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Transient responses of fished populations to marine reserve establishment

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Keywords
Age structure; linear population model; marine reserves; overfishing; transient dynamics.

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 equilibria (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 \( a \). All ages have natural mortality rate \( M \) and ages \( a \geq a_0 \) experience fishing mortality rate \( F \) (see Table 1 for glossary of symbols). The dynamics of the fished population are:

\[
\mathbf{N}_{t+1} = \mathbf{AN}_t + \mathbf{R},
\]

where \( \mathbf{N}_t \) is a \( n \times 1 \) vector of abundance in each age class \( a \) at time \( t \), \( \mathbf{N}_{t+1} \). \( \mathbf{A} \) is an \( n \times n \) matrix describing adult transition, and \( \mathbf{R} \) is a \( n \times 1 \) vector of the density of new recruits, \( \mathbf{R} \), 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

\[
\mathbf{N}_{t+1} = \mathbf{AN}_t,
\]

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 \( a \):

\[
\mathbf{A} = \begin{bmatrix}
  f_1 \\
  e^{-(M+F_1)} f_2 \\
  \vdots \\
  e^{-(M+F_{a-1})} f_a \\
  e^{-(M+F_{a_0})} 0
\end{bmatrix}.
\]

Defining \( a_0 \) as the age at maturity, \( f_a = 0 \) for \( a < a_0 \), and is a function of length, \( f_a = a L_a^2 \) for \( a \geq a_0 \) (\( a \) and \( \beta \) are constants; note that \( a \) also accounts for larval survival). The mean length of fish in each age class, \( L_a \), follows the von Bertalanffy equation:

\[
L_a = L_\infty (1 - e^{-k(a-a_0)}),
\]

where \( L_\infty \) 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

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_t$</td>
<td>$n \times 1$ vector of abundance in each age class, $a$</td>
<td>Sub-elements $N_{a,t}$; $N_0$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$R$</td>
<td>$n \times 1$ vector of recruit abundance</td>
<td>$R_1 = R$, zeros elsewhere</td>
</tr>
<tr>
<td>$A$</td>
<td>Population projection matrix</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$a$</td>
<td>Age class</td>
<td>$a_{m}$ is the age at maturity</td>
</tr>
<tr>
<td>$a_0$</td>
<td>Age at length 0</td>
<td>$a_{c}$ is the age at entry to fishery</td>
</tr>
<tr>
<td>$a_m$</td>
<td>Age at maturity</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$A$</td>
<td>Length-fecundity coefficient</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Length-fecundity exponent</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$f_a$</td>
<td>Fecundity at age $a$</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$k$</td>
<td>von Bertalanffy growth rate</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$L_a$</td>
<td>Length at age $a$</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$L_\infty$</td>
<td>Asymptotic maximum length</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$M$</td>
<td>Natural mortality rate</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$n$</td>
<td>Number of age classes</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Constant of proportionality between mean and standard deviation of length</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
</tbody>
</table>

Management factors

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_f$</td>
<td>Duration of fishing prior to reserve</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$F$</td>
<td>Fishing mortality rate</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
<tr>
<td>$F_a$</td>
<td>Age-specific fishing mortality rate</td>
<td>$A_{0,0}$ is the initial conditions when the reserve is implemented</td>
</tr>
</tbody>
</table>

Transient metrics

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_i$</td>
<td>$i$th right eigenvalue of $A$</td>
<td>$\lambda_1$ determines asymptotic geometric growth rate</td>
</tr>
<tr>
<td>$\lambda_{\text{init}}$</td>
<td>Initial trajectory of transient</td>
<td>$\lambda_2$ is often complex, and describes the primary oscillatory component of the transient</td>
</tr>
<tr>
<td>$w_i$</td>
<td>$i$th right eigenvector of $A$</td>
<td>Determined by $\phi$</td>
</tr>
<tr>
<td>$v_i$</td>
<td>$i$th left eigenvector of $A$</td>
<td>Deviation from $\lambda_1$ determines amplitude of oscillations</td>
</tr>
<tr>
<td>$D$</td>
<td>Distance from SAD</td>
<td>Proportional to SAD$^*$</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Angle between $N_0$ and SAD</td>
<td>&quot;As the road turns&quot; distance (Equation 7)</td>
</tr>
<tr>
<td>$P$</td>
<td>Period of transient oscillations</td>
<td>&quot;As the crow flies&quot; distance; determines $\lambda_{\text{init}}$ (Equation 6)</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Rate of return to SAD</td>
<td>Usually determined by complex part of $\lambda_2$ (Equation 9)</td>
</tr>
</tbody>
</table>

Notes: $^*$SAD = stable age distribution.

Now $A$ is a Leslie matrix, so the model has asymptotic (i.e., long-term) behavior described by the dominant eigenvalue $\lambda_1$ of $A$: geometric growth ($\lambda_1 > 0$) or decline ($\lambda_1 < 0$). In the long term, $N$ 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 $w_1$ of $A$. 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 $\phi L_a$, where $\phi$ 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
Transient dynamics in marine reserves

J. W. White et al.

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 \(a_m, M, k, \beta\). 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 \(\alpha\) 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 \(\lambda_1\). Generally speaking, a faster growth rate (larger value of \(\lambda_1\)) 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

\[
\lim_{t \to \infty} \frac{N'_t}{N'_0} = \frac{M + F}{M}.\]

(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:

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

(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](image_url)
Transient dynamics in marine reserves

J. W. White et al.

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 \( (a > a_c) \) only.

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 \( (F = 0.1 \text{ per year}; \text{Figure 3a}) \) or a continued decline followed by an oscillatory increase in density \( (F = 0.8 \text{ per year}; \text{Figure 3b}) \). Regardless, once the population reaches its SAD, it exhibits long-term dynamics determined by the dominant eigenvalue \( \lambda_1 \) of \( A \).

Any oscillations are due to the narrower age distribution produced by fishing during the years prior to reserve implementation. As the heavily fished population \( (F = 0.8 \text{ per year}) \) 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).
Transient dynamics in marine reserves

First, we calculate the similarity of initial conditions to the unfished SAD, which will determine the initial trajectory of change in population density, $\lambda_{\text{init}}$. The similarity to the SAD can be expressed as an angle, $\theta$, with smaller $\theta$ indicating that $\lambda_{\text{init}}$ will be closer to $\lambda_1$ (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 $\theta$ by finding the angle between the vectors $N_0$ and $\mathbf{w}_1$:

$$\theta = \arccos \left( \frac{N_0 \cdot \mathbf{w}_1}{\|N_0\| \|\mathbf{w}_1\|} \right),$$

where double vertical bars indicate a vector norm.

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

$$D = \left[ \lim_{t \to \infty} \sum_{i=0}^{T} \frac{N_i}{\lambda_1} \left( \mathbf{w}_i \mathbf{v}_1^\top \mathbf{N}_i \right) \right],$$

where $\mathbf{v}_1$ is the dominant left eigenvector of $N_0$. 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 $\theta$) 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 $\theta$ estimates the initial trajectory, $D$ affects the overall transient duration.

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

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

The actual rate of convergence may deviate slightly from this estimate due to the effect of the remaining eigenvalues. Smaller values of $\rho$ result in longer transients because the oscillatory components of $A$, represented by $\lambda_2$ (and its complex conjugate in typical cases), are large relative to the exponential growth component represented by $\lambda_1$ (compare Figures 4a–b; the latter has $a_0 = 8$ year and thus larger $\lambda_2$).

Last, we can calculate $P$, the period of oscillations in the transient, which is determined by $\lambda_2$:

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

where $\text{Im}(x)$ and $\text{Re}(x)$ 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 $\lambda_{\text{init}}$ from the asymptotic trajectory, $\lambda_1$ (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.
from \( N_0 \) and \( A \) (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 (\( a_m \)) produces large values of \( D \) and \( \theta \), moving \( \lambda_{\text{max}} \) away from \( \lambda_1 \), but has no effect on \( \rho \) or \( P \) (Figure 5). Longer \( T_f \) also increases \( D \) and \( \theta \), 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 \( \lambda_1 \) 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 \( \theta \) as well as greater \( \lambda_2 \) relative to \( \lambda_1 \), so \( \rho \) decreases (note that \( \rho \) is actually greatest for intermediate values of \( M \); Figure 5o) and \( P \) increases (Figure 5). The other model parameters, \( k \) and \( \beta \), 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).
**Transient dynamics in marine reserves**

J. W. White et al.

Unfished population

- Age
- Relative abundance
- Fishing rate
- Fishing duration
- Age at maturity

**Effects of fishing:**
- Small distance ($D$)
- Small angle ($\theta$)

**Fishing rate**

- Small distance ($D$)
- Large angle ($\theta$)

**Fishing duration**

- Age at maturity

**Age at maturity**

- Large distance ($D$)
- Large angle ($\theta$)

**Effects of fishing:**

- Large distance ($D$)
- Large angle ($\theta$)

"Open" Population

- Low self-replenishment
- High immigration

**Population density**

- Low $N_t/N_0$:
  - Minimal transient
  - Moderate to high $M$:
    - Small $\theta$
    - Fast $\rho$
    - Short $P$

**Properties of transient:**

1. Recruitment "fills in" age structure
2. Time scale: (max age – age of entry)
3. Maximum density ~ (M+F)/M

"Closed" Population

- High self-replenishment
- Low immigration

**Properties of transient:**

1. $\theta$ (angle of deviation from SAD): determines initial trajectory, amplitude of oscillations
2. $D$ (distance from SAD): $D$ and $\rho$ determine transient duration
3. $\rho$ (rate of convergence to SAD): $\rho$ and $D$ determine transient duration
4. $P$ (period of oscillations): $\rho$ mean age of reproduction

- Low $D$:
  - Minimal transient
- Young age at maturity, moderate to high $M$:
  - Small $\theta$
  - Fast $\rho$
  - Short $P$
- Old age at maturity, very low $M$:
  - Large $\theta$
  - Slow $\rho$
  - Long $P$

**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 & Sym 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 website:

- **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 $\beta$.

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

**Figure S6**: Sensitivity of first and second eigenvalues of $A$, $\lambda_1$ and $\lambda_2$, to variation in recruit survival.

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

**References**


