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LETTER

Transient responses of fished populations to marine reserve establishment

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Abstract

Implementation of no-take marine reserves is typically followed by monitoring to ensure that a reserve meets its intended goal, such as increasing the abundance of fished species. The factors affecting whether abundance will increase within a reserve are well characterized; however, those results are based on long-term equilibria of population models. Here we use age-structured models of a generic fish population to analyze the short-term transient response. We show that it may take decades for a fished population to reach postreserve equilibrium. In the meantime, short-term transient dynamics dominate. During the transient phase, population abundance could either remain unchanged, decrease, or exhibit single-generation oscillations, regardless of the eventual long-term result. Such transient dynamics are longer and more oscillatory for populations with heavier fishing, older ages at maturity, lower natural mortality rates, and lower larval connectivity. We provide metrics based on demographic data to describe the important characteristics of these postreserve transient dynamics.

Introduction

Marine reserves are growing in popularity as a conservation and management tool (Wood *et al.* 2008), hence there is a need to determine whether reserves meet their intended goals in an adaptive management process (e.g., Hamilton *et al.* 2010; McCook *et al.* 2010). The majority of marine reserves produce an increase in the density, size, and biomass of fished species within their boundaries, although there are exceptions (Lester *et al.* 2009). However, several meta-analyses have produced different conclusions regarding the time scale over which these increases occur, from rapid, asymptotic increases (Halpern & Warner 2002) to gradual increases over time (Micheli *et al.* 2004; Claudet *et al.* 2008) to no net effect of reserve age on population responses (Côté *et al.* 2001). Recently, Molloy *et al.* (2009) found that fish densities gradually increased with reserve age, but species differed greatly in their responses. A serious difficulty in evaluating these findings is the dearth of population dynamic models to predict the transient response of populations to marine reserves.

In ecology, there is increasing appreciation of the importance of transient dynamics. Changes in management will necessarily perturb ecological systems away from dynamic equilibrium (Hastings 2004, 2010; Caswell 2007; Ezard *et al.* 2010); therefore, transient dynamics may be especially important when harvest of a heavily exploited population is abruptly stopped, such as when a no-take reserve is implemented.

Most modeling analyses of fished populations within marine reserves have focused on long-term dynamic equilibria (e.g., Mangel 1998; Botsford *et al.* 2001; Gerber *et al.* 2003; Costello *et al.* 2010; White *et al.* 2010a, b).

Equilibrium conditions reflect the long-term effects of reserve designs, and in general they have indicated that the abundance of fished species will increase within a reserve (White *et al.* 2011). However, equilibrium-based analyses do not explore how quickly that effect will appear. The time it will take for abundance to increase within reserves is crucial information for monitoring programs. Understanding transient dynamics is particularly important as the goals of reserve monitoring become more sophisticated, moving from simply determining whether abundance increases within the reserve to evaluating whether and how to alter reserve management (Gerber *et al.* 2005).

Here we use age-structured population models to investigate the biological and management factors that affect the rate and pattern of that increase in abundance. We show that populations could exhibit slowly increasing, decreasing, or oscillatory trajectories immediately after reserve implementation even when abundance would eventually increase over the long term. We also describe metrics that could assist empirical assessments of reserve success by quantifying the expected duration and intensity of transient dynamics.

Methods

Size-selective fishing has two main effects on a population: (1) an immediate increase in mortality, reducing abundance and truncating the age distribution as older fish are removed, and (2) a longer term reduction in recruitment due to reduced abundance of reproductive age classes. When fishing stops, the time scale of the population response will reflect both processes: the "filling in" of the age distribution as it returns to the unfished state, and the gradual increase in reproduction due to increased abundance of adults, which might accelerate with the filling in of older, more fecund individuals. We investigated both these processes, focusing on the dynamics of the type of organism typically protected in marine reserves: a fish with a dispersive larval stage and relatively sedentary adult stage.

Case 1 (open population): filling in the age distribution

To investigate the filling in of the age distribution absent any changes in reproduction, we first consider the case of a single reserve that receives all of its larval recruits from elsewhere; that is, a demographically "open" population. This represents a reserve containing a small fraction of a larger population.

We model a population with n age classes; fish are targeted by the fishery after age a_c. All ages have natural mortality rate M and ages $a \geq a_c$ experience fishing mortality rate F (see Table 1 for glossary of symbols). The dynamics of the fished population are:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t + \mathbf{R}, \tag{1}$$

where $\mathbf{N}_t$ is a $n \times 1$ vector of abundance in each age class a at time t, $N_{a,t}$. $\mathbf{A}$ is an $n \times n$ matrix describing adult survivorship:

$$\mathbf{A} = \begin{bmatrix} 0 & & & & \\ e^{-(M+\hat{F}_1)} & & & & \\ & e^{-(M+\hat{F}_2)} & & & \\ & & \ddots & & \\ & & & e^{-(M+\hat{F}_{n-1})} & 0 \end{bmatrix}, \tag{2}$$

where $\hat{F}_a = 0$ for $a < a_c$ and $\hat{F}_a = F$ otherwise. $\mathbf{R}$ is an $n \times 1$ vector with the density of new recruits, R, in the first entry and zeros elsewhere.

Case 2 (closed population): filling in + changes in reproduction

Next, to focus on the combined effects of filling in and reproduction, we consider the case of a population within a reserve that has extremely high local retention and/or is isolated from external sources of larvae, so that the population is demographically "closed." Although we focus on marine reserves, this case could also represent the effects of a stock-wide fishing closure in a traditional, nonspatial management setting. The model in this case is

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t, \tag{3}$$

in which the first row of $\mathbf{A}$ now accounts for reproduction, and f_a is the per-capita fecundity, measured in recruits, of individuals in age class a:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & \dots & f_{n-1} & f_n \\ e^{-(M+\hat{F}_1)} & & & & \\ & e^{-(M+\hat{F}_2)} & & & \\ & & \ddots & & \\ & & & e^{-(M+\hat{F}_{n-1})} & 0 \end{bmatrix}. \tag{4}$$

Defining a_m as the age at maturity, $f_a = 0$ for $a < a_m$, and is a function of length, $f_a = \alpha L_a^{\beta}$ for $a \geq a_m$ (α and β are constants; note that α also accounts for larval survival). The mean length of fish in each age class, L_a, follows the von Bertalanffy equation:

$$L_a = L_\infty(1 - e^{-k(a-a_0)}), \tag{5}$$

where L_∞ is the asymptotic maximum size, k is the growth rate, and a_0 is the age at length zero.

Table 1 Symbols used in the article

Symbol	Description	Comments
State variables		
$\mathbf{N}_t$	$n \times 1$ vector of abundance in each age class, a	Sub-elements $\mathbf{N}_{a,t}$. N_0 is the initial conditions when the reserve is implemented
$\mathbf{R}$	$n \times 1$ vector of recruit abundance	$R_1 = R$, zeros elsewhere
Demographic parameters		
$\mathbf{A}$	Population projection matrix	
a	Age class	
a_0	Age at length 0	
a_c	Age at entry to fishery	
a_m	Age at maturity	
α	Length-fecundity coefficient	
β	Length-fecundity exponent	
f_a	Fecundity at age a	
k	von Bertalanffy growth rate	
L_a	Length at age a	
L_∞	Asymptotic maximum length	
M	Natural mortality rate	
n	Number of age classes	
ϕ	Constant of proportionality between mean and standard deviation of length	
Management factors		
T_f	Duration of fishing prior to reserve	
F	Fishing mortality rate	
$\hat{F}_a$	Age-specific fishing mortality rate	
Transient metrics		
λ_i	ith right eigenvalue of $\mathbf{A}$	λ_1 determines asymptotic geometric growth rate. λ_2 is often complex, and describes the primary oscillatory component of the transient
λ_{init}	Initial trajectory of transient	Determined by θ. Deviation from λ_1 determines amplitude of oscillations
$\mathbf{w}_i$	ith right eigenvector of $\mathbf{A}$	Proportional to SAD*
$\mathbf{v}_i$	ith left eigenvector of $\mathbf{A}$	
D	Distance from SAD	"As the road turns" distance (Equation 7)
θ	Angle between $\mathbf{N}_0$ and SAD	"As the crow flies" distance; determines λ_init (Equation 6)
P	Period of transient oscillations	Usually determined by complex part of λ_2 (Equation 9)
ρ	Rate of return to SAD	Determined by ratio of λ_1 to λ_2 (Equation 8)

Notes: *SAD = stable age distribution.

Now $\mathbf{A}$ is a Leslie matrix, so the model has asymptotic (i.e., long-term) behavior described by the dominant eigenvalue λ_1 of $\mathbf{A}$: geometric growth ($\lambda_1 > 0$) or decline ($\lambda_1 < 0$). In the long term, $\mathbf{N}$ will converge to a stable age distribution (SAD), i.e., a consistent proportion of individuals in each age class, given by the dominant right eigenvector $\mathbf{w}_1$ of $\mathbf{A}$. As this model lacks density dependence, there is no stable nonzero equilibrium density. However, it is adequate for describing the initial transient response of a population that is at low density because of harvesting (see Appendix S1, Figures S1, S2, S3).

Model analysis

We simulate the dynamics of a population that starts at an unfished SAD. Fishing at rate F begins at time $t = T_f$ ($T_{-f} < 0$) and continues until reserve establishment at $t = 0$, when the fishing rate changes from F to 0. We then examine the response of the population as it returns to the unfished SAD.

We focus on age-structure dynamics in our results, but also illustrate the consequences for size structure, since the latter is more commonly observed. When constructing size distributions, we represent natural variability in size by assuming that the standard deviation of L_a was equal to ϕL_a, where ϕ is a constant of proportionality (Table S1). Additionally, we show age-structured results for both total population abundance and the abundance of fished age classes only. The latter exhibits dynamics similar to the former, but monitoring programs may be more likely to observe only the latter. Total population abundance should also be more sensitive to stochastic variation in larval supply, so the deterministic patterns we describe here may be more easily observed in the dynamics of older age classes.

We investigate how the magnitude and tempo of the population response to reserve implementation depends on both management factors (F, a_c) and life-history parameters (a_m, M, k, β). As a baseline, we use life-history parameters for the kelp rockfish (*Sebastes atrovirens*), a nearshore species that is a focus of marine reserve protection in coastal California, USA (White & Rogers-Bennett 2010, Table S1). We also analyze the local sensitivity of results for all parameter values.

In order to examine the effects of life-history variation, independent of changes to the overall population growth rate, we adjust the larval survival parameter α so that all simulations of the closed population model had instantaneous growth rate $\lambda_1 = 1.02$ when $F = 0$. This growth rate is an arbitrary choice intended to show a modest positive increase within the reserve; our analytical results are not sensitive to the value of λ_1. Generally speaking, a faster growth rate (larger value of λ_1) would shorten the time scale over which the dynamics we describe would be observed.

Results

Case 1 (open population): filling in the age distribution

An example of the pattern of change in population age structure following reserve implementation in an open population is shown in Figure 1. The "missing" older age classes that were subject to fishing ($a \geq a_c$) gradually fill in as the population approaches the unfished SAD (Figure 1a). This filling-in produces a similar effect in the population size distribution (Figure 1b).

The change in age structure (Figure 1) is accompanied by an asymptotic increase in population density after reserve implementation (Figure 2). We derived an analytical description of this asymptotic increase (see Appendix S2) that shows that the difference between the abundance of the fished population and the unfished equilibrium declines exponentially with rate M after reserve implementation. For a continuous age distribution, the maximum proportional increase relative to the fished population at $t = 0$ is

$$\lim_{t\to\infty} \frac{N'_t}{N'_0} = \frac{M + F}{M}, \tag{6}$$

where N'_t is the total density of age classes $a \geq a_c$ at time t. For a discrete age distribution with no maximum age, the expression is more complex but has a similar interpretation:

$$\lim_{t\to\infty} \frac{N'_t}{N'_0} = \frac{1 - e^{-(M+F)}}{1 - e^{-M}}. \tag{7}$$

The time scale over which the maximum increase occurs is equal to $n - a_c$, the time required for all age classes

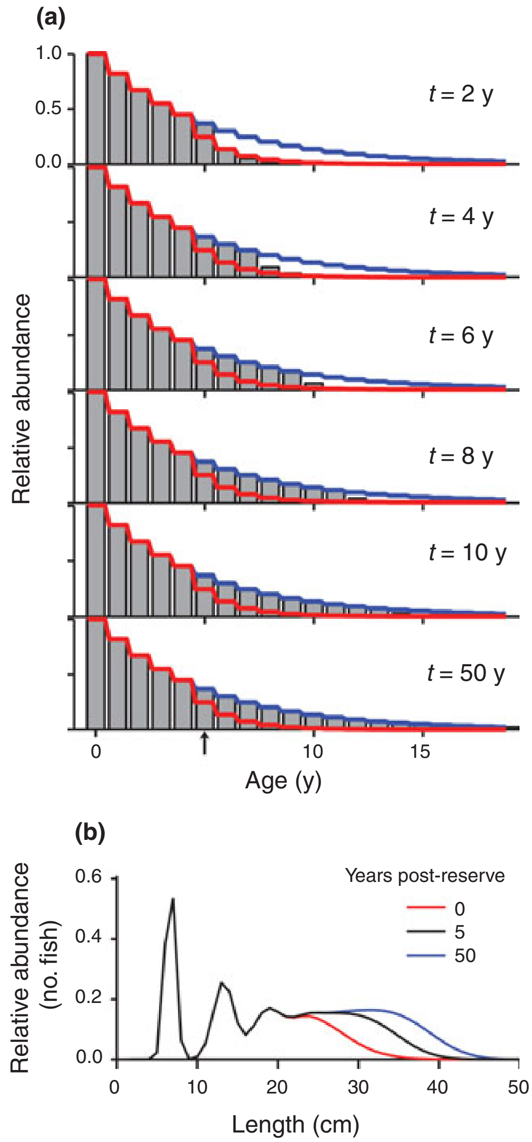

Figure 1 Example of the age and size distributions "filling in" after marine reserve implementation in the open population model. Time is expressed in years after reserve implementation, and abundance is shown relative to the abundance of the first age class. (a) Age distribution in each year (gray bars); also shown are the age distribution at $t = 0$ (after fishing at $F = 0.8$ per year for 50 years; red curve) and the unfished age distribution (blue curve). (b) Size distribution of the population 0, 5, and 50 years after reserve implementation (curves overlap for sizes < 20 cm). This simulation used the baseline parameters given in Table S1 for kelp rockfish; age of entry to the fishery, a_c, is indicated by arrow.

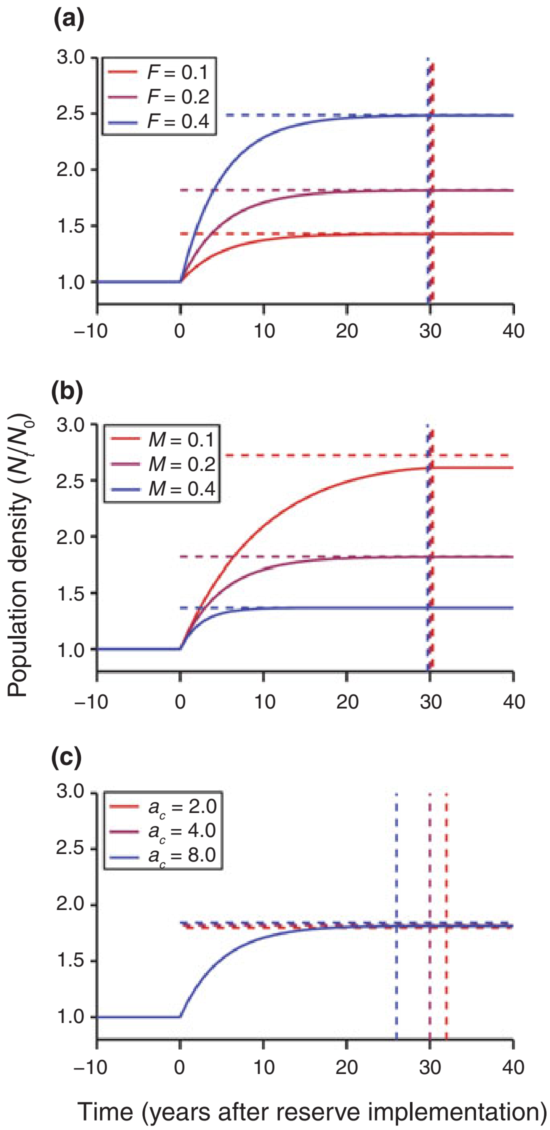

Figure 2 Change in population size following reserve implementation in the open population model. Each panel shows simulations with the same parameters (given in Table 1) except for (a) fishing rate, F (per year); (b) natural mortality rate, M (per year); and (c) age of entry to the fishery, a_c (y). Each simulation is shown as a solid curve for each different value of these variables as indicated by legend (all three curves overlap in panel c). Vertical dashed lines indicate the predicted end of the transient "filling in" period ($n - a_c$). Horizontal dashed lines indicate the predicted asymptotic postreserve density (Equations 5), with dashed lines corresponding to the solid curve of the same color. Population density is expressed as a ratio relative to density just prior to reserve implementation at $t = 0$ and is calculated for fished age classes ($a \geq a_c$) only.

to have existed without fishing (Figure 2). The approximation for the maximum increase (Equation 5) and time scale of the increase are less accurate if $T_f < (n - a_c)$ or if n is not much larger than a_c.

We derived these results using a linear model without density dependence, although by assuming constant recruitment from an external source we implicitly assume that there is density-dependent regulation elsewhere in the metapopulation. If density-dependent mortality occurs, it likely falls most heavily on the youngest age classes (Caley *et al.* 1996), not the fished age classes covered by our analysis. In a population with intra-cohort density-dependent mortality, density dependence should remain relatively constant with constant recruitment, and would not affect our predictions regarding the relative abundance of older age classes.

Case 2 (closed population): filling in + changes in reproduction

For a closed population there is a greater variety of potential responses to marine reserve implementation than in an open population. For example, two populations with the same demographic parameters but fished at different rates could show a rapid increase in density following reserve implementation ($F = 0.1$ per year; Figure 3a) or a continued decline followed by an oscillatory increase in density ($F = 0.8$ per year; Figure 3b). Regardless, once the population reaches its SAD, it exhibits long-term dynamics determined by the dominant eigenvalue λ_1 of $\mathbf{A}$.

Any oscillations are due to the narrower age distribution produced by fishing during the years prior to reserve implementation. As the heavily fished population ($F = 0.8$ per year) declines in abundance, the number of new recruits (a_1) is much smaller each year, so the older unfished cohorts ($0 < a \leq a_c$) are relatively more abundant than they would be with less fishing. This produces a bulge in the age distribution just before the age of entry to the fishery (Figure 3d; see Mori *et al.* [2001] for an example of this effect). When fishing ceases, that bulge produces a resonant effect in population abundance as it moves through the now-unfished reproductive age classes (Figures 3d, f). This effect is smaller in a more lightly fished population (Figures 3c, e).

The intensity and duration of the transient following reserve implementation depends on two factors: the initial conditions (at the time fishing stops) and the life history of the fished species. Fortunately, the transient response of linear models with Leslie matrices is well studied (Caswell 2001). Using theoretical results from linear population models, we derived several quantities that describe the transient behavior of fished populations (see Appendix S3 for mathematical details). We illustrate the use of these quantities with examples of model populations that have been fished at different rates, F, and have a range of life-history parameters (in particular a_m) (Figure 4).

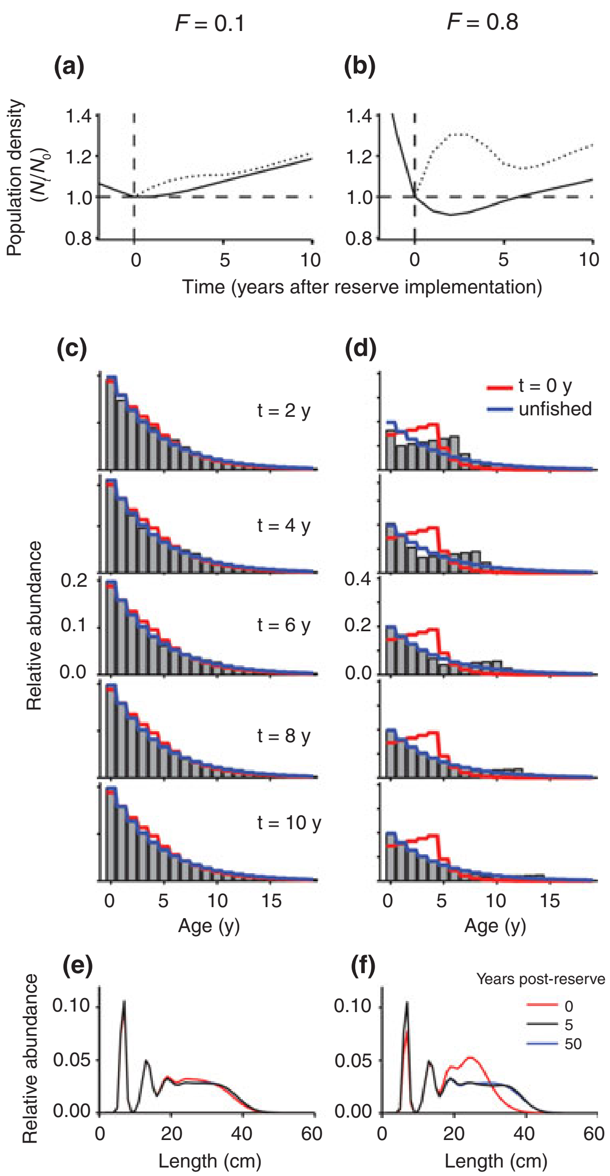

Figure 3 Differences in transient response due to differences in fishing rate, illustrated by the change in population size (a, b), age structure (c, d), and size structure (e, f) after reserve implementation in the closed population model. Simulations had the same demographic parameters (Table 1) but experienced fishing at rate (a, c, e) $F = 0.1$ per year or (b, d, f) $F = 0.8$ per year for $T_f = 50$ years prior to reserve implementation. In (a, b), population density is expressed as a ratio relative to density at $t = 0$, and is shown as density of all age classes (solid curve) or fished age classes only (dotted curve). In (c, d), the age distribution is shown in each year; the fished distribution at $t = 0$ (red curve) and unfished distribution (blue curve) are shown for comparison. Age and size distributions are shown as the proportion of total abundance in each age or size class.

First, we calculate the similarity of initial conditions to the unfished SAD, which will determine the initial trajectory of change in population density, λ_{init}. The similarity to the SAD can be expressed as an angle, θ, with smaller θ indicating that λ_{init} will be closer to λ_1 (Figures 4a,b). Note that in the examples shown here, $\lambda_{\text{init}} \leq \lambda_1$, so the overall population density continues to decline (Figures 4a,b); however, the fished age classes sometimes increase initially (Figure 4c) because of the propagation of a "bulge" in the age distribution like that in Figure 3d. We calculate θ by finding the angle between the vectors $\mathbf{N}_0$ and $\mathbf{w}_1$:

$$\theta = \arccos\left(\frac{\mathbf{N}_0 \cdot \mathbf{w}_1}{\|\mathbf{N}_0\| \, \|\mathbf{w}_1\|}\right), \tag{8}$$

where double vertical bars indicate a vector norm.

Second, we calculate D, the scalar distance from the SAD (Cohen 1979):

$$D = \left[\lim_{T\to\infty} \sum_{t=0}^{T} \left(\frac{\mathbf{N}_t}{\lambda_1^t} - \frac{\mathbf{w}_1 \mathbf{v}'_1}{\mathbf{v}_1 \mathbf{w}'_1} \mathbf{N}_0\right)\right], \tag{9}$$

where $\mathbf{v}_1$ is the dominant left eigenvector of $\mathbf{N}_0$. This distance is measured not "as the crow flies" (i.e., simply the difference in abundance of each age class, which is essentially measured by θ) but rather "as the road turns" (i.e., accounting for "the trajectory of age structures through which the population must pass" as it approaches the SAD; Cohen 1979, p. 172). Larger values of D are associated with longer transients (Figure 4). While θ estimates the initial trajectory, D affects the overall transient duration.

Third, we calculate ρ, the rate of convergence to asymptotic behavior. It is approximately proportional to the ratio of the first and second eigenvalues of $\mathbf{A}$:

$$\rho \approx \lambda_1 / |\lambda_2| \, . \tag{10}$$

The actual rate of convergence may deviate slightly from this estimate due to the effect of the remaining eigenvalues. Smaller values of ρ result in longer transients because the oscillatory components of $\mathbf{A}$, represented by λ_2 (and its complex conjugate in typical cases), are large relative to the exponential growth component represented by λ_1 (compare Figures 4a–b; the latter has $a_m = 8$ year and thus larger λ_2).

Last, we can calculate P, the period of oscillations in the transient, which is determined by λ_2:

$$P = 2\pi / \arctan\left(\frac{\mathrm{Im}\,(\lambda_2)}{\mathrm{Re}\,(\lambda_2)}\right), \tag{11}$$

where $\mathrm{Im}(x)$ and $\mathrm{Re}(x)$ denote the imaginary and real parts of x, respectively. P is approximately equal to the generation time (Caswell 2001; Figure 4). The amplitude of oscillations is determined by the deviation of the initial trajectory λ_{init} from the asymptotic trajectory, λ_1 (Figure 4).

The value of each of these transient metrics depends on the combination of fishing intensity and life-history parameters. These relationships can be calculated directly

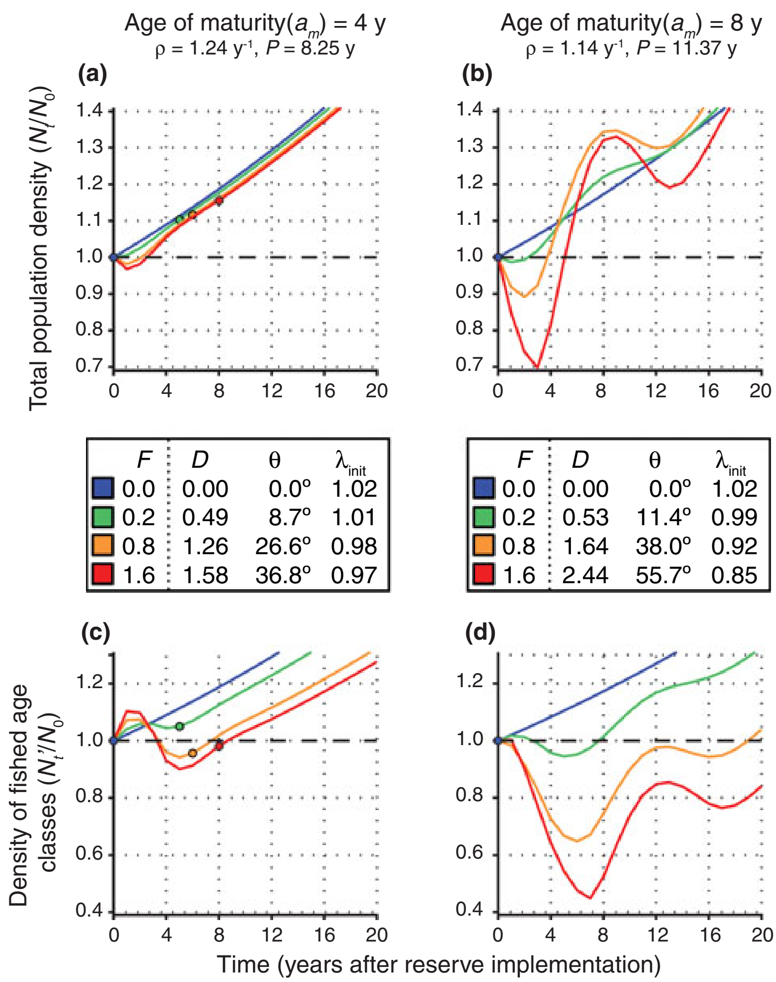

Figure 4 Change in population density over time after reserve implementation (relative to density at $t = 0$) for populations that experienced fishing at different rates (F, indicated by color) for $T_f = 50$ years prior to reserve implementation in the closed population model. Populations had the same demographic parameters (Table S1) except for age of maturity, a_m, which was either (a, c) 4 years or (b, d) 8 years. Densities shown are (a, b) all age classes; (c, d) fished age classes only. Metrics that characterize the transient (D, θ, λ_{init}, ρ, P, see Equations 6–9) were calculated for each simulation. The metrics D, θ, λ_{init} differ for each curve because they depend on F. The metrics ρ and P depend on life-history parameters (including a_m in particular; see Figure 5) but not F. Points on each curve indicate the time at which the population is growing at 99% of the asymptotic rate (i.e., the transient is essentially complete). These points are not visible in (b, d) but occurred at $t = 24$, 35, and 36 years for $F = 0.2$, 0.8, and 1.6 per year, respectively.

from $\mathbf{N}_0$ and $\mathbf{A}$ (Equations 5–9) for any population, but as an example we show the sensitivity of each to variation in the kelp rockfish parameters (Figure 5).

Higher F and/or younger age of entry (a_c) produces large values of D and θ, moving λ_{init} away from λ_1, but has no effect on ρ or P (Figure 5). Longer T_f also increases D and θ, although this effect quickly saturates at relatively high F. Increasing the age of maturity, a_m, and/or decreasing the natural mortality rate, M, concentrates reproduction in older, more fecund age classes (recall that λ_1 is fixed at a constant value) and lengthens generation time. Thus for a given F, older a_m or smaller M leads to higher values of D and θ as well as greater λ_2 relative to λ_1, so ρ decreases (note that ρ is actually greatest for intermediate values of M; Figure 5o) and P increases (Figure 5). The other model parameters, k and β, had minimal effects on transient behavior (Figure S4).

Discussion

We have shown that populations within reserves can exhibit a long period of transient dynamics after fishing ceases (e.g., Figures 3b, 4b). During this transient, abundance may not change or may actually decrease relative to the prereserve conditions, even when the long-term equilibrium outcome is a large increase in abundance. The possibility of such transients is crucial to the adaptive management of marine reserves: without accounting for them, a reserve could be judged to have failed to meet expectations over the short term, even if it would ultimately be successful. As such, we have provided several metrics to estimate the magnitude and duration of the transient. Some of these metrics are appropriate for demographically open populations (Equation 5), while others are intended for demographically closed populations (Equations 6–9); populations that are only partially open to immigration exhibit dynamics that are intermediate

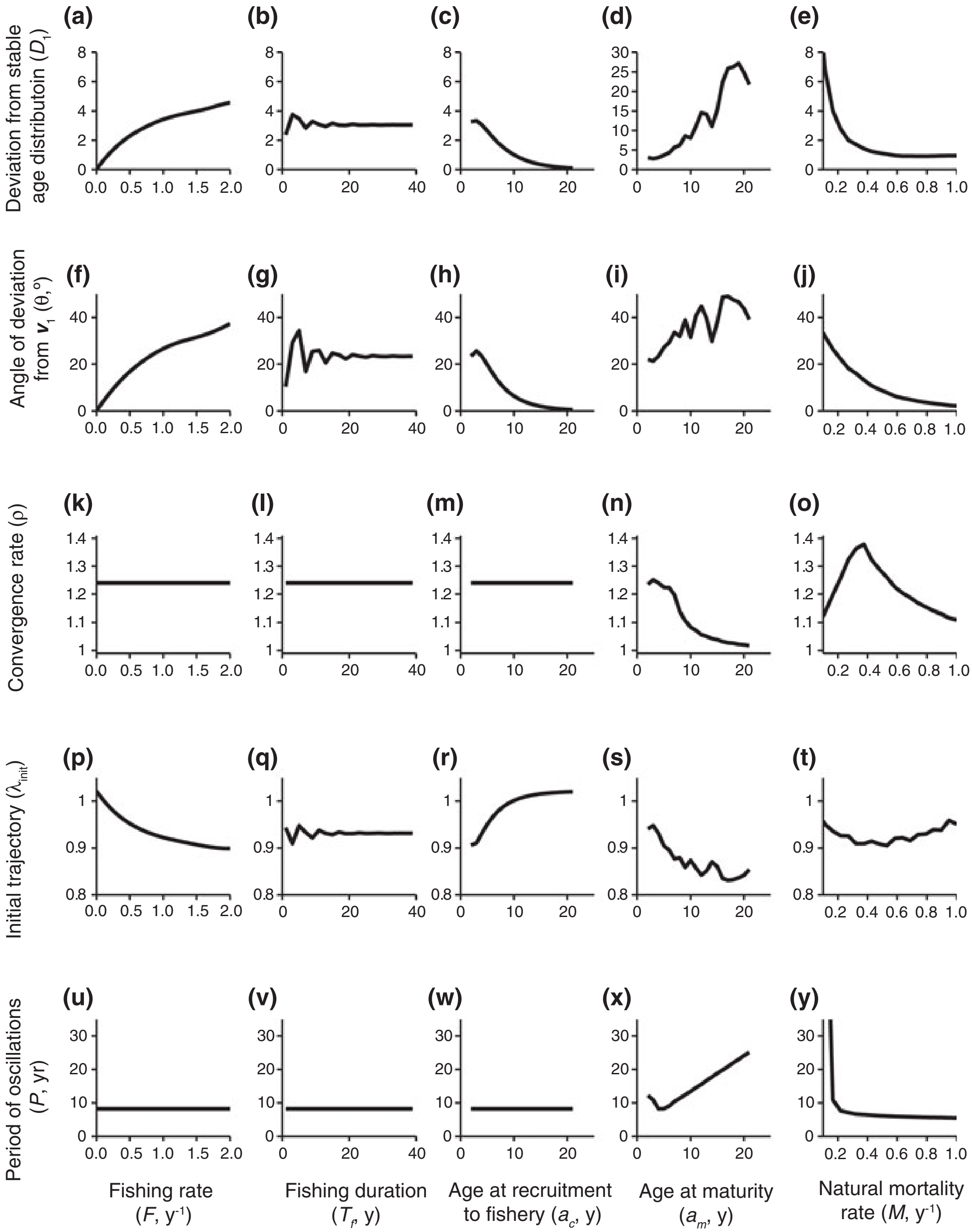

Figure 5 Sensitivity of transient dynamics to variation in fishery management and life-history parameters in the closed population model. Each panel shows the value of a transient statistic at the time of reserve implementation ($t = 0$) for a population with model parameters given in Table 1, except for the parameter being varied in that panel. In each column of panels, a single model parameter has been varied across a biologically reasonable range of values, holding other parameters constant. Note that horizontal and vertical axis scales are consistent across rows and columns, respectively, except for (d).

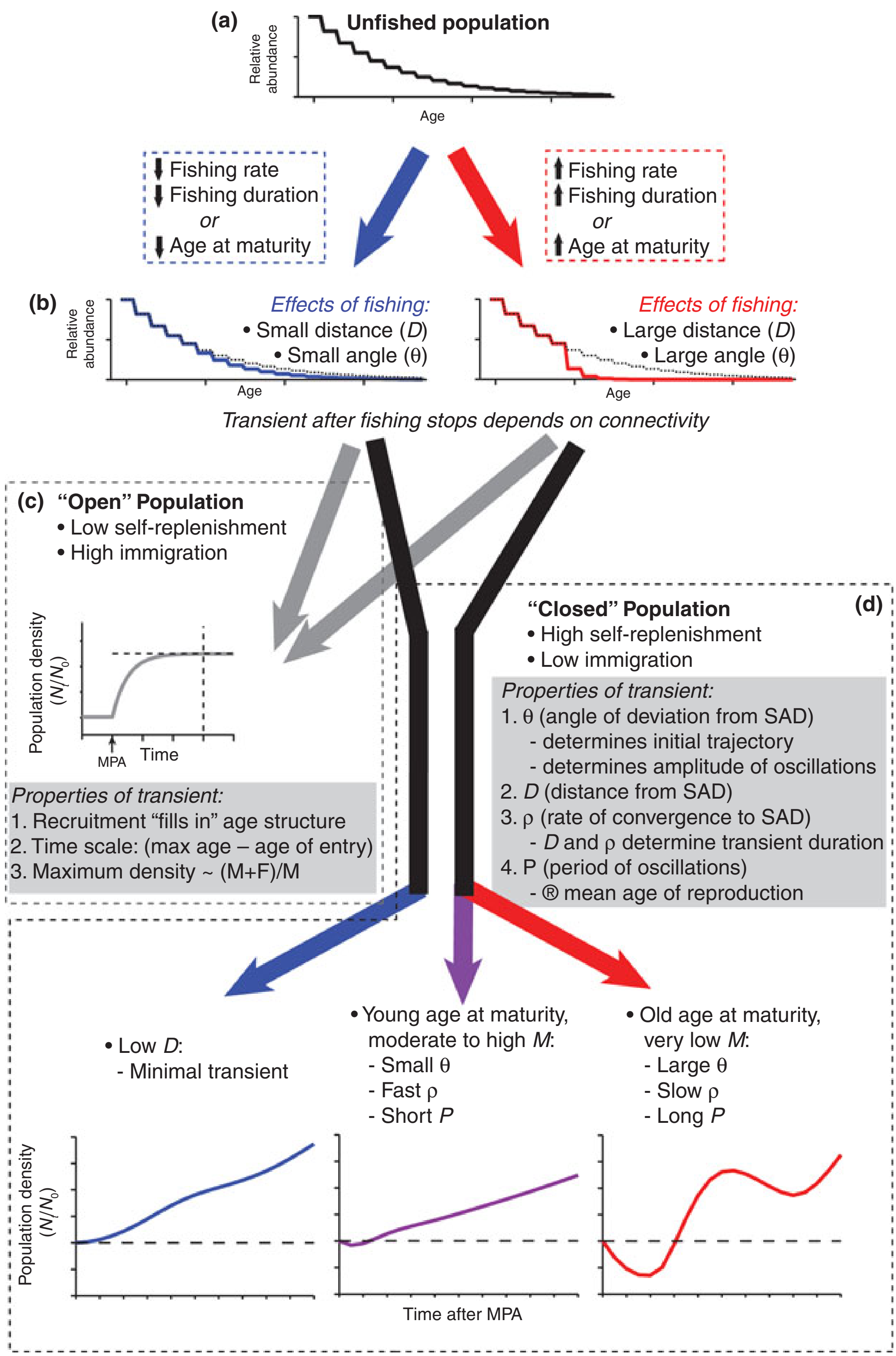

Figure 6 Schematic summary of results presented in this article. (a) Beginning with an unfished population (stable age distribution [SAD] is shown), the intensity of fishing and the age at maturity determine (b) the deviation of the fished age structure (blue and red curves) from the unfished SAD (dotted line). Once fishing is halted (e.g., due to a marine reserve), the transient behavior depends on connectivity patterns. (c) In an open population, the age structure "fills in." (d) In a demographically closed population, the duration and intensity of the transient will be minimal if *D* is small (blue arrow and curve); moderate if *D* is large but the age of maturity is young (purple arrow and curve); and extreme if *D* is large and the age of maturity is older (red arrow and curve). Gray panels in (c) and (d) give key mathematical descriptions of the transient derived in this article.

to the two extreme cases presented here (Appendix S4, Figure S5).

The transient metrics we have proposed could be used by resource managers in two general ways. First, in a relatively data-poor situation, one could calculate these metrics from a "snapshot" estimate of the population age structure near the time of reserve implementation. The metrics would then set expectations for the length of time required to observe increases in abundance within the reserve. Second, if more resources for monitoring and modeling are available, managers could use these metrics within an adaptive management program, with feedback from monitoring observations used to refine the population model and revise the predictions regarding transient dynamics (White *et al.* 2011).

Our analysis reveals the management conditions and demographic processes that most strongly affect the transient dynamics (summarized in Figure 6). In general, populations that have lower natural mortality rates, older ages at maturity, or that have been fished more intensely (e.g., some California rockfishes, such as *Sebastes mystinus*; Key *et al.* 2007; or species in a reserve placed in an area of high fishing pressure, such as southern California) should be more likely to exhibit longer transients with higher amplitude oscillations relative to faster maturing populations or those that have been fished less intensely (e.g., California halibut, *Paralichthys californicus*; CDFG 2011; or species in a reserve placed in an area of historically low fishing pressure, such as the northwest Hawaiian islands). Unfortunately from a monitoring perspective, the intensity and duration of the transient are best predicted by the age distribution, which is difficult to sample. However, it could be possible to use the size distribution as a proxy (Figures 1b, 3e–f) in cases where there is information on growth patterns. Our results also lend themselves to the intuitive interpretation that longer lags and age structures that are more truncated relative to unfished conditions (especially when this concentrates reproduction in just a few age classes) are more likely to cause cyclic behavior, because the population will generate periodic pulses of recruitment as the stock rebuilds and the age structure fills in.

Prior analyses of the rate of increase within reserves did not account for population age structure and so did not include the possibility of transients (Jennings 2001; Game *et al.* 2009). For simplicity, the models we used to examine transient dynamics also omit several factors that are known to affect population responses to marine reserves. For example, larval dispersal and adult movement have well-characterized effects on equilibrium biomass within reserve networks (reviewed by Grüss *et al.* 2011; White *et al.* 2011), and we examine them in the context of transient behavior elsewhere (Moffitt, White, and Botsford, unpublished manuscript). Here we addressed the role of larval dispersal indirectly. Species with extremely short dispersal distances should have relatively closed populations, with transients similar to those in Case 2. Species with extremely long dispersal distances will have more open demographics, with dynamics similar to those in Case 1; and species between those extremes will have intermediate dynamics (see Appendix S4, Figure S2). Our analysis also omitted temporal environmental variability such as that in larval survival and transport, which can dominate patterns of recruitment, especially in temperate populations (Carr & Syms 2006). We have explored the effects of such temporal stochasticity on transient dynamics within reserves elsewhere (White & Rogers-Bennett 2010); in general stochasticity amplifies the difficulty of detecting increases in density within reserves over short time scales, and may also change the frequency of transient oscillations. These changes are especially for noticeable for species with intermediate ages of maturity (Appendix S5, Figures S6, S7). Finally, the models used here lacked density dependence and so are appropriate only for representing the initial increase in abundance within a heavily fished population (see Appendix S1).

The intensity of fishing prior to reserve implementation bears an inverse relationship to the long-term increase in biomass within the reserve (Holland & Brazee 1996; Mangel 1998; White *et al.* 2010b), and fishing intensity is typically accounted for in empirical analyses of responses to reserve establishment (Côté *et al.* 2001; Micheli *et al.* 2004). However, such analyses typically report that some fished species do not exhibit increased biomass over short time scales (5–15 years; e.g., Molloy *et al.* 2009; Hamilton *et al.* 2010). These patterns could reflect the presence of transients, although testing that hypothesis would require examination of age distributions. Similarly, transient dynamics could explain the lag in recovery of many overfished stocks after the cessation of fishing, such as those reported for species with long generation times (Hutchings 2000; Frank *et al.* 2011). Indeed, many such stocks exhibit recoveries consisting of a continued decline followed by initial increase, just as in Figure 3b (Hutchings 2000). Collecting the data necessary to evaluate the likely magnitude and duration of transient effects is crucial for the development of monitoring programs that can judge effectively whether management actions are producing intended effects.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1: Analysis of deviation from linear approximation.

Appendix S2: Derivation of the asymptotic increase in abundance of an open population.

Appendix S3: Derivation of transient metrics for Case 2, the open population model.

Appendix S4: Analysis of populations with a mixture of open and closed demographics.

Appendix S5: Analysis of effects of stochastic variation in larval recruitment.

Table S1: Baseline model parameters for kelp rockfish, *Sebastes atrovirens*.

Figure S1: Example of transient dynamics with and without density dependence.

Figure S2: Deviation between transient dynamics with and without density dependence.

Figure S3: Transient population growth rate (N_{t+1}/N_t) with and without density dependence.

Figure S4: Sensitivity of transient dynamics to parameters k and β.

Figure S5: Results of simulations with a mixture of open and closed demographics.

Figure S6: Sensitivity of first and second eigenvalues of **A**, λ_1 and λ_2, to variation in recruit survival.

Figure S7: Examples of transient dynamics with stochasticity in larval recruitment.

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