

## Exploring the Use of a Size-Based Egg-per-Recruit Model for the Red Abalone Fishery in California

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**Abstract.**—Eggs-per-recruit (EPR) models are widely used for management of invertebrate fisheries to provide guidance to managers about the magnitude of egg production for a given level of instantaneous annual fishing mortality ( $F$ ). We constructed a deterministic size-based EPR model that utilizes size-specific natural mortality rates and egg production for red abalone *Haliotis rufescens* in California. We analyzed the sensitivity of the model to alterations in biological parameters, modeled the effect of incidental mortality of sublegal individuals on EPR, and modeled the effects of various management actions, including incorporation of a slot size limit, incorporation of a harvest refugium, and alternative legal minimum size limits. Model results were more sensitive to alterations in growth parameters and lower mortality estimates than to changes in upper mortality estimates or fecundity parameters. When  $F$  increased from 0.0 to 0.1 per year, EPR exhibited a large decline from 100% to 70%. Only the incorporation of a harvest refugium and an increase in the minimum size limit produced increases in the percent of maximum EPR. Implementing a slot limit of 152.4–203.2 mm maximum shell length (MSL) decreased the EPR value, indicating the importance of egg production by red abalone that are smaller than the current minimum size limit of 177.8 mm MSL. Because of the sensitivity of model predictions to changes in certain biological parameters, we recommend caution when applying EPR models to management, particularly for regions without spatially explicit parameter values. Despite this sensitivity, EPR models provide a heuristic framework for exploring the potential impacts of proposed fishery management strategies (e.g., harvest refugia), establishing biological reference points, examining how spatial and temporal variability in biological parameters affects egg production, and providing a guide for prioritizing research to improve data quality used for red abalone management.

Red abalone *Haliotis rufescens* are the target of California's last remaining abalone fishery, a recreational fishery along the northern coast (Cox 1960; Rogers-Bennett et al. 2002). Current management of red abalone in California includes a combination of measures, including a minimum size limit, daily and yearly bag limits, season closures, and gear restrictions (e.g., prohibition of scuba; California Department of Fish and Game 2005). Recent work examining the sensitivity of a size-based matrix model indicates that the present minimum legal size limit of 177.8 mm maximum shell length (MSL) protects smaller adults (150–178 mm MSL) that have the most influence on population growth (Rogers-Bennett and Leaf 2006).

Careful management of north coast red abalone populations is warranted, as stocks of *Haliotis* spp. have collapsed in southern California (Karpov et al. 2000) despite the use of management tools such as size limits and season closures. Egg-per-recruit (EPR) models are one option for exploring the population dynamics of a stock and egg production responses to a range of management strategies, such as changing instantaneous annual fishing mortality rates ( $F$ ) or minimum size limits (Prager et al. 1987; Annala and Breen 1989; Shepherd et al. 1995; Smith and Addison 2003). An analysis of an EPR model for the fishery in southern California, which eventually collapsed and was closed in 1997, indicated that 48% of maximum egg production was maintained by the management strategies (Tegner et al. 1989). The resulting collapse of this fishery suggests that abalone populations can be subject to extirpation even when populations are fished

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at intensities that maintain nearly half of egg productivity.

Historically, serial depletion of five abalone species occurred in southern California, resulting in the closure of both recreational and commercial red abalone fisheries in 1997 (Karpov et al. 2000). Currently, there is a process underway to explore the reopening of the red abalone fishery at San Miguel Island (SMI) in southern California. Management of the northern California recreational fishery and the SMI management process would benefit from a re-evaluation of EPR models and a description of model sensitivity to biological parameters. Additionally, EPR models can be used to examine alternative management strategies and identify critical areas for research.

Recently, a number of papers have described size-specific growth, fecundity, and natural mortality of red abalone from northern and southern California (Haaker et al. 1998; Rogers-Bennett et al. 2004b, 2007; Leaf et al. 2007); this information allows for the development of a size-based EPR model. Although a stock-recruitment relationship has not been determined for red abalone, stock collapse and recruitment failure have been identified in parts of the Channel Islands, where adults are at exceedingly low densities (Rogers-Bennett et al. 2004a). Egg-per-recruit models are used to help manage fisheries for abalone and other invertebrates (Tegner et al. 1989; Shepherd et al. 1991; McShane and Naylor 1995; Smith and Addison 2003) and to maintain a minimum level of egg production. For many invertebrates, size-based models are advantageous, because biological parameters (e.g., natural mortality and fecundity) are determined by size rather than age (Ebert 1998) and because growth rates vary among individuals (Quinn and Deriso 1999). A variety of size-based predictive models have been developed (Jones 1981; Chen 1997), and size-based demographic models have been used to describe the population dynamics of red abalone (Rogers-Bennett and Leaf 2006).

We constructed and analyzed a size-based EPR model for red abalone in California. Mean estimates of growth, natural mortality, and reproduction estimates from California populations were used to derive a base model. We performed a number of sensitivity trials to explore the response of this model to changes in biological parameters. We used the model to explore potential management strategies, such as changes in  $F$ , alternative size and slot limits, alternative fishing selectivity patterns, and the role of harvest refugia. Here, we discuss the advantages and disadvantages of EPR models for red abalone management and use the model results to identify priority research areas.

## Methods

*Red abalone biological parameters.*—Individual growth trajectories were described using a two-parameter von Bertalanffy growth function (VBGF) that describes the MSL at age  $t$  ( $L_t$ ):

$$L_t = L_\infty(1 - e^{-kt}), \quad (1)$$

where  $L_\infty$  is the average MSL of the largest individuals in the population,  $e$  is the base of natural logarithms, and  $k$  is the von Bertalanffy annual growth rate constant. Estimates of growth were derived from multiple studies of northern and southern California populations (Figure 1; Haaker et al. 1986; Rogers-Bennett et al. 2007). In the base model, we used VBGF parameters ( $k = 0.108$  per year,  $L_\infty = 254.2$  mm MSL) estimated from northern California (Rogers-Bennett et al. 2007; Figure 2A). These estimates were derived from 5–222 mm MSL, tagged individuals ( $n = 231$ ) sampled at Point Cabrillo Reserve (Figure 1). An alternative VBGF growth estimate based on tag-recapture work performed at Johnson's Lee on Santa Rosa Island (southern California) from 1978 to 1984 (Haaker et al. 1986) was used for the sensitivity analysis (Figure 1). These data were used to estimate VBGF parameters by Fabens' (1965) method using nonlinear, least-squares regression:

$$L_{\text{capture}} = L_{\text{tag}} + (L_\infty - L_{\text{tag}})(1 - e^{-k\Delta t}), \quad (2)$$

where  $L_{\text{capture}}$  is the MSL (mm) of an individual at the time of recapture,  $L_{\text{tag}}$  is the MSL of an individual at the time of marking, and  $\Delta t$  is the duration (years) between the time of marking and capture. Tag-recapture data from Johnson's Lee ( $n = 761$ ) were recorded at annual intervals. The resulting VBGF was assessed qualitatively using the growth vector method presented by Cailliet et al. (1992). Growth vectors represent the change in time since first capture ( $\Delta t$ , years) and the change in length during the time at liberty ( $\Delta L$ , mm), assuming that the age at first tagging is predicted by the VBGF.

Estimates of size-specific egg production in the base model were based on data reported by Rogers-Bennett et al. (2004b) from Van Damme State Park ( $n = 45$  red abalone; size range = 172–260 mm MSL) and from SMI (Figures 1, 2B;  $n = 16$  red abalone; size range = 123–215 mm MSL). The mean number of eggs ( $E_L$ ) produced annually by a female as a function of  $L$  (mm) was described using a three-parameter Gaussian curve (model parameters are  $A$ ,  $\mu$ , and  $\sigma^2$ ) assuming a lognormal error structure:

$$E_L = Ae^{[-(L-\mu)^2]/(2\sigma^2)}. \quad (3)$$

We assumed that  $E_L$  from females less than 100 mm

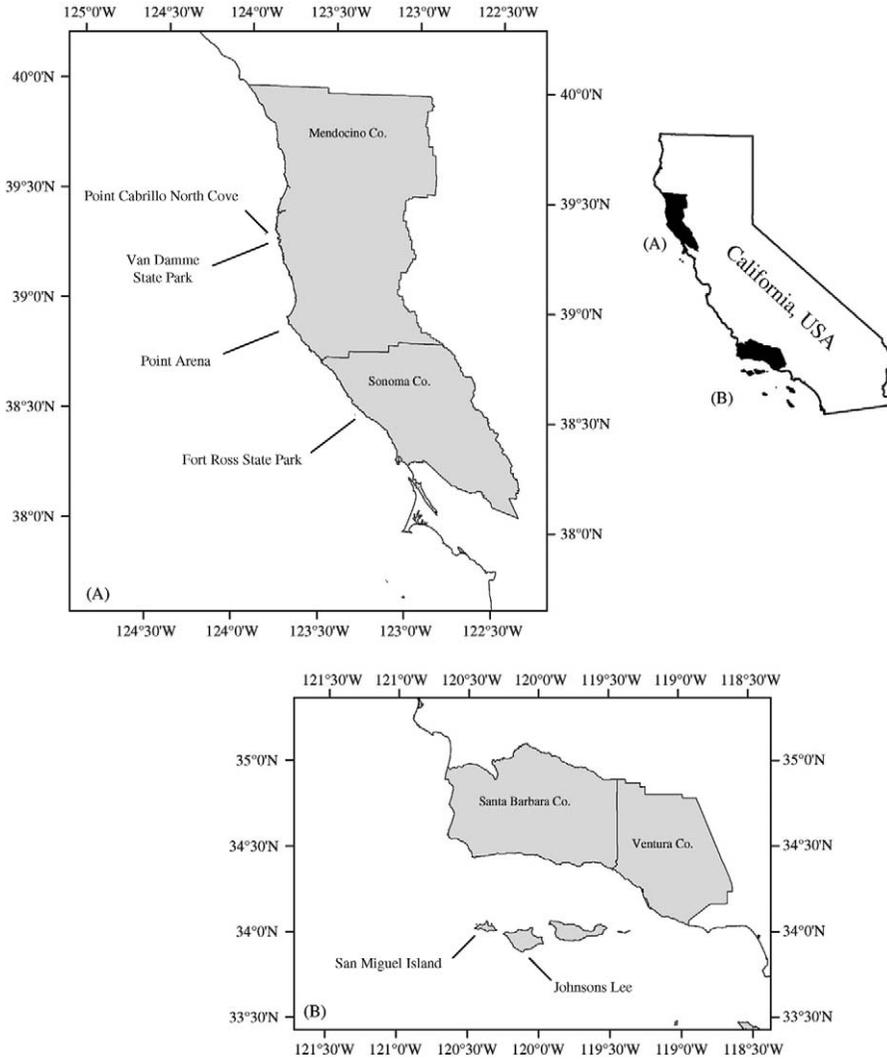


FIGURE 1.—Locations in (A) northern California and (B) southern California, from which red abalone individual growth, reproduction, and mortality estimates were derived for use in an egg-per-recruit model.

MSL was zero, as has been reported by Rogers-Bennett et al. (2004b). The 95% confidence intervals of  $E_L$  were determined using a nonlinear curve-fitting protocol in Matlab (version 7.1) and were used in sensitivity trials.

Leaf et al. (2007) reported estimates for instantaneous annual size-specific natural mortality ( $M$ ) for red abalone in northern California; these estimates were derived from Cormack–Jolly–Seber analysis of data from Point Cabrillo North Cove (Figure 1). Natural mortality estimates were determined for three size-classes: (1) larger than 178.0 mm MSL (mean  $M = 0.05$ ; mean  $- SE = 0.01$ ; mean  $+ SE = 0.14$ ); (2) 100.0–178.0 mm MSL (mean  $M = 0.37$ ; mean  $- SE =$

0.30; mean  $+ SE = 0.46$ ); and (3) smaller than 100.1 mm MSL (mean  $M = 0.65$ ; mean  $- SE = 0.56$ ; mean  $+ SE = 0.75$ ). We applied a three-parameter logistic curve to these point estimates to derive continuous mean, minimum (mean  $- SE$ ), and maximum (mean  $+ SE$ ) estimates of size-specific  $M (M_L)$ :

$$M_L = \alpha / [1 + (L/l_0)^\beta]. \tag{4}$$

For the logistic regression, the median value of each size-class (0.1–100.0, 100.1–178.0, and >178.0 mm MSL) was used as the independent variable,  $L$ . The point value of the independent variable of the largest size-class was 245.55 mm MSL, which is the median

value calculated based on (1) the smallest length in the largest size-class and (2) the largest recorded length of red abalone in California (313 mm MSL). We assumed that  $M_L$  was bounded such that (1) the  $M_L$  value for sizes less than 50.05 mm MSL was equal to the  $M_L$  for 50.05 mm MSL and (2) the  $M_L$  value for sizes greater than 245.55 mm MSL was equal to the  $M_L$  for 245.55 mm MSL (Figure 2C).

*Size-based egg-per-recruit model.*—A deterministic size-based EPR model was derived from the yield-per-recruit model presented by Chen (1997); the lengths of individuals in the model are divided into  $n$  segments (size-class  $g = 1, \dots, n$ ). The number of individuals in each size-class  $g$  is

$$N_g = \exp \left[ - \sum_{j=1}^{g-1} (F_j + M_j) \Delta T_j \right], \quad (5)$$

where  $F_j$  and  $M_j$  are the instantaneous rates describing size-class  $g$ . The time that an individual remains in size-class  $g$  ( $\Delta T_g$ ) is calculated as

$$\Delta T_g = \frac{1}{k} \log_e \left( \frac{L_\infty - L_g}{L_\infty - L_g - d_g} \right), \quad (6)$$

where  $k$  and  $L_\infty$  are the VBGF parameter estimates,  $d_g = 5$  mm and is the width of size-class  $g$ , and  $L_g$  is the minimum size in  $g$ .

Size-specific cohort egg production was calculated as the number of eggs produced by the median-sized individual in a size-class (from equation 3, where  $L = L_g + d_g/2$ ). Egg production of the median-sized individual in the size-class  $E_L$  was multiplied by the number of individuals in the size-class  $N_g$  to determine the total egg production of the size-class  $E_g$ :

$$E_g = E_L N_g. \quad (7)$$

The EPR value was calculated as the sum of the number of eggs produced in each size-class at a given  $F$  applied at a minimum legal size limit to individuals in the fishery:

$$\text{EPR} = \sum_{j=1}^g E_j. \quad (8)$$

The EPR values, each expressed as a percentage of the maximum EPR, were calculated for a range of sizes at entry into the fishery and a range of  $F$ -values.

*Model sensitivity.*—The sensitivity of the EPR model to changes in biological parameter values and the impact of alternative fishery selectivity scenarios were evaluated by altering the associated parameter values within the base model. The impacts of incidental mortality on sublegal individuals and the incorporation of minimum and maximum size limits (i.e., a slot

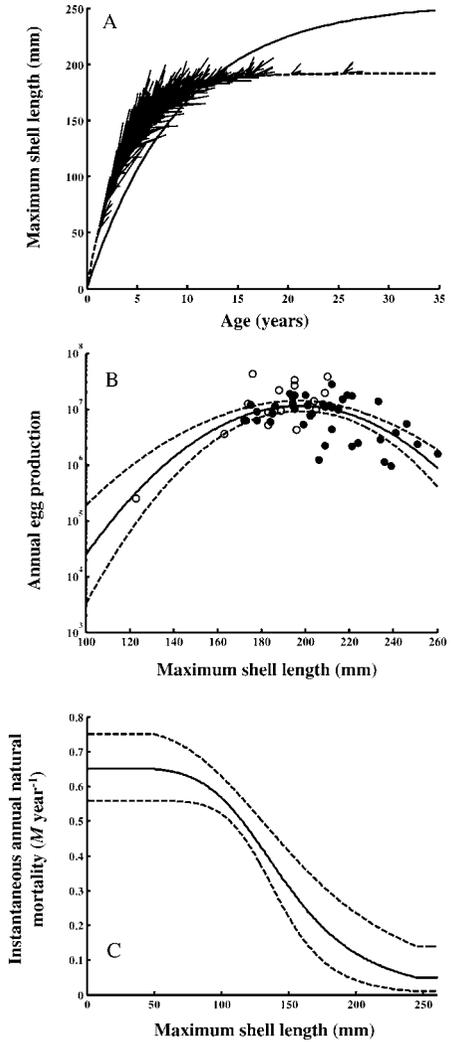


FIGURE 2.—California red abalone biological information used in a base egg-per-recruit (EPR) model and analyses of model sensitivity to changes in biological parameters: (A) von Bertalanffy growth function (VBGF) estimates (from tag-recapture studies) used in the base EPR model (solid line;  $k = 0.108$  per year,  $L_\infty = 254.2$  mm maximum shell length [MSL]; data from Point Cabrillo North Cove,  $n = 231$ ; Rogers-Bennett et al. 2007) and in the sensitivity analysis (dashed line;  $k = 0.27$  per year,  $L_\infty = 191.8$  mm MSL; data from Johnson's Lee,  $n = 761$ ; the fit to the tag-recapture data was assessed qualitatively using growth vectors determined from individual tag-recapture histories; Cailliet et al. 1992); (B) mean Gaussian estimate of size-specific egg production (solid line) and upper and lower 95% confidence limits (dotted lines) based on estimates from northern (open circles;  $n = 45$  red abalone) and southern (closed circles;  $n = 16$  red abalone) California; and (C) mean estimate of instantaneous annual size-specific natural mortality ( $M$ ; solid line) and the minimum (mean - SE) and maximum (mean + SE) estimates (dotted lines) from a three-parameter logistic equation.

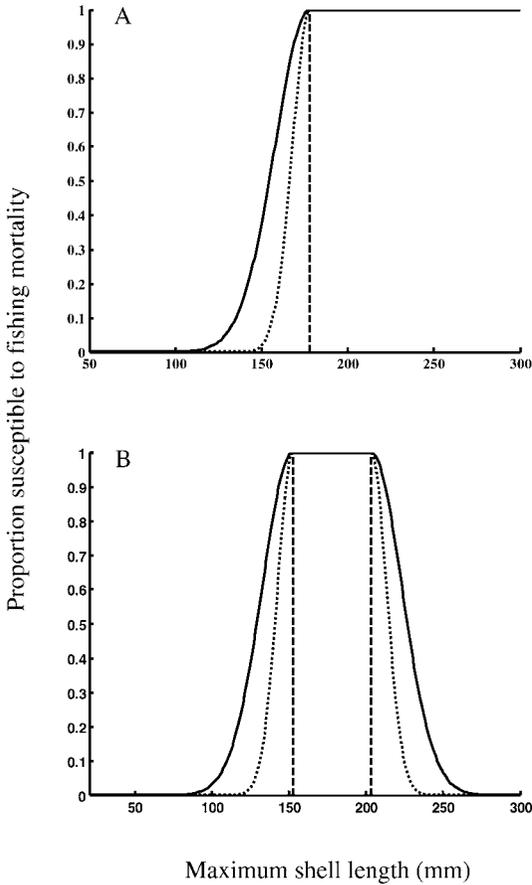


FIGURE 3.—Examples of the types of fishery selectivity incorporated into an egg-per-recruit model for California red abalone (dashed line = knife-edged selectivity) (A) at a target minimum size limit of 178 mm maximum shell length (MSL) and (B) a slot limit of 152.4–203.2 mm MSL (6–8 in). For both panels, dotted and solid lines represent selectivity curves defined by the truncated, scaled normal probability distribution at the target maximum size limit and slot limit with two levels of error (dotted line = SD of 10 mm; solid line = SD of 20 mm).

limit), including incidental mortality, on the percentage of maximum EPR were determined. For these analyses, a selectivity index for the median-sized individual in each size-class was determined using a truncated, scaled, normal probability distribution ( $P_L$ ) around the target size limit ( $L_{SL}$ ) at two levels of estimated error, SD (10 and 20 mm):

$$P_L = \exp\left[\frac{-(L - L_{SL})^2}{2SD^2}\right]. \tag{9}$$

To model the effect of incidental mortality at the current size limit ( $L_{SL} = 177.8$  mm MSL) on EPR,  $P_L$  was

calculated for  $L$ -values less than  $L_{SL}$ . For  $L$ -values that were equal to or greater than  $L_{SL}$ , the  $P_L$  was set to 1.0 (Figure 3A). The value of  $P_L$  was determined to estimate the effect of incidental mortality on the percentage of maximum EPR attained outside of the interval of the minimum size limit ( $L_{SL,min}$ ) and maximum size limit ( $L_{SL,max}$ ) using two hypothetical slot limits: 177.8–226.8 mm MSL (7–9 in) and 152.4–203.2 mm MSL (6–8 in). The  $P_L$  for  $L$ -values less than  $L_{SL,min}$  or greater than  $L_{SL,max}$  was determined using equation (9); the  $P_L$  for  $L$ -values equal to or falling in between  $L_{SL,min}$  and  $L_{SL,max}$  was set to 1.0 (Figure 3B). The proportion of individuals selected in each size-class was incorporated into the model for each trial by multiplying  $P_L$  for the median-sized individual in each size-class (equation 5) by the associated  $F$  for that individual.

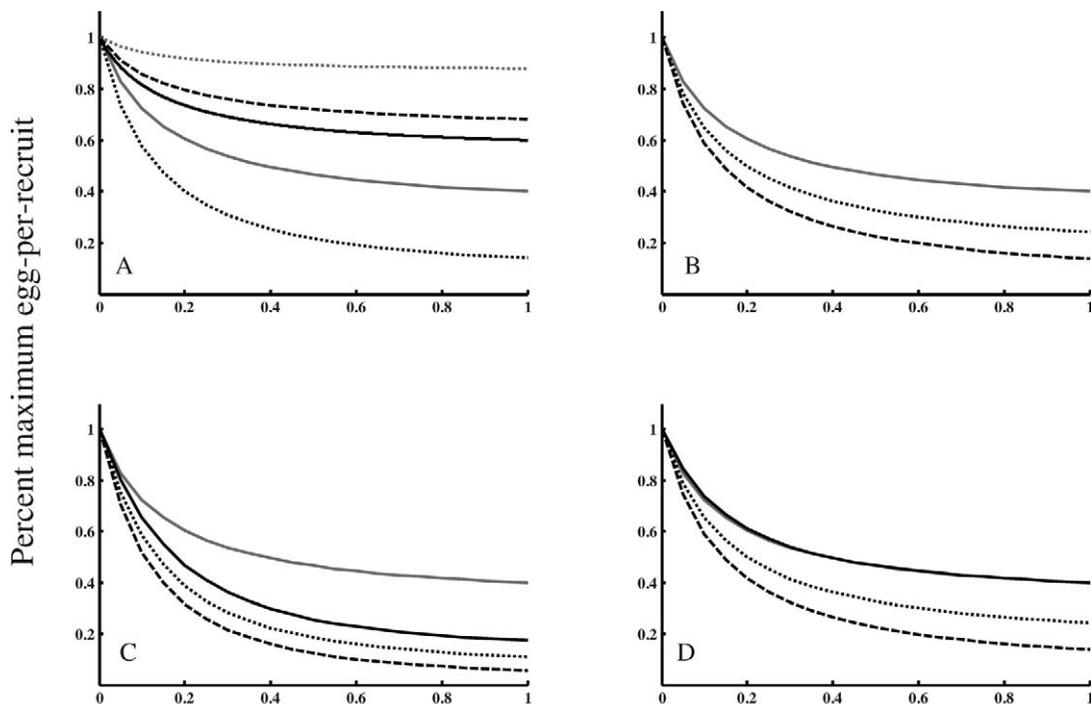
Because scuba is not allowed for recreational fishing in northern California, a proportion of the deepwater population is not subjected to mortality from fishing (Karpov et al. 1998). We modeled the effects of this harvest refuge on EPR values by assuming that one-third of the population is kept as a reserve and the remaining two-thirds of the population (i.e., in shallow water) are subjected to fishing mortality.

Model sensitivity to changes in biological parameters was evaluated by altering growth, size-specific egg production, or mortality individually in a number of sensitivity trials. Changes in model estimates in response to changes in VBGF parameters were evaluated by using an alternative growth trajectory (Figure 2A). The minimum (mean – lower 95% confidence limit [CL]) and maximum (mean + upper 95% CL) size-specific egg production estimates (Figure 2B) and the minimum (mean – SE) and maximum (mean + SE) size-specific  $M$  estimates (Figure 2C) were also substituted into the base model. Model sensitivity to alterations in a biological parameter was evaluated in two ways. First, we determined the relative difference between EPR estimates at different levels of  $F$  ( $F = 0.05, 0.01, 0.25, \text{ or } 0.50$ ) for a specific size at entry into the fishery (177.8 mm MSL) and the EPR value of the base model at the same values of  $F$  and size at entry into the fishery:

$$RD = \frac{EPR|_{simulation,F=x}}{EPR|_{base,F=x}}. \tag{10}$$

Second, we determined the intensity of fishing ( $F_{x\%}$ ) that would result in the production of 35, 55, and 75% ( $F_{35\%}$ ,  $F_{55\%}$ , and  $F_{75\%}$ ) of the EPR in each simulation relative to the maximum EPR value of each simulation evaluated at a 177.8-mm size at entry into the fishery:

$$F_{x\%} = F_{(EPR|_{simulation,F=x})/EPR|_{simulation,F=0}}. \tag{11}$$



### Instantaneous annual fishing mortality ( $F$ )

FIGURE 4.—Percentage of the maximum egg-per-recruit (EPR) value exhibited at a given level of instantaneous annual fishing mortality ( $F$ ) for red abalone in California. In each analysis, the solid gray line represents the estimated percent of maximum EPR of the base model at a given  $F$  in comparison to (A) incorporating a harvest refugium where one-third of the population is protected from fishing (solid black line) and using one of three alternative minimum size limits [MSL]; black dotted line = 152.4 mm or 6 in maximum shell length [MSL]; black dashed line = 203.2 mm or 8 in; gray dotted line = 228.6 mm or 9 in; (B) incorporating alternate selectivity patterns (black dotted line = SD of 10 mm; black dashed line = SD of 20 mm) in the base model; (C) use of a 152.4–203.2-mm MSL (6–8-in) slot limit, incorporating knife-edged selectivity (solid black line) and two levels of error (black dotted line = SD of 10 mm; black dashed line = SD of 20 mm); and (D) use of a 177.8–226.8-mm MSL (7–9-in) slot limit with knife-edged selectivity and two levels of error (line definitions are the same as those in C; note that the line of the percentage of maximum EPR at a given  $F$  for the base model and that of the knife-edged selectivity overlap).

## Results

### Biological Parameters

Mean individual growth of red abalone in southern California was determined for the sensitivity analysis, and annual size-specific egg production by red abalone in northern California was determined for the base model. The resulting VBGF parameter estimates from southern California were 0.27 per year for  $k$  and 191.8 mm MSL for  $L_{\infty}$ . The resulting growth vectors, when fitted to the mean VBGF estimate, indicated that individual growth was variable relative to the mean estimate (Figure 2A). For the three-parameter Gaussian curve (both data sets combined) mean  $A$  was  $1.14 \times 10^7$  eggs/year, mean  $\mu$  was 197 mm, and mean  $\sigma^2$  was  $5.94 \times 10^5$  mm<sup>2</sup>. The 95% CLs of size-specific egg

production were used in the sensitivity analysis (Figure 2B).

### Egg-per-Recruit Model and Sensitivity Analysis

The incorporation of incidental mortality, a slot limit with upper and lower size limits, the choice of a minimum legal size limit, an implicit harvest refugium, and target  $F$  all had major impacts on the percent of maximum EPR produced by the stock. The percent of maximum EPR in the base model was reduced from 100% at an  $F$  of 0.0 to 60% at an  $F$  of 0.20 or greater (Figure 4A). The steepness and magnitude of the decline in percent of maximum EPR were reduced when size limits of 203.2 mm MSL (8 in) and 228.6 mm MSL (9 in) were imposed (Figure 4A, top two curves). A similar result was obtained when a harvest

TABLE 1.—Results of sensitivity analyses in which the following biological parameters of an egg-per-recruit (EPR) model for California red abalone were altered relative to a base model: (1) von Bertalanffy growth parameters (determined at Johnson's Lee, Santa Rosa Island:  $L_{\infty}$  = average size of the largest individuals in the population,  $k$  = annual growth rate constant), (2) size-specific instantaneous annual mortality (mean  $M \pm$  SE), and (3) fecundity (mean  $\pm$  95% confidence limits [CLs]). Relative difference (RD; %) in cohort EPR is expressed in relation to a size limit of 178 mm maximum shell length (MSL) for instantaneous annual fishing mortality rates ( $F$ ) of 0.05, 0.10, 0.25, and 0.50. The  $F$  resulting in a specified maximum percentage of EPR (35, 55, or 75%) for each analysis is also shown.

Parameter change	$F$				Maximum EPR (%)		
	0.05	0.10	0.25	0.50	35	55	75
Base					>2.0	0.55	0.17
Growth at Johnson's Lee, ( $k = 0.27$ , $L_{\infty} = 191.8$ mm MSL)	359	382	427	467	>2.0	>2.0	>2.0
Mean $M +$ SE	31	33	37	40	0	0	0
Mean $M -$ SE	431	401	364	348	>2.0	>2.0	>2.0
Fecundity – lower 95% CL	72	71	69	66	0.65	0.15	0.05
Fecundity + upper 95% CL	148	150	156	162	>2.0	>2.0	1.96

refugium was imposed (Figure 4A); the decline in EPR relative to the base model was reduced and was maintained at 60% of maximum EPR even at much higher levels of  $F$ . Conversely, when the minimum size limit was decreased to 152.4 mm (6 in), the percent of maximum EPR was dramatically reduced even when  $F$  was low (Figure 4A, bottom curve). The incorporation of incidental mortality into the base model at the two levels of variance greatly reduced the percent of maximum EPR estimated by the model. The decline in percent of maximum EPR for the model with incidental mortality using a normal selectivity curve (SD = 20 mm) resulted in declines similar to those predicted when the size limit was reduced to 152.4 mm MSL (Figure 4B). The incorporation of the 152.4–203.2-mm MSL slot limit did not result in an increase relative to the base model estimates of percent maximum EPR (Figure 4C); however, the percent of maximum EPR produced under a 177.8–228.6-mm slot limit was nearly identical to base model estimates but marginally greater than the base model estimate at low  $F$  (<0.10; Figure 4D). Both estimates were decreased when incidental mortality was incorporated into the model (Figure 4D).

Predictions of the EPR models relative to the base model were sensitive to alterations in biological parameters (Table 1). The use of alternate individual growth parameters and  $M$ -values resulted in large differences relative to the base model. Alteration of the fecundity parameter also resulted in large differences relative to the base model, but the magnitude was not as great as that resulting from alteration of growth or  $M$ .

### Discussion

Egg-per-recruit models have not been used to support the management of the recreational red abalone

in the northern California. Current management using a minimum size limit tacitly assumes that (1) several spawning events take place before an individual enters the fishery and (2) this management strategy is adequate to sustain recruitment and maintain stocks (Breen 1992). However, abalone species may experience very high local  $F$ , incidental sublegal mortality, and local metapopulation structure (Morgan and Shepherd 2006). Furthermore, spatial and temporal differences in biological parameter estimates exist (McShane et al. 1988, 1994, 1995; Leaf et al. 2007) such that the conceptual model of abalone species management by size limits does not ensure sustainability (Nash 1992), as evidenced by the collapse of southern California red abalone stocks.

The demands of management necessitate the use of predictive models, such as the EPR model presented here, to help evaluate size limits and other management measures. The results of our EPR base model suggest that a relatively small increase in  $F$  (from 0.0 to 0.1) can reduce egg production by 30% (Figure 4A). The only management scenario that enhanced EPR relative to the base model was an increase in the minimum legal size from 178 mm MSL to either 203 or 228 mm MSL (8 or 9 in) and the incorporation of a harvest refugium (Figure 4A). These management actions maintained the percent of maximum EPR at over 60%, even when  $F$  was very high. These modeling results support the prohibition of scuba as one management strategy to maintain egg production under conditions of high  $F$  (Figure 4B). This management strategy was not in place for the red abalone fishery in southern California, where stocks collapsed.

Other management actions that were incorporated into the EPR model, including slot limits, did not increase the percent of maximum EPR (Figure 4B–D)

relative to base model estimates, because they did not reduce mortality on sublegal red abalone. The inclusion of incidental mortality of sublegal red abalone in the model greatly reduced the percent of maximum EPR, indicating the importance of these individuals to a population's egg production. These results are similar to those observed using size-based matrix models, where increasing the mortality of the sublegal size-class had the most deleterious effect on population growth (Rogers-Bennett and Leaf 2006). The results of EPR and matrix models suggest that more-precise estimates of incidental mortality of sublegal red abalone and better estimates of unreported take (poaching) are needed (Daniels and Floren 1998). Furthermore, these results support the need for education of recreational divers and enforcement measures designed to reduce mortality of sublegal size-classes and maintain the deepwater reserve population.

The EPR model's high sensitivity to the biological parameter estimates used in its construction is another result that is applicable to management. Such sensitivity is not a desirable feature, especially if individual growth and reproduction of red abalone differ over small or large spatial scales, as has been reported for red abalone (Tegner et al. 1992) and other abalone species (McShane et al. 1994; McShane and Naylor 1995). The EPR estimates were most sensitive to alterations in growth parameters and  $M$  but were not as sensitive to changes in fecundity estimates; thus, locally derived estimates of growth and  $M$  are needed for accurate EPR model estimates. This is especially relevant for the analysis of the potential fishery at SMI: it may not be appropriate to borrow biological parameters from geographically disparate populations. Additionally, an examination of changes in EPR estimates should be evaluated temporally; reproduction, growth, and mortality can vary over time as a function of ocean temperature and productivity (Haaker et al. 1986; Vilchis et al. 2005; Leaf et al. 2007).

An additional caveat should be made regarding the deterministic EPR model presented here. This model did not consider fertilization dynamics. The necessity of the close proximity of broadcast spawners for successful reproduction is not addressed with our base model. Abalone densities may fall below some minimum density (Allee threshold), and fertilization success can subsequently decline precipitously (Babcock and Keesing 1999; Gascoigne and Lipcius 2004). Stock-recruit dynamics are not well understood for red abalone, but it is possible that recruitment can be reduced to zero well before the stock becomes locally extirpated (Rogers-Bennett et al. 2004a). The sensitivity analysis that incorporated a reserve effect mimics

the deepwater reserve that is protected from fishing. The density of individuals in the depth refuge may help ameliorate depensatory processes, including Allee effects, but further research is needed to assess this.

The benefits of using an EPR model are that the model quantitatively formalizes the conceptual model of management and allows for the incorporation of a limit reference point (the perceived maximum safe exploitation level) and a target reference point (some exploitation level that is less than the maximum; Caddy 2004) for management. The limit reference point and its corollary, the target reference point, can be set in terms of a percent of maximum EPR (for example, 70% of maximum EPR). Members of the genus *Haliotis* are fished worldwide (Morgan and Shepherd 2006), and generally the limit reference points have been determined by EPR analysis. However, the failure of size limits to ensure sustainability of the abalone fisheries in southern California (Tegner 1989a; Davis et al. 1992) and elsewhere (Shepherd and Baker 1998) indicates that use of size limits alone is inadequate to ensure sustainability and that additional measures are necessary. Furthermore, the southern California example suggested that EPR values of 48% and lower were not sufficient to protect stocks from collapse (Tegner et al. 1989b). Case studies of declines in the abalone fisheries of Baja California, Mexico (Shepherd et al. 1998), and Australia (Shepherd and Rodda 2001) are well documented and suggest the necessity of adaptive management strategies (Shepherd et al. 2001) or even deepwater areas that are protected from harvest to rebuild collapsed stocks (Tegner 1993) and limit recruitment overfishing (Shepherd and Brown 1993). Northern California's additional regulation prohibiting the use of scuba appears to be a strategy that works in the region and could be used to guide the establishment of EPR reference points.

Because of the metapopulation structure exhibited by abalone species (Morgan and Shepherd 2006) and the potential episodic recruitment of red abalone, the maintenance of a population segment that is inaccessible to fishing is probably necessary for local population persistence. By means of EPR models, protected proportions of the population can be incorporated into models for management. The existence of a de facto deepwater reserve (Karpov et al. 1998) is an important attribute that is distinct from other types of protected areas, as it is continuous along the geographic range of the local abalone stock and thus contains part of the local metapopulation structure of each geographically isolated population. Therefore, the resilience of the local population may not necessarily be compromised by limited larval dispersal. It is likely that this management measure, in conjunc-

tion with a minimum size limit, has provided a necessary reserve of egg productivity to maintain a sustainable red abalone fishery in northern California; this type of regulation and EPR modeling approach can act as a model for abalone management worldwide.

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