best described by size in abalone rather than age or stage. We assume a pre-breeding, birth-pulse population. First, growth transition rates were determined using tag recapture data of abalone growing for one year. Growth transition probabilities were then multiplied by annual survivorship. We incorporated size as a covariate (except survival from the egg to one year) with annual survivorship. Next, mean fecundities for females in the center of each

size category were determined using the Gaussian growth curve. The number of mature eggs was then divided by two to represent the number of female offspring produced by a female in a year (F_x; assuming that half of the offspring are female). In the pre-breeding census, F_x was multiplied by the survival of eggs during the first year (P_0). The first row and column of the size transition matrix representing growth and survival, P_0, of individuals 0.1 to size 25 mm is then dropped from the matrix.

First-year survivals P_0 (representing fertilization success, survival in the larval stage, and early post-settlement survival during the first year) are difficult parameters to quantify. No direct measures of P_0 are available from this study or the literature. Therefore, P_0 was solved for by iteration setting the "dominant eigenvalue" of the matrix, also known as the population growth rate, λ to 1.0 which assumes the population is at a stable equilibrium (neither growing nor decreasing) (Vaughan and Saila 1976).

White abalone matrix

A deterministic size-based matrix model was constructed for white abalone assuming a pre-breeding, birth-pulse population. Growth transitions were determined from a small sample (N = 21) of white abalone grown in the laboratory for one year (Tutschulte 1976). Abalone remaining, transitioning (growing) into the next class, or skipping a size class were tabulated. Size categories in the matrix were selected to minimize both sampling and distribution error. In this case, we use a size class interval width of 35 mm since the sparse growth data would not support smaller size class intervals.

Fecundity estimates were derived from a four-year study of wild white abalone in which the number of eggs per female per year was estimated by determining the gonad index and then multiplying the total number of eggs in each female. The mean number of eggs per gram of female (N = 197) body weight was 9052 eggs (SE = 1603 eggs) (Tutschulte 1976). The relationship between shell length and body size was determined for a large sample of white abalone (N = 99) (Tutschulte 1976):

$$\ln(\text{body weight}) = [4.0243 \times \ln(\text{shell length})]$$
$$- 14.5069.$$

This relationship was used to determine the number of eggs per female within each size class. The number of eggs destined to be females produced by the mean size female for each size class was used in the matrix model.

There are no survival estimates of white abalone from the literature (Hobday and Tegner 2000), however survival estimates exist for red and pink abalone congeners. We based the white abalone survival estimates on the logit-link using size as a covariate in the model of red abalone. In addition, we tested the white abalone

matrix model's behavior using the survival estimate for pink abalone of $\Phi = 0.7$ for all size classes (Tutshulte 1976).

Sensitivity, elasticity, and parameter uncertainty

Sensitivity is defined as the partial derivative of a population's finite growth rate (λ) to changes in matrix elements (a_{ij}) (Caswell 1978, 2000):

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle w, v \rangle}$$

where v_i and w_j are the ith and jth elements in the stage (or size) specific reproductive value (**v**) and the stable age (stage) distribution, (SAD) (**w**) vectors, respectively, and where $\langle w, v \rangle$ is the scalar of w multiplied by v.

The damping ratio (ρ) is proportional to the rate of convergence to a stable size structure and is the ratio between the dominant real eigenvalue and the modulus of the largest subdominant eigenvalue (Caswell 1986, Ebert 1999):

$$\rho = \frac{\lambda_1}{|\lambda_2|}.$$

Rapid convergence is seen with larger values of ρ, while a value equal to 1.0 indicates no convergence.

Elasticity is defined as the sensitivity scaled to take into account the magnitude of both λ and the matrix element and is frequently used instead of sensitivity since reproduction and growth transitions are measured at different scales:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial\lambda}{\partial a_{ij}}.$$

Sensitivities and elasticities for the red and white abalone projection matrixes were calculated using PopTools (*available online*).[4] The elasticity values of fecundity and first-year survival ($f_x \times P_0$) were summed with survivorship within a size class and growth and survivorship in subsequent size classes were determined. The elasticities of all elements in a matrix must sum to 1.0 (de Kroon et al. 1986).

To examine how variation in vital rate estimates contributed to changes in the value of elasticities, we performed matrix simulations using the minimum and maximum fecundity and survival vital rate estimates (Mills et al. 1999, Hunter et al. 2000). In the red abalone matrix, we varied fecundity and survival ± the standard error of the estimates while growth transitions were varied by 5% (either 5% more transitioning into the next size class [maximum] or 5% more remaining in a size class [minimum]).

Red abalone matrix perturbations

To examine the theoretical impacts of a number of factors on the population dynamics of red abalone in

[4] ⟨http://www.cse.csiro.au/poptools/⟩

the model, vital rates in the matrix were increased or decreased mimicking different potential biological, fishery, and environmental scenarios. Changes in the population growth rate resulting from the new deterministic matrix were examined. We simulated the impacts of senescence of the largest females by eliminating the reproductive contribution of the >200 mm size class abalone. To mimic the impact of fishing in the model, the survival rate of legal size (>178 mm) red abalone was decreased by 50% simulating fishing removals. The impact of incidental fishing mortality in combination with legal fishing was examined by decreasing the survival of sublegal abalone (150–178 mm) by 50%, simulating fishing mortality due to the mortal wounding of sublegal abalone. We created a matrix mimicking conditions during a warm water regime in which we (1) decreased fecundity by 1000 times, (2) reduced survival by 50%, and (3) removed jumps in growth and skipping a size class (in the sub-subdiagonal). Finally, we examined the potential impact of successful settlement events on the relative importance (elasticity) by increasing the survival of the smallest size class by 50% and increasing the reproductive output of all mature size classes 10 times.

White abalone matrix perturbations

Matrix manipulations altering vital rates were conducted to assess the potential effects of (1) proposed recovery actions and (2) potential threats faced by the white abalone population in the wild. The elasticity values of the resulting deterministic matrix were examined. The first set of matrix manipulations were designed to examine the elasticities associated with enhancing wild white abalone populations by stocking abalone of different sizes. The second set of matrix manipulations was to examine the potential impacts of threats to the population; either current or future threats.

To simulate restoration options for white abalone, the survival of each of the size classes was increased by 20% and the resulting change in population growth was examined. Threats were then assessed by manipulating the vital rates to mimic current or future threats. Poaching, sea otter predation, and disease would all likely result in decreased survival. Poaching was simulated by decreasing survival of the largest size class by 50%, sea otter predation by decreasing survival of the three largest size classes 50%, and disease by decreasing survival of all the size classes 50%.

RESULTS

Red abalone matrix construction

A size-based matrix model with nine size classes of 25 mm intervals was constructed for red abalone. Growth transitions based on tag recapture data were determined for red abalone following growth over one year (Table 2). In some cases, at the largest size classes,

TABLE 2. Mean transition matrices for (A) red and (B) white abalone, based on shell length (SL).

A) Red abalone

Size class (SL, mm)	Transition size class (SL, mm)							
	25–50	50.1–75	75.1–100	100.1–125	125.1–150	150.1–178	178.1–200	>200.1
25–50	0.191	0.000	0.000	0.800	3.790	12.33	24.02	30.33
50.1–75	0.191	0.045	0.000	0.000	0.000	0.000	0.000	0.000
75.1–100	0.000	0.360	0.148	0.000	0.000	0.000	0.000	0.000
100.1–125	0.000	0.045	0.342	0.180	0.000	0.000	0.000	0.000
125.1–150	0.000	0.000	0.037	0.405	0.321	0.000	0.000	0.000
150.1–178	0.000	0.000	0.000	0.013	0.343	0.670	0.048	0.000
178.1–200	0.000	0.000	0.000	0.000	0.000	0.060	0.726	0.010
>200.1	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.735

B) White abalone

Size class (SL, mm)	Transition size class (SL, mm)			
	35–70	70.1–105	105.1–140	140.1–175
35–70	0.071	0.252	0.874	2.298
70.1–105	0.354	0.226	0.000	0.000
105.1–140	0.000	0.301	0.000	0.000
140.1–175	0.000	0.000	0.626	0.717

the data suggest some backward growth transitions for 6% and 12% of the two largest size classes, respectively. Growth transitions were multiplied by survival estimates.

Survival probabilities were determined using the logit-link covariate protocol in Program MARK (White and Burnham 1999). We assumed that annual survivorship was constant during the study (Φ). The probability of recapture varied for each census period (p_t). We used initial size at first tagging as a covariate. Maximum likelihood estimates of the mean and 95% confidence intervals of annual survivorship for each size class were determined based on logit-link parameters (slope = 0.453 ± 0.078) and (intercept = 0.598 ± 0.089) (White and Burnham 1999).

A Gaussian function was used to describe the number of eggs per female abalone of a given size. Reproduction increased with increasing abalone size until the maximum shell length of 215 mm with 2.85×10^6 eggs, after which the number of eggs began to decline with increasing shell length. Reproduction estimates were calculated as the number of eggs produced by the average size female in the size class.

The ''dominant eigenvalue'' was then set to 1.0 and P_0, was calculated by iteration. Population growth rate $\lambda = 1.0008$ was set, and after iteration P_0 was equal to 2.13×10^{-5}.

The stable stage distribution ''right eigenvector'' for the red abalone matrix is dominated by the small size classes and decreases with decreasing size while the reproductive value ''left eigenvector'' suggests that the larger sizes have the most reproductive value with the >200 mm size class having the highest reproductive value (40%).

The damping ratio (ρ) for red abalone is 1.0008/0.731 = 1.369 with the subdominant root in the denominator (imaginary root of 0). It will take t number of years for the λ_1 to have 1000 times the influence on

population growth as λ_2: $t = \ln(1000)/\ln(\rho) = 6.9078/0.3141 = 2.19$ yr. Note that there are no complex roots so there is no period of oscillation.

Red abalone matrix: elasticity analysis

The proportional elasticity of the red abalone matrix suggests that the matrix element composed of vital rates of remaining in and surviving in the seventh size class (150–178 mm) had the largest elasticity (0.254) and therefore the most influence on population growth rate λ of the model (Fig. 2A). Survival made up 89% of the elasticity value while reproduction comprised 11%. In general, elasticities for survival (p_x) were much greater than for reproduction (f_x) (Fig. 2A). Eliminating the backward growth transitions did not alter the relative ranking of size class elasticities and their influence on λ

Simulations changing vital rates from their mean to the maximum and minimum values of reproduction, survival and growth did not change the relative importance of the seventh size class on population growth in the model (Fig. 3).

Red abalone matrix perturbations

Manipulations of survival rates had the most impact on population growth. Large changes in fecundities did little to influence population growth. Similarly, changes in growth including the elimination of jumps in size classes (the fastest growers) did not dramatically alter the population growth rate (Table 3). Eliminating the reproductive output of the largest size class, mimicking reproductive senescence, resulted in little change in population growth relative to the base model. The scenario mimicking a warm regime substantially decreased population growth relative to the base model.

Including fishing in the matrix model decreased the population growth rate which when combined with incidental fishing related mortality of sublegal abalone
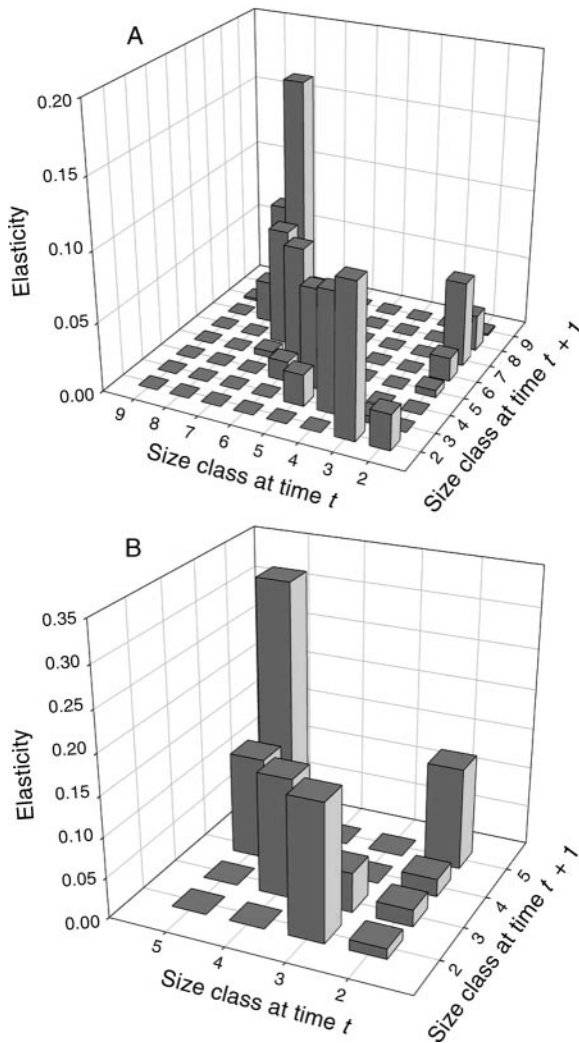
FIG. 2. Elasticity values for abalone matrix elements. (A) Red abalone and (B) white abalone fecundity (f_x) elasticity values are shown in the first row for size class 1 at time t. Survival (p_x) elasticity values for red abalone size classes 2–9 and for white abalone in size classes 2–5 are in the remaining rows.

reduced the population growth rate even further. The last scenario, a recruitment boom, resulted in a large increase in population growth rate mostly attributable to the 10-fold increase in reproduction (Table 3).

White abalone matrix: elasticity analysis

A five size class matrix model for white abalone was constructed with size class intervals of 35 mm. This size class interval minimized sampling error since the white abalone growth data could not support smaller size classes (e.g., widths of 30 or 20 mm). Distribution error was less in the 35 mm size class matrix as compared with a matrix using 40 mm size class intervals. Changes in the widths of the size class intervals had little influence on elasticity values and did not alter the

relative rankings of their importance. In each case, the largest size class had the largest elasticity value. Similarly, the addition of artificial data points in the growth data to supplement size classes with little data, thereby artificially improving the distribution error (e.g., adding 2 to remain in the 105–140 mm size class) also did little to influence elasticity values and the final rankings.

Transition probabilities reflected relatively fast growth into the next size classes with few small individuals remaining in the same size class, as has been observed with white abalone growing in aquaculture facilities (Tutschulte 1976, McCormick and Brogan 2003). Survival estimates used in the final matrix taken from red abalone increased with increasing abalone size. Changes in survival estimates did not appear to influence elasticities values since a number of other potential survival rates (including $\Phi = 0.7$ for all size classes taken from estimates for pink abalone congeners; Tutschulte 1976, Shepherd and Breen 1992) yielded comparable elasticity rankings. We used reproduction estimates based on a large sample of fecund females taken over a four-year period. The population growth rate was then set to $\lambda = 1.0007$, and P_0, was calculated by iteration to be 1.35×10^{-6}.

The stable stage distribution of the white abalone matrix was dominated by the largest size class (52%). The size frequency distributions of white abalone observed on the offshore banks today lacks the small and intermediate size classes (Behrens and Lafferty 2005). The largest size class has the greatest reproductive value (46%).

The damping ratio (ρ) for the white abalone matrix model is $1.0007/0.50046 = 1.999$ with the modulus of the complex subdominant root in the denominator. It will take t number of years for the λ_1 to have 1000 times the influence on population growth as λ_2: $t = \ln(1000)/\ln(\rho) = 6.9078/0.693 = 9.97$ yr. The complex root of the subdominant eigenvalue suggests that as the population converges on the stable size distribution it may oscillate.

The proportional elasticity of the red abalone matrix suggests that the matrix element composed of vital rates remaining in and surviving the fifth and largest size class (140–175 mm) had the largest elasticity (0.32) and therefore the most influence of population growth rate λ (Fig. 2B). Elasticities for survival (p_x) were much greater than for reproduction (f_x), as was the case with the red abalone matrix (Fig. 2B). Reproduction had very little influence on population growth λ such that the size class with the largest reproductive elasticity (140–175 mm size class) had one-third the survival elasticity.

We did not have enough data to explore the impacts of maximum and minimum survival and growth vital rate values on elasticities for the endangered white abalone. Reproduction maximums of 10 120 eggs and minimums of 7170 eggs per gram of female body
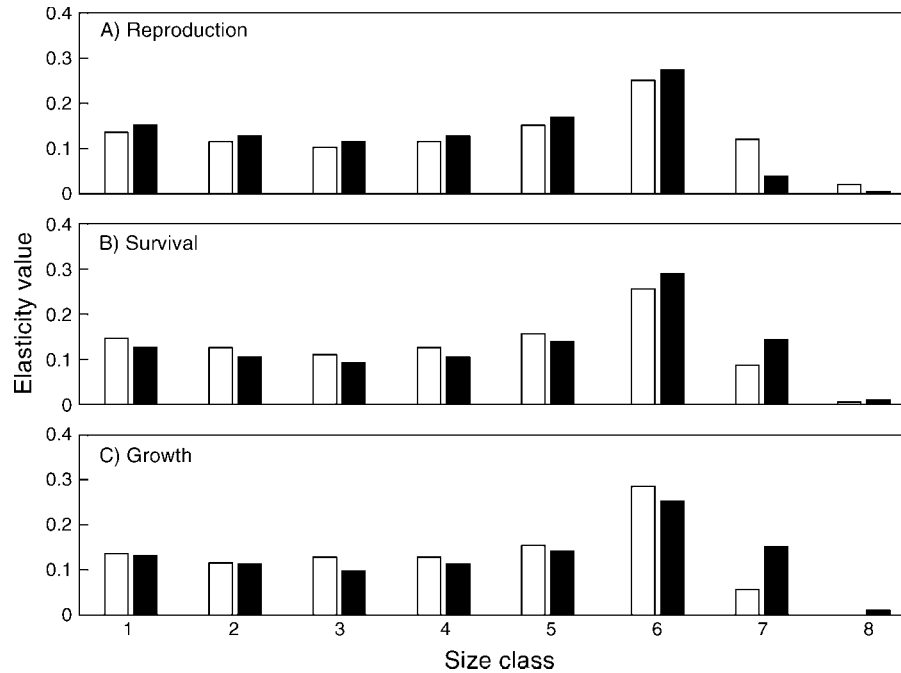
FIG. 3. Elasticity values of the mean vital rates for red abalone (open bars) shown along with bars indicating elasticities using minimum and maximum vital rate estimates (black bars): (A) elasticity values of minimum and maximum number of eggs produced per female in each size class, (B) elasticity values of minimum (mean − SE) and maximum (mean + SE) survival estimates, and (C) elasticity values of minimum and maximum growth frequencies. Minimum growth values had 5% more abalone staying in the same size class while the maximum growth increased the number of abalone growing into the next size class by 5% as compared with the mean.

weight (Tutschulte 1976) did little to change the elasticity values.

White abalone matrix perturbations

Matrix manipulations suggest that restoration measures focused on stocking as represented by increasing

TABLE 3. Perturbations of vital rates were conducted simulating potential effects of management options, fishing scenarios, and environmental effects for (A) red abalone and (B) white abalone and the resulting change in population growth rate (λ) from 1.0 (population at equilibrium).

Matrix perturbation	Change from $\lambda = 1$
Red abalone	
Reproductive senescence	−0.0012
Fishing	−0.0216
Fishing + bar cuts mortality	−0.1014
Warm regime	−0.2647
Settlement boom	0.4635
White abalone	
Stocking by SL†	
35–70 mm	0.0341
70–105 mm	0.0386
105–140 mm	0.0238
140–175 mm	0.0719
Poaching mortality	−0.1214
Sea otter predation	−0.1994
Disease	−0.3272

† Shell length, a measure of size class.

survival 20% in the matrix model increased population growth compared with the base model (Table 3). Increasing survival of the largest size class 140–175mm increased population growth the most (Table 3) while increases in the 35–70 mm, 70–105 mm and 105–140 mm size classes had less of a positive impact on population growth. Matrix manipulations simulating threats to white abalone decreased population growth the more size classes were impacted by decreases in survival. The largest decline in population growth was associated with disease which we simulated by decreasing survival in all of the size classes (Table 3).

DISCUSSION

Management implications for red abalone

Elasticity analysis of the red abalone matrix model revealed that survival of adults (150–178 mm) had the greatest elasticity value while fecundity elasticities were low (Fig. 2A). Adult survival in other long-lived marine organisms such as loggerhead sea turtles (Crouse et al. 1987) and gorgonians (Gotelli 1991) also had the most influence on population growth.

These results support the hypothesis of a relationship between life history strategy and elasticity values (Heppell et al. 2000, Cortes 2002). In a similar analysis of red sea urchins (Ebert 1998), the largest rather than the mid-size adult class had the most influence on population growth rates. In that case, the sea urchin matrix

results suggested that the commercial fishery could benefit from an upper limit, in addition to the existing lower size limit (Ebert 1998).

Vital rates for abalone are known to be plastic in both space and time. To address the robustness of our matrix model to variations in vital rates, we used the high, mean, and low values of growth, survival, and reproduction estimates (Mills et al. 1999). These simulations did not affect the ranking of the elasticity values suggesting that our model is robust to changes in vital rates over the range of values examined (Fig. 3). Large changes in growth, not seen in our data, such as increasing growth in the first few size classes, did yield higher elasticity values for the larger size class (178–200 mm), while high rates of retention 85% (slow growth) in the juvenile size classes increased the importance of the juveniles.

It is known that many marine invertebrates including abalone may vary with respect to life history parameters even over small spatial scales. While our growth data come from a number of sites, the reproduction and survival estimates come from just one site. Likewise, temporal changes in growth rates have been observed in abalone (Haaker et al. 1998). This potential temporal variation highlights the need for a mechanistic understanding of abalone vital rates under conditions of environmental stochasticity (Harley and Rogers-Bennett 2004) and may cause problems with the interpretation of elasticity values (Benton and Grant 1996).

Model selection itself (specifying the number of stage/size classes and their widths) had an effect on the elasticity results. This has also been seen in plant population models where few wide size classes have a greater probability of retention and therefore greater elasticity values for juveniles (Enright et al. 1995). Better understanding of the differences in growth rates in space and time should be made a research priority (Hunter et al. 2000) for future red abalone work. With more data, future directions could include examining the effects of spatial differences in size at maturity and incorporating estimates of carrying capacity or Allee thresholds into matrix models to explore other important aspects of abalone population dynamics (Morris and Doak 2003). We caution, as others have (Mills et al. 1999, deKroon et al. 2000), that this elasticity analysis is derived from a density independent, deterministic (time-invariant) matrix model.

Model perturbations were performed to examine changes in population growth under various vital rate scenarios (Table 3). Reproductive senescence of the largest size classes did little to influence population growth. Manipulations simulating fishing (>178 mm size classes) coupled with fishing-related mortality of sublegal abalone (150–178 mm) negatively influenced population growth more than fishing alone. In contrast, large increases in fecundity combined with enhanced juvenile survival simulating a recruitment boom dramatically increased population growth. Perturbations

mimicking a warm regime, including decreased survival, slow growth (no skipping size classes; Haaker et al. 1998) and a reduction in reproduction dramatically decreased population growth.

Enhancing the survival of sublegal red abalone in the model had the most impact on population growth suggesting the current minimum legal size (178 mm) is set appropriately protecting the size class that has the most influence on population growth in the model. This suggests minimizing incidental fishing related mortality of sublegal abalone (150–178 mm) should be a priority. Abalone injured but not taken in the fishery may bleed to death since they have no blood clotting mechanism. Novice diver education programs, interpretive displays, and renewed enforcement could remind inexperienced fishers (divers and shorepickers) that existing regulations prohibit (1) removal of sublegal size abalone and (2) exchanging legal size abalone for bigger abalone or ''high grading.'' Marine protected areas (Gerber and Heppell 2004) that could also be used to reduce incidental mortality of the critical size class.

Conservation implications for white abalone

Elasticity analysis of the white abalone matrix model revealed that survival of the largest size class had the greatest elasticity value (Fig. 2B). Restoration actions focused on enhancing and protecting large adults should be preferred over those focused on smaller size classes. The abalone model was robust to changes in reproduction and survival parameters, but was sensitive to changes in growth transitions. We caution that this white abalone model was constructed with limited growth data and that results from models based on depauperate data, such as those presented, should be interpreted with caution. Elasticity analyses can be a helpful first step in the modeling of endangered species with minimal data (Heppell et al. 2000) and the model results can help focus data collection and research efforts.

The white and red abalone population models both converged on the stable size distribution slowly, with the white abalone model converging slightly faster than the red abalone model, as indicated by the larger damping ratio. The complex subdominant eigenvalue of the white abalone matrix however, indicates that oscillations may be a feature of the population dynamics potentially increasing the risk of collapse (or falling below some threshold).

Constructing matrix models that encompassed variations in vital rates allowed for an evaluation of enhancement options as well as an assessment of threats (Table 3). Our results suggest that several stocking strategies resulted in small increases in population growth. These model results suggest stocking larger abalone might be more effective than smaller abalone although this would have to be balanced against hatchery production costs. In contrast, threats mimicked by decreases in adult survival resulted in decreased pop-

ulation growth. Increased knowledge of the impact of these threats to adult white abalone should be an important research priority. The influence of shell boring organisms for example, such as clams (Alvarez-Tinajero et al. 2001) and sponges that infest old large adults potentially would be good candidates for further studies. Future modeling work may also incorporate recruitment and the role of Allee thresholds since recruitment failure appears to be one of the major threats to the population as described under the ESA listing (Hobday and Tegner 2000, Hobday et al. 2001, Lafferty et al. 2004). The feasibility of restoration practitioners enhancing vital rates and ameliorating threats must also be considered.

Clearly, more work needs to be done to improve vital rate estimates for white abalone. The most obvious need is in generating survival estimates which are lacking and generating more growth data. Reproduction estimates are based on four years of data, however these data are 30 years old and need to be updated. While the data needs for this endangered species are obvious, it is unclear how or if this is attainable because the species is now rare, lives in deep water, and has few individual in small and mid size classes. Few tools exist to aid white abalone populations other than closing the fishery and captive rearing (McCormick and Brogan 2003) which have been done or are ongoing. With limited prospects for acquiring more data, conservation efforts can take advantage of quantitative elasticity analyses based on limited data for this species and its congeners to help make informed conservation and research priority choices, as has been done with other endangered species (Caswell et al. 1998, Heppell et al. 2000).

Literature Cited

Alvarez-Tinajero, M. D. C., J. Caceres-Martinez, and J. G. Gonzalez-Aviles. 2001. Shell boring clams in the blue abalone *Haliotis fulgens* and the yellow abalone *Haliotis corrugata* from Baja California, Mexico. Journal of Shellfish Research **20**:889–893.

Behrens, M. D., and K. D. Lafferty. 2005. Size frequency measures of white abalone with implications for conservation. Pages 427–432 *in* Proceedings of the Sixth California Islands Symposium. Institute for Wildlife Studies, Ventura, California, USA.

Benton, T. G., and A. Grant. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life-histories in a variable environment. American Naturalist **147**:115–139.

Benton, T. G., and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution **14**:467–471.

Burnham, K. P., and G. C. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Campbell, A., editor. 2000. Workshop on rebuilding abalone stocks in British Columbia. Canadian Special Publication Fisheries and Aquatic Sciences **130**:1–158.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology **14**:215–230.

Caswell, H. 1986. Life cycle models for plants. Lectures on Mathematics in the Life Sciences **18**:171–233.

Caswell, H. 2000. Prospective and retrospective perturbation analysis: their roles in conservation biology. Ecology **81**:619–627.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications **8**:1226–1238.

Cortes, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conservation Biology **16**:1048–1062.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412–1423.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications **4**:437–445.

de Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology **67**:1427–1431.

de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods and model limitations. Ecology **67**:1427–1431.

Dugan, J. E., and G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences **50**:2029–2042.

Ebert, T. A. 1998. An analysis of the importance of Allee effects in management of the red sea urchin *Stongylocentrotus franciscanus*. Pages 619–627 *in* T. Mooi, editor. Echinoderms: San Francisco. Balkema, Rotterdam, The Netherlands.

Ebert, T. A. 1999. Plant and animal populations. Academic Press, San Diego, USA.

Enright, N. J., F. Franco, and J. Silvertown. 1995. Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. Oecologia **104**:79–84.

Gerber, L. R., and S. S. Heppell. 2004. The use of demographic sensitivity analysis in marine species conservation planning. Biological Conservation **120**:121–128.

Gotelli, N. J. 1991. Demographic models for *Leptogorgia virgulata*, a shallow-water Gorgonian. Ecology **72**:457–467.

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

Harley, C. D. G., and L. Rogers-Bennett. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. Cal-

ifornia Cooperative Oceanic Fisheries Investigations Reports **45**:98–110.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology **81**:654–665.

Heppell, S. S., and L. B. Crowder. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications **6**:556–565.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for Red-cockaded Woodpeckers: a modeling approach. Journal of Wildlife Management **58**:479–487.

Hobday, A. J., and M. J. Tegner. 2000. Status review of white abalone (*Haliotis sorenseni*) throughout its range in California and Mexico. NOAA Technical Memorandum NOAA-TM-SWR-035. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. National Marine Fisheries Service, Southwest Region Office, Long Beach, California, USA.

Hobday, A. J., and M. J. Tegner. 2002. The warm and the cold: influence of temperature and fishing on local population dynamics of red abalone. California Cooperative Oceanic Fisheries Investigations Reports **43**:74–96.

Hobday, A. J., M. J. Tegner, and P. L. Haaker. 2001. Overexploitation of a broadcast spawning marine invertebrate: decline of the white abalone. Review Fish Biology and Fisheries **10**:493–514.

Hunter, C. M., H. Moller, and D. Fletcher. 2000. Parameter uncertainty and elasticity analyses of a population model: setting research priorities for shearwaters. Ecological Modelling **134**:299–323.

Karpov, K. A., P. L. Haaker, I. K. Taniguchi, and L. Rogers-Bennett. 2000. Serial depletion and the collapse of the California abalone (*Haliotis* spp.) fishery. Canadian Journal of Fisheries and Aquatic Sciences **130**:11–24.

Lafferty, K. D., M. D. Behrens, G. E. Davis, P. L. Haaker, D. J. Kushner, D. V. Richards, I. K. Taniguchi, and M. J. Tegner. 2004. Habitat of endangered white abalone, *Haliotis sorenseni*. Biological Conservation **116**:191–194.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia **75**:601–607.

Lebreton, J. D., K. P. Burnham, J. Colbert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62**:67–118.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**:1–18.

McCormick, T. B., and J. L. Brogan. 2003. Early reproduction in hatchery-raised white abalone, *Haliotis sorenseni*, Bartsch, 1940. Journal of Shellfish Research **22**:825–829.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. The reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology **13**:815–829.

Moloney, K. A. 1986. A generalized algorithm for determining category size. Oecologia **69**:176–180.

Morris, W. F., and D. F. Doak. 2003. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Morris, W. F., D. F. Doak, M. Groom, P. Kareiva, J. Fieberg, L. Gerber, P. Murphy, and D. Thomson. 1999. A practical handbook for population viability analysis. The Nature Conservancy, Washington, D.C., USA.

Rogers-Bennett, L., editor. 2001. Review of some California fisheries for 2000: market squid, sea urchin, prawn, white abalone, groundfishes, ocean salmon, Pacific sardine, Pacific herring, Pacific mackerel, nearshore live-fishes, halibut, yellowfin tuna, white seabass, and kelp. California Cooperative Oceanic Fisheries Investigations Reports **42**:12–28.

Rogers-Bennett, L., B. A. Allen, and G. E. Davis. 2004*a*. Measuring abalone (*Haliotis* spp.) recruitment in California to examine recruitment overfishing and recovery criteria. Journal of Shellfish Research. **23**:1201–1207.

Rogers-Bennett, L., R. F. Dondanville, and J. V. Kashiwada. 2004*b*. Size specific fecundity of red abalone (*Haliotis rufescens*): evidence for reproductive senescence? Journal of Shellfish Research **23**:553–560.

Rogers-Bennett, L., P. A. Haaker, T. O. Huff, and P. K. Dayton. 2002. Estimating baseline abundances of abalone in California for restoration. California Cooperative Oceanic Fisheries Investigations Reports **43**:97–111.

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

Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**:642–653.

Shepherd, S. A., and P. A. Breen. 1992. Mortality in abalone: its estimation, variability and causes. Pages 276–304 *in* S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo, editors. Abalones of the world: biology, fisheries and culture. Fishing News Books, Victoria, Australia.

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

Tegner, M. J., P. A. Breen, and C. E. Lennert. 1989. Population biology of red abalones, *Haliotis rufescens*, in Southern California and management of the red and pink, *H. corrugata*, abalone fisheries. Fishery Bulletin **87**:313–339.

Tutschulte, T. C. 1976. The comparative ecology of three sympatric abalones. Dissertation. University of California, San Diego, California, USA.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. Oecologia **32**:79–84.

Vaughan, D. S., and S. B. Saila. 1976. A method for determining mortality rates using the Leslie matrix. Transactions of the American Fisheries Society **3**:380–383.

Vogel, G. 2000. Migrating otters push law to the limit. Science **289**:1271.

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

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**(Supplement):120–138.