Appendix B. Detailed description of the fish population model.

We developed an age-based non-linear matrix population model of *L. peru* with projection intervals of one year because age-specific demographic information was available for *L. peru* and related snappers. We then reduced the age-based model to stages that correspond to the size classes recognized in the market. Although the age-based model contains more information than the stage-based model, which averages the age-specific information into three stages, the stage-based model is used because it allows harvest to be added.

Both models are nonlinear because we assume a dependency between recruitment and adult stock in which the density of the adult stock negatively affects the average fecundity of individuals and/or pre-recruit survival and consequently the size of the recruited class (Levin and Goodyear 1980, Reed 1980, Myers and Cadigan 1993, Hilborn and Walker 2001). Our models employ a compensatory Beverton and Holt function (see equation (B.2) below) that determines pre-recruit survival based on total egg density, M .

Age-based Model

The population was divided into age classes up to a maximum age of 26 (Rocha-Olivares 1998).

$$
\begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_{26} \end{pmatrix}(t+1) =
\begin{pmatrix} l_1 f_1 & l_1 f_2 & \cdots & l_1 f_{26} \\ l_2 & 0 & \cdots & 0 \\ & & \ddots & \\ 0 & \cdots & l_{26} & 0 \end{pmatrix}
\begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_{26} \end{pmatrix}(t)
\tag{B.1}
$$

Survival from age class i to $i+1$ is given by l_{i+1}, $i = 1,...,25$ and average fecundity of each age class i is given by f_i, $i = 1,...,26$. Pre-recruit survival is defined by the following Beverton and Holt function:

$$l_1 = \frac{\alpha}{\beta + M}$$

(B.2)

where egg density, M, is defined as $M = \sum_{i=1}^{26} f_i n_i$. The parameter α represents the maximum

number of recruits in the population and β is the number of eggs needed to produce $\alpha / 2$ recruits. We

use a Beverton and Holt function that determines pre-recruit survival from egg density, M, rather than

adult stock, N, because adults and pre-recruits inhabit separate habitats (Parrish 1987, Rocha-Olivares

1998, Saucedo-Lozano et al. 1998). The different habitats of adults and pre-recruits suggests that pre-

recruit mortality is affected by egg density, through starvation or vulnerability to predators, rather than

the adult stock, through problems such as cannibalism.

Parameters Estimates

We derived estimates of the age-specific parameters, survivorship and fecundity, and the Beverton-Holt

parameters, α and β, from the literature on *Lutjanus peru* and related species to create the age-based

model.

Survivorship is the complement of mortality. Natural mortality estimates were taken from a

relationship between natural mortality and weight in marine fish (Lorenzen 1996)

$$Z = 3.69 \times W^\wedge \gamma$$

(B.3)

where Z is annual mortality, W is total weight in kilograms, and $\gamma = -0.305$.

Fecundity was estimated using a relationship between fecundity and weight determined for the

vermillion snapper, *Rhomboplites aurorubens* (Grimes and Huntsman 1980)

$$f = \exp(10.21 + 0.002W)$$

(B.4)

where W is total weight in kilograms and f is annual fecundity. Because our models count only females, the fecundity estimate was scaled by the sex ratio given by Cruz-Romero et al. (1996) to account only for the eggs that would grow into adult females. The maximum length of the snappers sampled by Grimes and Huntsman (1980) was 57 cm, whereas *Lutjanus peru* may reach 95 cm (Allen 1985, Rocha-Olivares 1998). We truncated the fecundity estimate at age 10, at which point red snappers are 65 cm in length (determined by equation (B.6) below) because extrapolating beyond the range of data adds uncertainty. We assumed that the fecundity of individuals greater than age 10 remained constant for the remaining ages. We considered this truncation to be plausible because over ninety-nine percent of the population is between the ages 1–10 (see Model Characteristics) and fish may experience a natural decrease in fecundity due to senescence despite substantial increases in fecundity with age (Reznick et al. 2002).

We transformed the weight-specific mortality and fecundity from Eqs. (B.3) and (B.4) into age-specific estimates of mortality and fecundity using known weight–length and length–age relationships. Rocha-Olivares (1998) reports the following weight-length relationship and von Bertalanffy growth function (VBGF) for *L. peru:*

$$W = 1.816 \times 10^{-5} L^{2.905} \tag{B.5}$$

$$L_T = 92.85(1 - e^{-0.12(t+0.14)}) \tag{B.6}$$

Where L is total length given in centimeters, t is age given in years, and W is total weight in kilograms. These equations were used along with fecundity and survival equations to determine age-specific parameters for the matrix model.

Figure B1 shows the resulting age-specific survivorship and fecundity estimates. Fecundity is an increasing function of age after the first year. Fecundity increases at an increasing rate with gains in fecundity increasing dramatically after age 5.

The parameters for the Beverton and Holt function were specific to *Lutjanus peru* and taken from Diaz Uribe et al. (2004). The Beverton and Holt function presented by Diaz Uribe et al. (2004) was in terms of total population size N, so we nondimensionalized the parameters in order to use them in a Beverton and Holt function in terms of total egg production, M. In addition we scaled the parameters to account for only females because the model in Diaz Uribe et al. (2004) counted total population. The resulting parameter values were $\alpha_{\text{age}} = \alpha_{\text{stage}} = 5.94 \times 10^5$ individuals, $\beta_{\text{age}} = 6.59 \times 10^9$ eggs, and $\beta_{\text{stage}} = 5.29 \times 10^9$ eggs (the values of β differ because the fecundity estimates differ slightly between the two models).

Stage-based Model

We derived a stage-based model from the age-based model in order to incorporate the available harvest data into the population model. Fishermen recognize three size classes or stages: small "chico" (<20 cm), medium or plate-sized "mediano" or "orden" (20–35 cm), and large "grande" (>35 cm). Using equation (B.6), we estimated the corresponding ages to be: small, 0 to 1 yrs; plate-sized 2–5 yrs; and large, 6 yrs to 26 yrs. Just as in the age model, we truncated the stages at a maximum of 26 years to reflect the oldest observed individual. The following non-linear matrix population model is used to represent the evolution of the population as determine by stage-specific parameters:

$$
\begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}^{(t+1)} = \begin{pmatrix} P_1 & l_1 F_2 & l_1 F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}^{(t)} \tag{B.7}
$$

where pre-recruit survival, l_1, is defined the same as in the age-based model (see equation (B.2)) above.

Because the length of time an individual is in a stage does not necessarily equal the projection interval, in this case one year, a stage-based model must take into account the probability of surviving and progressing to the next stage, G, as well as the probability of surviving but remaining in the same stage, P. To calculate P and G the processes of growth and survival must be separated.

$$\sigma_i = \text{Prob(survival of an individual in stage } i) \qquad \text{(B.8)}$$

$$\gamma_i = \text{Prob(growth from stage } i \text{ to } i+1 \,|\, \text{survival in stage } i) \qquad \text{(B.9)}$$

$$G_i = \sigma_i \, \gamma_i \qquad \text{(B.10)}$$

$$P_i = \sigma_i(1 - \gamma_i) \qquad \text{(B.11)}$$

Note that σ_i is the same as l_i in the age-based model and γ_i is not directly measurable but may be inferred through other data (Caswell 2001).

We derived the parameters for the stage-based model from the age-based model, assuming that in-stage age distributions are the same as the age distribution that results from the age-based model. The age range of each stage was found using the growth function (Eq. B.6) and the stable age distribution of the nonlinear age-based model (i.e., the eigenvector associated with the eigenvalue λ=1) was used to weight the averages of the age-specific parameters for each stage:

$$F_j = \frac{\Sigma_{i=t}^{t+S} f_i d_i}{\Sigma_{i=t}^{t+S} d_i}$$

$$\sigma_j = \frac{\Sigma_{i=t}^{t+S} l_i d_i}{\Sigma_{i=t}^{t+S} d_i}$$

$$W_j = \frac{\Sigma_{i=t}^{t+S} w_i d_i}{\Sigma_{i=t}^{t+S} d_i}$$

5

Where f_i, l_i, and w_i the fecundity, survivorship and weight of age each class i, $i = 1,...,26$, and

F_j, σ_j and W_j the fecundity, survivorship and weight of each stage j, $j = 1, 2, 3$, which contains

individuals age t to $t + S$. The parameters P and G for the stage-based model were estimated with

σ_j and equations (B.10) and (B.11).

Figure B2 shows the resulting parameters for the stage-based model. Fecundity in the third

stage is much higher than in the second stage and fecundity in the first stage is zero. The probability of

growing to the next stage decreases with the stage and is inversely related to the probability of staying

in the stage. The probability of staying in the first stage is zero because the duration of this stage is only

one year.

Model Characteristics

Running both the age- and stage-based models to equilibrium gives the population size and structure of

a pristine population, that is, one free of fishing pressure (*note:* both models count only females) (Figs.

B3, B4). The estimates of the population size; however, depend on initial conditions (i.e., the scale of the

system). Given that the purpose of these models is to simulate relative changes due to fishing rather

than estimate the actual population near La Paz, Mexico, we will focus on differences between the

models and different scenarios rather than on absolute estimates from the models.

Ideally, the age- and stage-based models would produce the same population estimates,

however, in averaging the parameters to reduce the age-based model to a 3-stage model, information is

inevitably lost. The equilibrium population sizes for both models were similar ($\hat{N}_{age} = 6.75 \times 10^5$

individuals and $\hat{N}_{stage} = 6.81 \times 10^5$ individuals) (Figs. B3-i, B4-i); however, the resulting total biomass

and total egg production for the two models differed more. Total biomass for the age- and stage-based

models was $\hat{B}_{\text{age}} = 8.63 \times 10^4$ kg and $\hat{B}_{\text{stage}} = 1.20 \times 10^5$ kg, respectively (Figs. B3-ii, B4-ii). The stage-based model overestimates the number of individuals in Stage 3 and consequently overestimates the biomass of this stage and the total biomass of the population, as well (Figs. B3-B4). Total egg production was underestimated by the stage-based model, $\hat{M}_{\text{stage}} = 4.06 \times 10^{10}$, as compared to the age-based model, $\hat{M}_{\text{age}} = 5.01 \times 10^{10}$.

In the age-based model, the population is concentrated within the younger age classes. In fact, 99.65% of the population is found within ages 1 to 10. Similarly, in the stage-based model, 93.98% of the population falls within the first two stages, in which individuals range from ages 1 to 5. Sixty-seven percent of the population's biomass, however, resides in Stage 3, because, even though there are fewer individuals in this stage, they are heavier than individuals in Stages 1 and 2.

Sensitivity Analysis of Stage-based model

We examined the elasticity, or proportional sensitivity, of the output variables (total population size, N, total egg production, M, and total biomass, B) to the stage-based model parameters (F, α, β, P, G) (Table B1). It is difficult to interpret the elasticity of the output variables to P and G because these parameters must sum to σ and cannot be altered independently; therefore, we present the elasticity of the output variables to σ. Elasticities of N and B were calculated manually while the elasticity of M was derived analytically. It should be noted that in a linear model, elasticities are less than one, but because our models is nonlinear, elasticities may exceed unity.

Total egg production and biomass were more sensitive to the survival parameter of Stage 3, σ_3, than to the survival parameters of the other two stages, but total population was less sensitive to this parameter. Stage 3 is has the largest average weight and the highest fecundity, explaining why altering

survival and consequently the size of this stage may have the largest effect on M and B. The number of individuals, which is determined by egg production, in Stage 1 and their survival has the largest effect on N because the size of this stage bounds the size of the subsequent stages and thus total population size.

Reducing or augmenting the survival of Stage 3 will only directly affect the size of Stage 3, however, this may alter total egg production, M, which could affect the size of Stage 1. This presents the question of why survival of Stage 3 doesn't have a greater effect on N. The Beverton and Holt function bounds the amount of eggs that can survive to Stage 1, creating a saturation point after which an increase in M will not affect the number of recruits. If total egg production of the equilibrium population is greater than the saturation level, the new M produced by changes in survivorship of Stage 3 may also be above saturation and Stage 1 will not be affected.

The elasticity of M, N, and B with respect to fecundity of Stage 3 is greater than that of Stage 2, suggesting that the fecundity of the older, more reproductive fish is more crucial to population dynamics than that of smaller, less reproductive fish.

The total population size was the most elastic to the Beverton and Holt parameter α, which bounds the number of recruits to the population and thus the population size. Total biomass and egg production were also highly elastic to α, because the effect of α on total population size will in turn affect total egg production and total biomass. Total population size, total biomass, and total egg production were least elastic to the Beverton and Holt parameter β. As M grows, β becomes insignificant and Stage 1 approaches equilibrium value α. At large values of M, the magnitude of β determines how quickly Stage 1 reaches α rather than population size.

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Tables and Figures

TABLE B1. Elasticity of total egg production (M), total population size (N), and total population biomass (B) with respect to the model parameters.

Parameter	M	N	B
σ (1)	1.13	0.36	1.02
σ (2)	1.39	0.29	1.07
σ (3)	1.65	0.28	1.19
F(1)	NA	NA	NA
F(2)	0.02	0.00	0.00
F(3)	1.12	0.13	0.13
α	1.13	1.13	1.13
β	-0.13	-0.13	-0.13
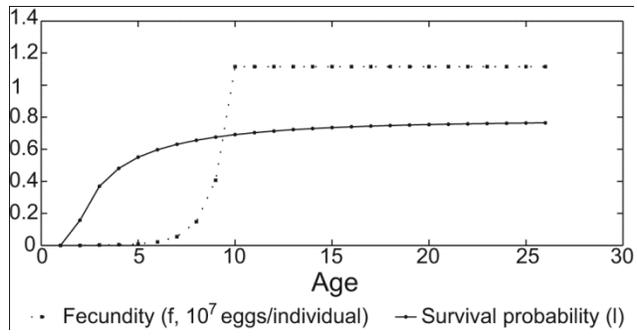
F<small>IG</small>. B1. Estimates of survival probability and fecundity for *L. peru* by age.
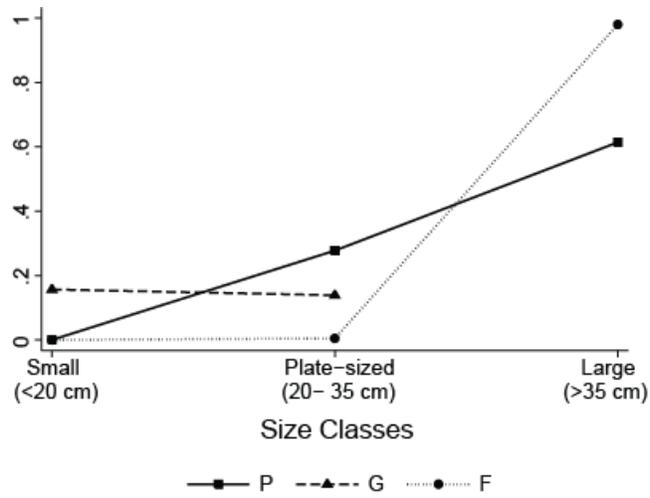
F<small>IG</small>. B2. Stage-based model parameters: P, probability of staying in a stage; G, probability of surviving and growing to the next stage; and F, fecundity (millions of eggs).
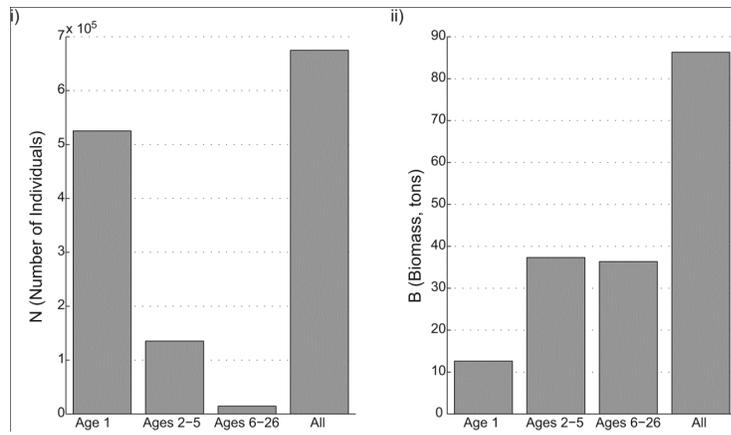
FIG. B3. Equilibrium population estimates from the age-based model: (i) number of individuals and (ii) biomass.
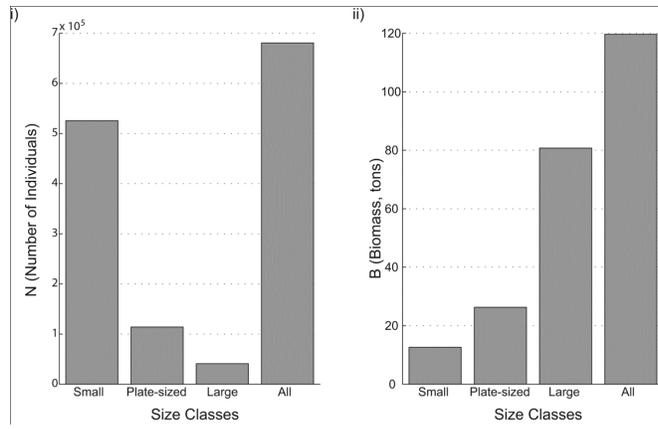
FIG. B4. Equilibrium population estimates from the stage-based model: (i) number of individuals and (ii) biomass.