

USING LIFE HISTORY AND PERSISTENCE CRITERIA TO PRIORITIZE HABITATS FOR MANAGEMENT AND CONSERVATION

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Abstract. In many marine and terrestrial systems, individuals of a focal species may be found in habitats that are neither essential nor of particular concern for conservation. For example, finding fish in a location does not make that location essential. This recognition begs the question of how one identifies the most important habitats for a particular species. We introduce new tools for use when prioritizing habitats for conservation and management, with application to Essential Fish Habitat (EFH). If density-dependent effects can be ignored, then elasticities of population growth rate with respect to adult survival, fecundity, and juvenile survival provide a means of identifying how susceptible the growth rate of the population is to perturbations in vital rates of particular life stages. We develop such a theory and apply it to 16 species of commercially harvested *Sebastes* rockfishes. We also show that the conclusions may differ significantly depending upon the estimate of mortality rate that is used. This suggests that although estimating mortality rates of fish in the field is difficult, it is crucial to do so. When density-dependent effects are important, we use a stochastic life history model to compute the moderate-term persistence of the stock, an important metric of population biology, as a function of the demographic parameters determined by the habitat. Although developed with fish in mind, the ideas here also apply to other taxa and systems.

Key words: conservation; commercially harvested fish; density dependence; eigenvalues; elasticity; essential fish habitat; life history; persistence, population growth rate; *Sebastes* spp.; stochastic iteration; stochasticity.

INTRODUCTION

Habitat is the stage upon which ecological dramas are played out (Southwood 1977). Heterogeneity of habitat in time and space often have profound consequences for predator–prey interactions (e.g., Karels et al. 2000), competition (e.g., Bonesi and Macdonald 2004), reproduction (e.g., Arthur et al. 2004), recruitment, and many other ecological processes. We should thus expect linkages between habitat and vital demographic rates and, as a consequence, between habitat and the persistence of a population. Given the link between habitat and persistence, management of habitat has become a key tool in the conservation of at-risk species, which often face massive habitat alteration. Setting aside habitat in reserves or easements, restoring habitat in locations where it once existed, and creating new habitat in areas where it never existed are now standard instruments to maintain viable populations.

That the crucial nature of high-quality habitat is already recognized is evident in such legislation as the U.S. Endangered Species Act (ESA) and the Sustainable Fisheries Act (SFA). These laws require federal agencies to designate specific areas within the range of species

that are essential to the persistence of species. Although the legal emphasis on habitat holds the promise of making habitat considerations a key part of management decisions in fisheries and maintaining their prominence in species conservation, actually determining what is “essential” has proven to be difficult because sufficient information about habitat requirements of focal species is often lacking. Indeed, “critical habitat” has been designated for only a small fraction of species listed under ESA (Hoekstra et al. 2002). In the case of exploited fishes, the SFA requires designation of “Essential Fish Habitat” (EFH), defined to be “those waters and substrate necessary to fish for spawning, breeding, feeding and/or growth to maturity.” Clearly, the ability of fisheries managers to identify EFH depends upon knowledge of what habitats fish use. Researchers typically describe habitats of organisms based on attributes known to be ecologically meaningful. Attributes as structure, hydrodynamics, and general hydrology usually form the corpus of fish habitat descriptions. However, if all habitats used by all life history stages are included in EFH descriptions, it is defined very broadly. Thus, for example, Pacific salmon freshwater EFH includes all those streams, lakes, ponds, wetlands, tributaries, and other water bodies currently and historically used by salmon within Washington, Oregon, Idaho, and California, USA (Roni et al. 1999). Designating a habitat as essential simply

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because an organism occurs there at some stage of the life history ignores the observation that some habitats may be more important to species than others (e.g., Tupper and Boutilier 1995, Levin and Stunz 2005), or that organisms may not respond strongly to some kinds of habitat (Petrik et al. 1999). Given the finite resources of management agencies, effective management of terrestrial and marine habitat requires prioritization (Newbold and Eadier 2004, Stauffer et al. 2004), but a framework in which all habitats that organisms use are considered equivalent does not allow a science-based ranking of habitats. Alternatives are needed. For example, Able (1999) provides four levels of impact assessment to determine whether a habitat is "essential" for a given species: (1) presence/absence, (2) relative abundance, (3) relative vital rates (growth, survival, reproduction), and (4) relative productivity. Here we introduce a tool (elasticity analysis) that allows evaluation of level-3 information and a tool (population persistence) that allows evaluation of level-3 and level-4 information.

The issue is further complicated because many species have evolved in fluctuating environments and have local populations (sources and sinks) that are linked by dispersal. How to prioritize locations where metapopulations show consistent abundance is still unclear (Bergmann et al. 2004) and must be done while coping with considerable levels of uncertainty (Harwood and Stokes 2003). It is also not clear how one identifies sources and sinks in a practicable manner; the focus on "critical" or "essential" fish habitat makes this a question that is especially relevant at a number of levels, from empirical science through modeling to policy. One difficulty, common to fish and some terrestrial species (e.g., insects) is that different life stages may use widely different components of the environment. Thus, many locations may be essential for the long-term health of the population, but organisms may also be found in a location that is not essential or critical. Recognizing the differences is key. Our goal here is to introduce new and relatively simple (Froese 2004) tools and develop ways of thinking about how to identify high-priority habitat for conservation. We focus on using persistence as a fundamental metric; another example of this approach (for salmon) is found in Hill et al. (2003). The tools presented here may offer a first step for assessments of habitat.

We begin, in the next section, by considering the case of density-independent population dynamics, such as might apply to fish stocks that have been overfished, but for which habitat destruction is not severe, or for recruitment-limited populations in which density effects are weak (Doherty 1981, Victor 1983). Of course, if recovery occurs over time, the stock will increase and reach a size where density-dependent effects are important. There will be an initial phase, however, during which density-dependent factors can be ignored. During this phase, we adapt the method of (Heppell et

al. 2000a) to focus on life history stages of individual species and, through them, physical locations. The method allows us to compute the elasticity of the growth rate of a population with minimal data on life history. We illustrate this method using rockfishes (*Sebastes* spp.) along the U.S. Pacific coast, showing how elasticity computations allow us to identify which habitat supporting which stages of the life history of which stocks should be the focus of conservation efforts.

We then turn to the case of density dependence in population dynamics. The model of population dynamics provides a link between habitat characteristics and the suite of vital rates. In that sense, vital rates become a proxy for habitat; this is analogous to the use of life history correlates (by Denney et al. 2002) to infer maximum growth rates of populations.

DENSITY-INDEPENDENT CASE: SELECTING LIFE HISTORY STAGES (AND THROUGH THEM, HABITAT)

We begin by asking how we can classify life history stages of species according to their likely response to perturbation in vital rates, which may be determined by habitat. A relatively simple way to do this is to construct an age- or stage-structured matrix model and examine how population characteristics respond to changes in vital rates (Caswell 2000). Elasticities predict the rate of change of population growth rate λ with respect to a change in a matrix element (Caswell 2000). Because elasticities sum to 1, they represent the relative contribution of each matrix element to the population growth rate (Caswell 2000, Heppell et al. 2000b). Estimating elasticities of matrix elements is now a standard procedure for evaluating and prioritizing conservation research and management (Mills et al. 1999, Heppell et al. 2000a, b).

For most species, the detailed demographic data necessary to parameterize matrix models are lacking, and given the time necessary to gather the information, the prospects for obtaining such data for most species are poor. However, Heppell et al. (2000a) developed a simple procedure to predict relative responses to perturbations based on elasticity analysis of approximate models. Given average adult survival, age at maturity, and an estimate of λ , it is possible to calculate elasticities of adult and juvenile stages (Heppell et al. 2000a, b). Because these basic estimates can be obtained for nearly all exploited species, a broad prioritization among life history stages of different species is possible, if one uses an age-structured model.

Following Heppell et al. (2000a), we estimated the elasticity (e) of λ to changes in mean adult survival of 16 rockfishes (*Sebastes* spp.) as

$$e_{\bar{s}_A} = (1 - \alpha e_F) \quad (1)$$

where \bar{s}_A is age-invariant mean adult survival, α is age at first reproduction, and e_F is the elasticity of mean annual fertility:

TABLE 1. Life history parameters used in the density-independent case for 16 species of *Sebastes*.

Common name	Species	Age of maturity (yr)	Maximum age (yr)	λ	Mean annual adult mortality	
					Pauly	Hoening
Bocaccio	<i>S. pauispinis</i>	8	50	0.83	0.209	0.083
Canary rockfish	<i>S. pinniger</i>	11	84	0.89	0.237	0.049
Chilipepper rockfish	<i>S. goodei</i>	4	35	1.05	0.285	0.119
Darkblotched rockfish	<i>S. crameri</i>	5.5	105	1.00	0.288	0.039
Greenstriped rockfish	<i>S. elongatus</i>	7	54	1.08	0.357	0.077
Pacific Ocean perch	<i>S. alutus</i>	9	100	0.96	0.308	0.041
Redbanded rockfish	<i>S. babcocki</i>	19	106	0.98	0.269	0.039
Rosethorn rockfish	<i>S. helvomaculatus</i>	7	87	1.02	0.370	0.047
Rougheye rockfish	<i>S. aleutianus</i>	20	205	1.05	0.199	0.020
Sharpchin rockfish	<i>S. zacentrus</i>	6	58	1.01	0.346	0.071
Shortbelly rockfish	<i>S. jordani</i>	1	32	1.09	0.414	0.130
Splitnose rockfish	<i>S. diploproa</i>	9	86	1.05	0.341	0.048
Stripetail rockfish	<i>S. saxicola</i>	2	38	1.03	0.423	0.109
Widow rockfish	<i>S. entomelas</i>	5.5	60	1.01	0.281	0.069
Yelloweye rockfish	<i>S. ruberrimus</i>	22	118	0.99	0.190	0.035
Yellowtail rockfish	<i>S. flavidus</i>	11	64	1.01	0.263	0.065

$$e_{\bar{F}} = \frac{\bar{S}_A - \lambda}{(\alpha - 1)\bar{S}_A - \alpha\lambda} \tag{2}$$

We focus on two of the three stages of the life history: settled juveniles and sedentary adults, as would apply to many species of *Sebastes* (Love et al. 2002) and reef fishes (Sale 2002). In the next section, we add consideration of pelagic larvae.

Adult survival in this framework is age invariant, and thus a cohort declines exponentially at constant rate. If \bar{S}_A is high, a singularly large recruitment can have a substantial influence on λ for many years. Heppell et al. (2000a) compensated for this by discounting \bar{S}_A for maximum life span according to Caswell (2000):

$$\gamma = \frac{\left(\frac{S}{\lambda}\right)^{T_s} - \left(\frac{S}{\lambda}\right)^{T_s-1}}{\left(\frac{S}{\lambda}\right)^{T_s} - 1} \tag{3}$$

Here S is annual survival and T_s is stage length. To estimate γ , we used \bar{S}_A as S and $T_s = (\omega - \alpha + 1)$ where ω is maximum age. We then computed an adult survival rate as

$$\hat{S}_A = \bar{S}_A(1 - \gamma) \tag{4}$$

Because elasticities sum to 1, the elasticity of λ to juvenile survival rates \bar{J} is

$$e_{\bar{J}} = 1 - (e_{\bar{S}} + e_{\bar{F}}) \tag{5}$$

We obtained estimates of age at first reproduction and maximum age for 16 species of exploited rockfish from Love et al. (2002). Direct estimates of natural (i.e., non-fishing) adult mortality are difficult to obtain for most exploited fish. As a consequence, we estimated average adult mortality using two approaches. First, we used an updated version of Pauly's (1980) empirical equation derived from >175 fish stocks based on the parameters of the von Bertalanffy growth function and on mean annual water temperature (Froese and Pauly 2002):

$$\log_{10}(1 - \bar{S}_A) = 0.566 - 0.718 \log_{10}(l_{\text{inf}}) + 0.02C \tag{6}$$

where l_{inf} is asymptotic length and C is water temperature in degrees centigrade. We used a mean value of 8°C for our estimates, recognizing that temperature may fluctuate on a variety of temporal and spatial scales. Second, we used the method of Hoening (1983) in which mortality rate is estimated from maximum observed longevity.

We estimated λ using the time series of adult abundance available from trawl surveys performed triennially within five strata along the continental shelf of the U.S. west coast by NMFS (National Marine Fisheries Service) from 1977 to 2001 and followed the approach outlined by Dennis et al. (1991) to estimate the population growth rate. When estimating λ , we treated counts as the sum of stratum means, estimated using a delta distribution (Pennington 1996, Stefansson 1996) that were weighted by stratum area. Even with these corrections, the estimated values of population growth rate were very noisy. In general, the value of λ has little influence on elasticities, relative to age at maturity or adult survival (Heppell et al. 2000a), and because $\lambda = 1$ is often used as a fitness boundary in life history analyses, we applied Eqs. 1–5 using the estimated value of population growth rate and the value assuming $\lambda = 1$, which we will call the stationary case.

The life history parameters that we used to estimate elasticities of rockfish are shown in Table 1 and the results in Figs. 1 and 2. The elasticities that we obtained when we assumed a stationary population and when we estimated λ are highly correlated ($R = 0.74$ with all 16 species; $R = 0.94$ when bocaccio, an outlier, is removed from the analysis; Fig. 3), which might suggest that current age distributions are not too far from stationary. Over the 16 species, the elasticity of λ to changes in adult survival averaged about 0.30 ± 0.16 (mean \pm SD), elasticity of λ to changes in juvenile survival averaged 0.58 ± 0.22 , and elasticity of fertility averaged $0.12 \pm$

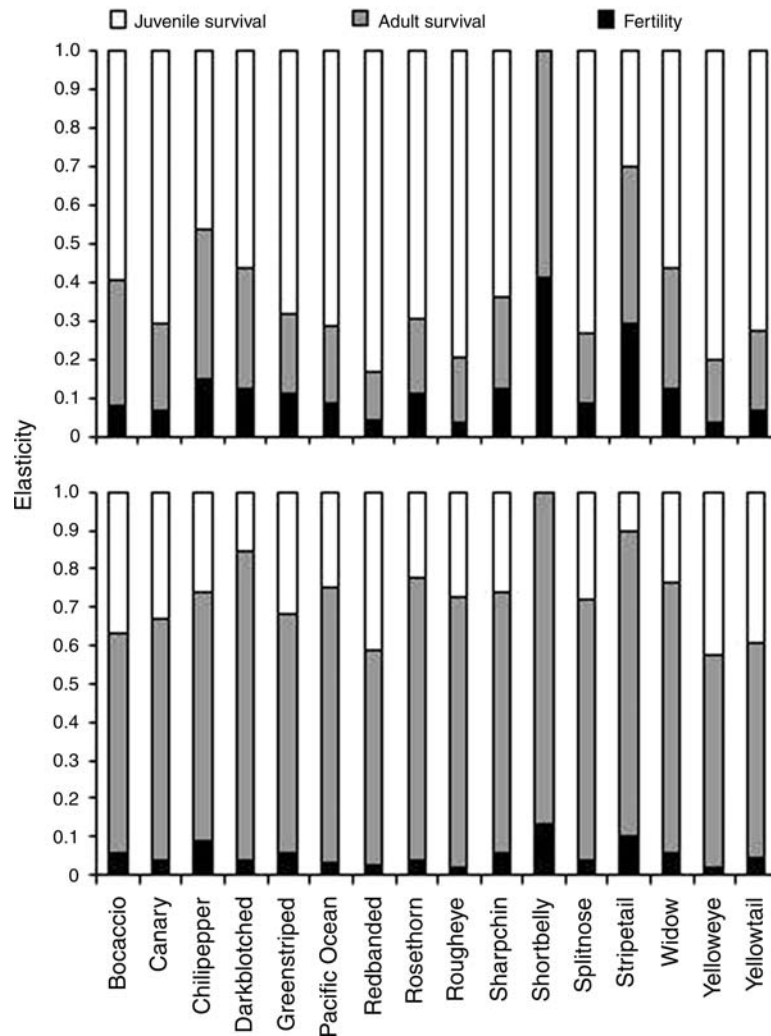


FIG. 1. The top panel shows elasticity results for 16 species of rockfish when mortality is estimated using the method of Pauly (1980); the bottom panel shows corresponding results using the method of Hoening (1983).

0.10. However, the relative importance of stage-specific vital rates differed greatly among species (Fig. 1) and depended upon the method that we used to estimate mortality rate. For instance, elasticities for stripetail rockfish were approximately evenly distributed among adult survival, juvenile survival, and fertility, but elasticity of juvenile survival was low in species such as bocaccio and high in species such as redbanded rockfish. When maximum age is log-transformed, nearly 60% of the among-species variance in juvenile elasticity is explained by maximum age ($r^2 = 0.58$, $P < 0.001$; Fig. 4); this is not unexpected because elasticity depends upon age at maturity (Heppell et al. 2000a), which is generally correlated with maximum age (Beverton 1992).

Heppell et al. (1999) used a plot similar to Fig. 1 in a comparative analysis of elasticities for long-lived marine species, and Gerber and Heppell (2004) use elasticities to compare the relative effects of protection through marine reserves. In the latter paper, the elasticities were

calculated for changes in mortality rates, rather than survival rates.

DENSITY-DEPENDENT CASE

We now turn to the case in which density dependence is important for population dynamics, which would apply if at least part of the reason for the decline in population size is due to habitat destruction or if the population is near carrying capacity.

The general situation

We let $A(t)$ denote the population size of adults at time t . If the age at maturation is τ , then we can write

$$A(t+1) = e^{-M_A}A(t) + R[A(t-\tau), \xi(\tau)] \quad (7)$$

where M_A is the annual rate of adult mortality (which includes natural and fishing mortality) and $R[A(t-\tau), \xi(\tau)]$ is the reproduction by adults at time $(t-\tau)$, where $\xi(\tau)$ represents all of the stochastic processes that occur

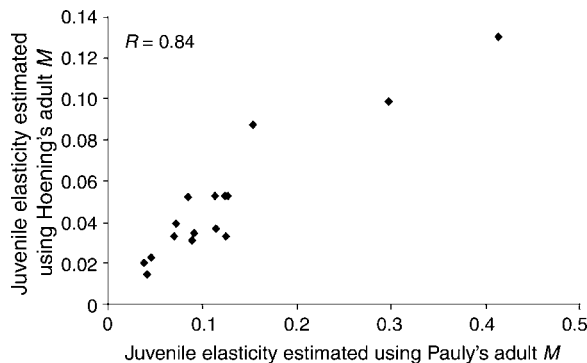


FIG. 2. Although results in Fig. 1 show strong qualitative differences, there is significant correlation in the juvenile elasticities estimated using the two methods for estimating mortality, M .

between reproduction and recruitment to the adult population. The precise form of the recruitment function will depend upon the life history characteristics of the species of interest. We next give an example for the rockfish.

A Sebastes-like life history

We now use three life history stages: surviving pelagic larvae, settled juveniles, and sedentary adults. We understand all variables to represent densities, use an annual time scale (as appropriate for temperate fish), and assume that the number of presettlement larvae, $L(t)$, produced by $A(t)$ adults in year t is

$$L(t) = fe^{-M_L}A(t)e^{X_\sigma(t)} \tag{8}$$

where f is average adult fecundity, M_L is mortality during the pelagic phase, and $X_\sigma(t)$ is a normally distributed random variable with mean $-(\sigma^2/2)$ and variance σ^2 (so that $E\{e^{X_\sigma(t)}\} = 1$), that accounts for variability in fecundity and larval survival.

We assume that density dependence acts during the settlement phase (Hixon and Webster 2002, Osenberg et al. 2002) and that the pelagic phase is relatively short, so that larvae produced in year t also settle in year t . We

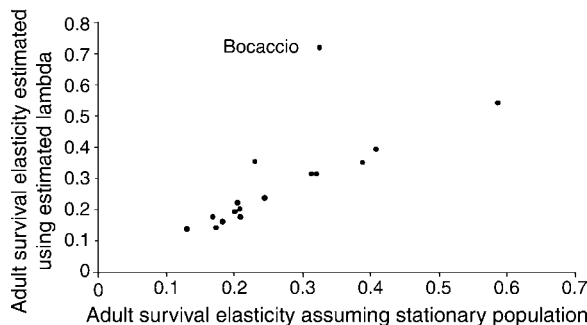


FIG. 3. There is also strong and significant correlation between the adult survival elasticity when the empirically estimated value of λ is used and the value of $\lambda = 1$ is used.

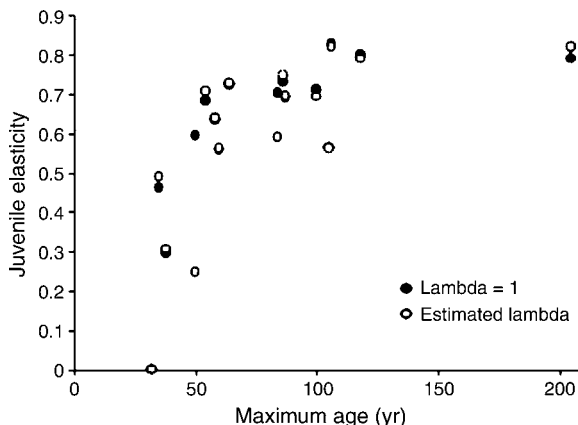


FIG. 4. Nearly 60% of the among-species variance in juvenile elasticity is explained by maximum age ($r^2 = 0.58$, $P < 0.001$).

describe density dependence at settlement by $x/(1 + bx)$ so that juveniles in year t , $J(t)$, are given by

$$J(t) = \frac{L(t)}{1 + bL(t)} = \frac{fe^{-M_L + X_\sigma(t)}A(t)}{1 + bfe^{-M_L + X_\sigma(t)}A(t)} \tag{9}$$

where b measures the intensity of density dependence of larval settlement.

Because the age at maturation is τ , adults in year t , $A(t)$, are given by

$$A(t) = e^{-M_A(t-1)}A(t-1) + S_J(t-\tau, t)J(t-\tau) \tag{10}$$

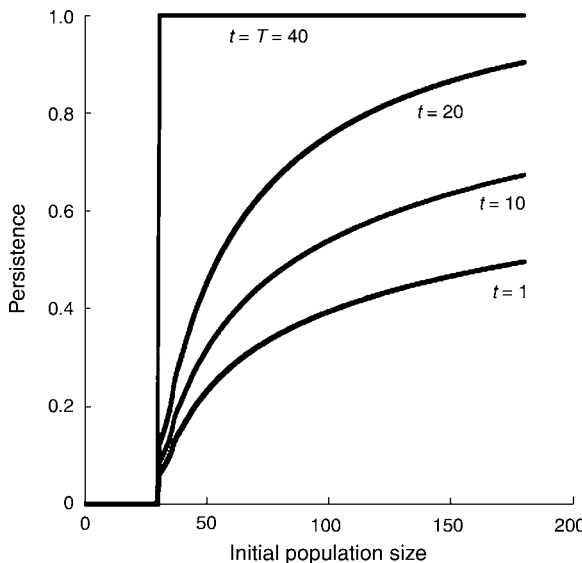


FIG. 5. Results of the backward iteration for the computation of persistence, for $M_A = 0.2$, $M_J = 1.6$, $f = 2 \times 10^7$, $\exp(-M_L) = 2.5 \times 10^{-7}$, $b = 0.006$, and $\sigma = 2$; here the deterministic steady state is about 150. We use a time horizon of $T = 40$ years and critical value of 20% of the deterministic steady state. Initial population size refers to $A(t)$, where $t = 40$, 20, 10, or 1. Persistence is $\Pr\{A(s) > A_c \text{ for } t \leq s \leq T | A(t) = a\}$.

where $S_j(t - \tau, t)$ is the fraction of juveniles that survive from year $t - \tau$ to year t . If $M_j(t)$ is the juvenile mortality rate in year t , then

$$S(t - \tau, t) = \exp\left[-\sum_{k=t-\tau}^{t-1} M_j(k)\right]$$

where k is the index of time (years). Once again, these mortalities are understood to reflect total mortality (natural plus direct and indirect fishing).

We combine these equations to obtain a single equation for the dynamics of $A(t)$, in terms of $A(t - \tau)$:

$$A(t) = e^{-M_A(t-1)}A(t-1) + S(t - \tau, t) \frac{fe^{-M_L+X_\sigma(t-\tau)}A(t-\tau)}{1 + bfe^{-M_L+X_\sigma(t-\tau)}A(t-\tau)}. \quad (11)$$

The population characterized by Eq. 11 is limited by density-dependent processes at the stage of settlement. That is, when X_σ happens to be large, the recruitment associated with Eq. 10 approaches $1/b$. In the computations that follow, we pick parameters that characterize a “generic” rockfish species (Halderson and Love 1991, Adams and Howard 1996, Love et al. 2002), but none in particular.

In a fully general situation, we could append dynamics for the mortality rates and random variables. Alternatively, we could consider an open population in which local adult population size and larval input are uncoupled, as would be most appropriate for a small and isolated local habitat. Each of these cases is included in the Appendix. We also note that there are circumstances in which larvae, rather than adults, are the subject of a census for purposes of estimating population dynamics (e.g., Ralston et al. 2003). In that case, one would rewrite the equation in terms of larval dynamics.

Persistence with a one-year time lag

We now specialize to the case of a one-year time lag. There are no rockfish species for which this situation applies, but there are other species; by using a one-year time lag, we are able to explain the methods, which generalize (see Mangel and Clark [1988], Clark and Mangel [2000]), as simply as possible. If the time lag in recruitment to the adult population is only one year, the general case becomes

$$A(t + 1) = e^{-M_A}A(t) + R[A(t), X_\sigma] \quad (12a)$$

and for the rockfish life history,

$$A(t) = e^{-M_A}A(t-1) + e^{-M_j} \frac{fe^{-M_L+X_\sigma}A(t-1)}{1 + bfe^{-M_L+X_\sigma}A(t-1)}. \quad (12b)$$

The dynamics described in Eq. 12b depend upon the habitat-related parameters of adult mortality, juvenile mortality, fecundity, and density-dependent juvenile settlement. We thus characterize the habitat by the

values of $\{M_A, M_j, f, b, \sigma\}$, considering that larval mortality is a global parameter and not localized to a particular habitat.

We now append two conditions exogenous to the biological dynamics. First, we introduce a time horizon T over which persistence, defined precisely below, is evaluated. Setting a value of T is not a scientific question; rather it is a policy issue. Second, we introduce the probability that the population remains above a critical size A_c between the current time t , at which the population size is $A(t) = a$, and the time horizon. Setting the value of the critical level is also a policy decision. If the habitat parameters determine the suite of vital rates, which in turn determine the successful persistence of the population, then these parameters become a metric with which habitats can be evaluated.

To compute persistence (p), we define (Mangel and Clark 1988, Mangel and Ludwig 1992, Clark and Mangel 2000):

$$p(a, t | A_c, T) = \Pr\{A(s) > A_c \text{ for } t \leq s \leq T | A(t) = a\}. \quad (13)$$

The critical value A_c , like the time horizon T , needs to be determined exogenously of the population dynamics (unless there is an Allee level), but once it is determined, the computation of persistence is endogenous to the habitat. One choice is $A_c = 1$, so that $A(t)$ falling below the critical value corresponds to local extirpation of the stock in the habitat under consideration. Other values of A_c , greater than 1, correspond to varying levels of population size. For example, if we replace Eq. 12a by its deterministic equivalent,

$$A(t + 1) = e^{-M_A}A(t) + R[A(t)] \quad (14)$$

it is then a simple matter to compute the steady-state population size \bar{A} for which $\bar{A}(1 - e^{-M_A}) = R(\bar{A})$. For example, the deterministic steady state of Eq. 11 is

$$\bar{A} = \frac{1}{bfe^{-M_L}} \left(\frac{e^{-M_j - M_L} f}{1 - e^{-M_A}} - 1 \right) \quad (15)$$

as long as the term in brackets in Eq. 15 is positive (in which case, the steady state at $A = 0$ is unstable). For shorthand, we refer to as \bar{A} the deterministic steady state. Thus, another choice of A_c is that it is a fraction (e.g., 20%, 35%, or 60%; see Mangel [1998, 2000a, b] for a discussion of these choices) of the deterministic steady state. This choice is a mixture of endogenous (habitat parameters determining the deterministic steady state) and exogenous (the fraction of the steady state determining the critical level) factors. In either case, A_c is a management concept; there is no biologically “good” choice, except perhaps the one that ensures the stock is not extinct.

The persistence criterion can be evaluated rapidly and efficiently by a method analogous to stochastic dynamic programming (Mangel and Clark 1988, Mangel and Ludwig 1992, Clark and Mangel 2000). First, when $t =$

T , $p(a, T | A_c, T) = 1$ if $a > A_c$ and $p(a, T | A_c, T) = 0$ otherwise. Second, for times previous to T , $p(a, T | A_c, T)$ satisfies the stochastic iteration equation

$$p(a, t | A_c, T) = E_{X_\sigma} \{ p(ae^{-M_A} + R(a, X_\sigma), t + 1 | A_c, T) \} \tag{16}$$

where $E_{X_\sigma}\{\cdot\}$ denotes the average over the distribution of X_σ . For the rockfish life history, Eq. 16 specializes to:

$$p(a, t | A_c, T) = E_{X_\sigma} \left[p \left(ae^{-M_A} + e^{-M_J} \frac{fe^{-M_L + X_\sigma a}}{1 + bfe^{-M_L + X_\sigma a}}, t + 1 | A_c, T \right) \right]. \tag{17}$$

We solve Eqs. 16 or 17 recursively in t , starting at $t = T - 1$. When $t = 1$ is reached, we have computed the probability that the adult population will stay above the critical level for the entire planning horizon (Fig. 5), given the initial population size $A(1) = a$ and, in the case of Eq. 17, the habitat parameters $\{M_A, M_J, f, b, \sigma\}$. Note that the curves for $T = 1, 10$, or 20 in Fig. 3, regardless of the choice of critical value, have the same general shape. This is a general property of the persistence probability. In particular, when $t \ll T$ and a is bounded away from the critical value,

$$\frac{p(a, t - 1 | A_c, T)}{p(a, t | A_c, T)} \approx \delta < 1 \tag{18}$$

where δ is a constant, with interpretation that it is the probability that the population will persist for one more time step after having persisted for a long time (Mangel and Clark 1988, McNamara 1991). Thus, when $a > A_c$ and $t < T$, $p(a, t | A_c, T) \approx \delta^{T-t}$.

The solution of Eq. 17 allows us to explore how the suite of habitat parameters $\{M_A, M_J, f, b, \sigma\}$ shapes the probability of persistence over the time horizon. In this manner, it will allow us to identify the most essential habitats.

DISCUSSION

In this paper, we have attempted to add two new tools to the ecological toolbox (*sensu* Norris 2004) to help in the identification of habitats of conservation priority. For harvested species, densities may drop below the point where density dependence is important (but see Levin and Grimes 2002, Achord et al. 2003). In these instances, elasticities of the population growth rate with respect to adult survival and fecundity and juvenile survival provide metrics that can be used to identify the most sensitive species and the most sensitive life history stage within a species. By corollary, the habitats associated with the most sensitive species and life history stages then become the ones of highest concern. That said, the evaluation of the importance of different habitat types needs to be carefully considered. For example, one should not misconstrue results to mean that protection of some life stages is unimportant, as

long as the “most sensitive life stages” are protected. Elasticity analysis provides information on the *relative* sensitivity of population growth rate to proportional changes in survival or other vital rates. It does not tell us that other life stages (or habitats) are expendable. The cause and effect that is implied by equating high elasticities with “importance” of habitat is a retrospective calculation and thus provides a means for prioritizing habitat protection or restoration for enhancement. More importantly, elasticity analysis alone does not provide enough information to “rank” management proposals; the relative change in the vital rates affected must also be estimated (Heppell 1998). For example, in rougheye rockfish, juvenile survival elasticity is around four times greater than adult survival elasticity. But, if management can increase the survival of adult four times more than it can increase the survival of juveniles, management action aimed at protecting adults (e.g., reduction of harvests) would have an equivalent result (or nearly so—actually, a bit higher). Furthermore, for a population that is not at equilibrium, the elasticities measured during a nonequilibrium phase will reflect the proportional “opportunism” of various life history stages, when density has lesser effect. Thus conservation efforts aimed to protect stages with high elasticity should be seen as a strategy to allow a stock to rebuild, but should also plan that as abundance increases, elasticities may change. As the stock rebuilds, a further analysis may reveal a different elasticity profile, even if density-dependent effects are not important.

The simplified life history models used in the elasticity analysis require an average fertility rate for all adults, even though fecundity clearly increases with age/size in fishes and survival of larvae may also increase (Berkeley et al. 2004), and such average rates neglect the response of λ to temporally fluctuating environments (Pico et al. 2003, Tuljapurkar et al. 2003, Tolimieri and Levin 2005). However, these simple models allow a quick calculation with minimal data. A comparison of the results of such simple models with those from full age-structured models (Leslie matrices) that include an increase in fecundity with age would be worthwhile (especially if done with a known operating model), but this is beyond the scope of this paper. A similar useful comparison would be between the use of minimum age of first reproduction, instead of the age when 50% of a cohort is mature. Recent work (Grant and Benton 2003) on density-dependent elasticity analysis may represent the beginning of a unification of the two approaches that we described here.

When density-dependent factors cannot be ignored, the metric of persistence allows one to identify those habitats for which the associated vital rates lead to the highest level of long-term presence of the species under consideration. Given enough information about vital rates, one can compute the probability of persistence rapidly and accurately using a method of stochastic iteration. Furthermore, because this model shows the

interplay of the habitat parameters $\{M_A, M_J, f, b, \sigma\}$, it could be useful for identifying the minimum acceptable levels of adult mortality and juvenile mortality to assure persistence, which could be achieved through protection of one "habitat" (perhaps defined broadly) or a suite of habitats. This model can also be helpful for identifying the "essentialness" of a habitat based on how limiting it is (which elasticity analysis cannot help with at all). As $b \rightarrow 0$, the life history model becomes identical to the model that underlies the elasticity analyses, so that for weak density dependence, the two approaches converge, but allow different representations of the life histories. Although we illustrated the method using one-year time lags, this was done for simplicity. With multiyear time lags, the equations of stochastic iteration become more complicated, but the principle for the computation remains unchanged.

Because management is an "incredibly tortuous negotiation process" (A. Rosenberg, *personal communication*), we must be pragmatic in the sense of Farber (1999):

Being pragmatic does not mean the rejection of rules or principles in favor of ad hoc decision making or raw intuition. Rather, it means a rejection of the view that rules, in and of themselves, dictate outcomes . . . Hard policy decisions can't be programmed into a spreadsheet . . . But we also need an analytic framework to help structure the process of making environmental decisions . . . Rather than rigid rules or mechanical techniques, we need a framework that leaves us open to the unique attributes of each case, without losing track of our more general normative commitments.

In the context of this work, we understand that being pragmatic means that the kinds of tools developed here will help to guide thinking about habitat management, but will not be applied with automatic behavior (see Caddy 2002, Quinn 2004).

We have ignored multispecies and other ecological effects (Chesson 2000), although, in principle, they could be included in a generalization of the model, e.g., through adaptive dynamics and invasibility plots that would allow one to examine trade-offs between competition and predation (Keeling 2000), competition and colonization (Levine and Rees 2002), or competition and longevity (Bonsall and Mangel 2004). Similarly, the results can be extended to include characteristics such as larval quality (Shima and Findlay 2002) by using methods similar to those in dynamic state variable models of behavior (Mangel and Clark 1988, Mangel and Ludwig 1992, Clark and Mangel 2000). We have explicitly ignored metapopulation considerations, including the explicit treatment of the spatial variation of fishing mortality (other than through its inclusion in the mortality rates). When population dynamics are fluctuating so that extinction is ultimately certain, the notion of sources and sinks becomes less clear. Certainly, to

identify sinks as essential without protecting sources is guaranteed to lead to disaster (Mangel et al. 1996, Cooper and Mangel 1999, Mangel 2003). Putting persistence into a metapopulation context remains an open question. Finally, we have ignored changing life history traits as a result of fishing pressure (Conover and Munch 2002). Each of these represents an important extension of the basic ideas introduced here.

Persistence is only the first component of reproductive value (Fisher 1930 [1958 reprint]) and there are arguments for incorporating reproductive value into management (Leaman 1991, Berkeley et al. 2004). The methods that we discuss here can be extended to include reproductive value, although the computations become more cumbersome (e.g., Mangel 1987:Appendix 1; Mangel and Clark 1986).

Interest in conserving and managing the world's habitats is intense and widespread, but limited time and money require the judicious use of these resources (McClure et al. 2003). Simple assessments that are based on the presence of a targeted species may have heuristic appeal, but do not aid, and may actually hinder, the work that needs to occur (Beck et al. 2001, Smallwood 2001). The presence of individuals may connote a functional significance of the habitat, but it may just as easily be a meaningless metric if the habitat does not alter vital rates or if the location is an ecological sink. Although detailed quantitative approaches linking habitat to demography are available (e.g., Haas et al. 2004, Levin and Stunz 2005), such approaches require detailed data that are lacking for most species of conservation concern. The approaches that we develop here provide the ability to use existing knowledge to prioritize habitat protection. A shortage of data may initially make our approach somewhat coarse; however, it acknowledges that conservation depends not only on protecting sites where organisms occur, but also on protecting the ecological processes that allow populations to persist and possibly expand.

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APPENDIX

Extensions of the approach described in *Methods* (Ecological Archives A016-031-A1).