

Influence of protogynous sex change on recovery of fish populations within marine protected areas

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Abstract. Marine protected areas (MPAs) are increasingly implemented as a conservation tool worldwide. In many cases, they are managed adaptively: the abundance of target species is monitored, and observations are compared to some model-based expectation for the trajectory of population recovery to ensure that the MPA is achieving its goals. Most previous analyses of the transient (short-term) response of populations to the cessation of fishing inside MPAs have dealt only with gonochore (fixed-sex) species. However, many important fishery species are protogynous hermaphrodites (female-to-male sex-changing). Because size-selective harvest will predominantly target males in these species, harvesting not only reduces abundance but also skews the sex ratio toward females. Thus the response to MPA implementation will involve changes in both survival and sex ratio, and ultimately reproductive output. We used an age-structured model of a generic sex-changing fish population to compare transient population dynamics after MPA implementation to those of an otherwise similar gonochore population and examine how different features of sex-changing life history affect those dynamics. We examined both demographically open (most larval recruitment comes from outside the MPA) and demographically closed (most larval recruitment is locally produced) dynamics. Under both scenarios, population recovery of protogynous species takes longer when fishing was more intense pre-MPA (as in gonochores), but also depends heavily on the mating function, the degree to which the sex ratio affects reproduction. If few males are needed and reproduction is not affected by a highly female-biased sex ratio, then population recovery is much faster; if males are a limiting resource, then increases in abundance after MPA implementation are much slower than for gonochores. Unfortunately, the mating function is largely unknown for fishes. In general, we expect that most protogynous species with harem mating systems will be in the first category (few males needed), though there is at least one example of a fish species (though not a sex-changing species) for which males are limiting. Thus a better understanding of the importance of male fish to population dynamics is needed for the adaptive management of MPAs.

Key words: fishing; marine protected area; marine reserve; protogynous hermaphrodite; sex change; transient population dynamics.

INTRODUCTION

Marine protected areas (MPAs), particularly no-take marine reserves, have been increasingly implemented as a management tool to conserve biodiversity and, in some cases, benefit fisheries (Klein et al. 2015). Empirical assessments and meta-analyses of MPA performance suggest that biomass and biodiversity of fished species generally, but not always, increases inside MPAs, though the level and tempo of that increase vary in magnitude

depending on reserve size, age, environmental conditions, fishing intensity pre-MPA implementation and in fished areas outside the MPA, etc. (e.g., Halpern and Warner 2002, Denny and Babcock 2004, Claudet et al. 2006, 2011, Tetreault and Ambrose 2007, Lester et al. 2009, Hamilton et al. 2010, McCook et al. 2010, Edgar et al. 2014, Caselle et al. 2015). Because most MPAs are relatively young, and because there is rarely funding for long-term monitoring of older MPAs, most MPA monitoring and assessment programs necessarily focus on the short-term (i.e., years, not decades) responses of fished populations after MPA establishment (e.g., Hamilton et al. 2010, Caselle et al. 2015). Typically, this is also the time scale most relevant to adaptive management of

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MPAs (Grafton and Kompas 2005), because time scales of policymaking may be faster than ecological time scales. For example, California has a 5-yr assessment cycle for its recently implemented network of 124 MPAs (Botsford et al. 2014b, CDFW and OPC 2018). In contrast, the theoretical models used in MPA planning processes are typically limited to making predictions about MPA effects under long-term, stable equilibrium conditions (e.g., Botsford et al. 2001, Gerber et al. 2003, Klein et al. 2008, White et al. 2013a, Krueck et al. 2017), but do not predict how quickly the outcomes should be expected (White et al. 2013a). To better inform the adaptive management of marine reserves, there is a need to match the timescales of empirical and theoretical analyses (White et al. 2011).

When abrupt changes in management are imposed, such as the placement of no-take MPAs in previously exploited areas, populations exhibit transient dynamics while they return to equilibrium (Hastings 2004, 2010, Ezard et al. 2010, White et al. 2013b, Hopf et al. 2016a, b, Hastings et al. 2017). Understanding the short-term, transient responses of previously harvested populations is critical information for monitoring programs. Without accounting for transient dynamics, an MPA could be deemed ineffective if increases in population density or biomass are not immediately seen (or if abundance initially decreases following protection), even if the reserve would ultimately be successful (White et al. 2013b, Nickols et al. 2019). Alternatively, initial increases could mask longer-term declines (Moffitt et al. 2013). Prior modeling work has identified the primary factors determining the pattern of post-MPA transient dynamics (White et al. 2013b, Kaplan et al. 2019). The first is the historical intensity and duration of fishery harvest, with more intense fishing producing a greater post-MPA increase. The second is the natural mortality rate, with longer-lived species exhibiting longer transient dynamics. The third is whether the population in the MPA is demographically open or closed, i.e., what proportion of settling larvae were spawned in the MPA; as that proportion increases, there is greater potential for oscillations due to cohort “echo” effects. Finally, stochastic variation in demographic rates, particularly larval recruitment, can produce tremendous transient variability that makes population trajectories difficult to discern (Kaplan et al. 2019).

Despite the recent increase in the analysis and description of transient dynamics in ecology (Hastings et al. 2017), models describing transient dynamics of marine fisheries (e.g., Jennings 2001, Frank et al. 2011, White et al. 2013b) are usually simplified by assuming sexes are fixed and in equal proportions, and by ignoring the effects of harvest on sex-specific survival, reproductive patterns, and fertilization success. However, many commercially and recreationally important species are protogynous hermaphrodites, that is, they reproduce as females first and then change sex to male. When subjected to size-selective harvest, populations

of protogynous species can experience reductions in the operational sex ratio (the proportion of the reproductively active population that is male) because larger individuals are predominately male and because many fisheries remove the largest individuals due to gear selectivity (e.g., Coleman et al. 1996, McGovern et al. 1998, Hawkins and Roberts 2003, Hamilton et al. 2007). Consequently, both conventional and spatial (MPA-based) fishery management of protogynous species must account for changes in sex ratio, and thus per capita reproduction (Alonzo and Mangel 2004, 2005, Alonzo et al. 2007, Easter and White 2016). A less-common life history among fished species is protandry, in which individuals mature as males then change sex to females; this has been addressed previously (e.g., Molloy et al. 2007) and we do not analyze it here.

The short-term responses of protogynous populations to MPA implementation involves both the “filling in” of the older, previously exploited age classes as the population returns to the stable age distribution, as in gonochore (non-sex-changing) populations (White et al. 2013b), as well as the recovery of normal, pre-exploitation sex ratios and reproductive output. Easter and White (2016) showed that a determining factor in the long-term response of protogynous populations to MPAs was the mating function, which is the relationship between the sex ratio and per-capita reproductive output, i.e., how many males a population needs (Miller and Inouye 2011, Easter and White 2016, White et al. 2017). Specifically, protogynous populations with a mating function in which males quickly become limiting when fishing reduces the sex ratio require more, larger MPAs for long-term population persistence (Easter and White 2016). Based on that result, we expected that transient dynamics inside MPAs would also depend heavily on the shape of the mating function. There has been some prior investigation of the transient dynamics of protogynous fish in MPAs, most notably by Hopf et al. (2016a,b) who examined the dynamics of protogynous coral trout (*Plectropomus* spp.) in no-take MPAs on the Great Barrier Reef. They used a fixed estimate of the mating function (based on an earlier modeling study that assumed the relationship was fairly steep; Chan et al. 2012), but did not examine the influence of the shape of the mating function on the transient population dynamics, as we do in this study.

Here, we examine how the transient population dynamics of protogynous populations in newly implemented MPAs compares to those of gonochores. We did this using age-structured models of a generic protogynous and gonochore fish populations, keeping the latter identical to the former in all ways except mating system: growth, mortality, etc. We explored the importance to transient dynamics of several biological quantities, particularly the shape of the mating function (i.e., how important males are) and how flexible the protogynous fish was with respect to the timing of sex

change. Some fish change sex at a fixed size, while others respond to social cues within the population; these lead to differences in a species' sensitivity to harvest-based changes in sex ratio (Alonzo and Mangel 2005, Easter and White 2016). We also compared scenarios in which harvest targeted fish above or below the size at sex change, which we expected would influence how quickly sex ratios recover to pre-fishing levels inside MPAs. Finally, we also varied the historical rate of fishing, which is known to influence the within-MPA population trajectory in both gonochores and sex-changing fish (White et al. 2013b, Hopf et al. 2016a). We followed the analytical framework of White et al. (2013b) to quantify the duration and magnitude of the post-MPA transient population dynamics. As in previous studies of the population dynamics of sex-changing species (Easter and White 2016), we found that our results depended greatly on the shape of the mating function, a quantity that is also unfortunately not well known for most species.

METHODS

Population model

As a first approximation to understand population dynamics inside MPAs, White et al. (2013b) considered two scenarios that represent opposite ends of a continuum with respect to demographic connectivity. The species of interest is a typical coastal benthic marine fish, with a relatively sedentary adult stage (i.e., the scale of adult movement is much smaller than the scale of an MPA) and a dispersive, planktonic larval stage. If larval dispersal is very widespread, then the population in the MPA would be demographically “open,” receiving most larval recruitment from elsewhere. If larval dispersal was highly restricted (or the MPA is very isolated from other populations) then all recruiting larvae would be produced inside the MPA itself (demographically “closed”). Of course, any real population will fall somewhere between those extremes, but it is useful (and analytically tractable) to consider those two endpoints (the appendix of White et al. 2013b presented results that fell between those extremes; in general, dynamics are more “closed” if self-connectivity is >50%).

We modified the model of White et al. (2013b) to incorporate protogyny, and used a discrete time, non-spatial, age-structured model of a generic protogynous hermaphrodite population and an otherwise identical gonochore population. While the model results of White et al. (2013b) were derived from the theory of linear projection models (Caswell 2001, Botsford et al. 2019), adding sex change renders the model nonlinear. As such, some of the conventional analytical metrics of transient dynamics in linear models (Caswell 2001, White et al. 2013b, Botsford et al. 2019) cannot be used directly, so we developed numerical approximations to

them. All symbols used in the paper are defined in Table 1.

We modeled a population with n age classes; the state variable is $\bar{\mathbf{N}}_t$, an $n \times 1$ vector of abundance in each age class at time t . The dynamics of the population are described by

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t + \mathbf{R}_t \quad (1)$$

where $\mathbf{A}$ is a $n \times n$ matrix that has terms $e^{-(M+\psi_a F)}$ along the first sub-diagonal and 0 elsewhere. That is, post-recruitment individuals experience constant, age- and density-independent natural mortality M and fishing mortality F with age-dependent fishery selectivity ψ_a . Selectivity has a value of 0 in ages for which the average length-at-age is less than the size at entry to the fishery, L_F , and 1 otherwise (we provide the age-length relationship below in Eq. 4).

The $n \times 1$ vector $\mathbf{R}_t$ has the number of recruits to age 1 at time t , R_t , in the first row and 0s elsewhere. In an *open* population, all larval recruitment originates elsewhere and is unaffected by the MPA implementation, so R_t is modeled as a time-invariant constant. In a *closed* population in which all larvae are locally produced, R_t is given by

$$R_t = \mathbf{N}_t^\top \cdot [(1 - \mathbf{p}_{\text{male},t}) \circ \mathbf{E}] P_t \alpha \quad (2)$$

which is the dot (scalar) product of the vector of abundances, $\mathbf{N}_t$ ($\top$ is the vector transpose operator) and the vector of per capita fertilized egg production at each age. The latter is the elementwise (Hadamard) product of the sex ratio at each age, $\mathbf{p}_{\text{male},t}$ (defined as proportion male, hence subtracted from 1), and female fecundity in each age class, $\mathbf{E}$, multiplied by the scalars P_t , the proportion of eggs produced at time t that are successfully fertilized, and α , the probability of survival through the egg and larval stages. In the next section we explain how $\mathbf{p}_{M,t}$, $\mathbf{E}$, and P_t are determined.

Reproductive strategies

We compared two sexual strategies: gonochore and protogynous hermaphrodite. In the gonochore case, the sex ratio was assumed to be 50:50 female:male, both sexes were fixed at birth, and the probability of being mature at a given age, a , $p_{\text{mat}}(a)$, was determined by the length of an individual at that age, $L(a)$:

$$p_{\text{mat}}(a) = \frac{1}{1 + \exp(-q(L(a) - L_{\text{mat}}))} \quad (3)$$

where L_{mat} is the length at which 50% of individuals are mature and q is a constant that determines the steepness of the function. The $p_{\text{mat}}(a)$ values comprise the elements of the vector $\mathbf{p}_{\text{mat}}$ (for simplicity we have dropped the time subscripts t in this section). Length-at-age, $L(a)$ is described by a von Bertalanffy function with

TABLE 1. Symbols and parameter values used in the model based on available data for California sheephead (*Semicossyphus pulcher*).

Parameter	Parameter values	Definition
State variables		
$\mathbf{N}_t$		$n \times 1$ vector of abundance in each age class, a , at time t
$\mathbf{A}$		population projection matrix
R_t		number of larval recruits at time t (open population model only)
n		number of age classes
X		biomass sex ratio (proportion male)
$L(a)$		length at age a
k	0.05	von Bertalanffy growth rate (Cowen 1990)
L_∞	90 cm	von Bertalanffy asymptotic length (Cowen 1990)
L_0	8 cm	larval size at recruitment
Survival		
M	0.35	natural adult mortality (Cowen 1990)
α		larval survival (adjusted to ensure $l = 1.02$)
Reproduction		
$\mathbf{E}$		$n \times 1$ vector of per capita egg production in each age class, with elements E
$\mathbf{p}_{\text{mat}}$		$n \times 1$ vector of the proportion of each age class that is reproductively mature, with elements p_{mat}
$\mathbf{p}_{\text{male}}$		$n \times 1$ vector of the proportion of each age class that is male, with elements p_{male}
P_t		probability of fertilization
u	7.04	constant in fecundity relationship
v	2.95	exponent in allometric relationship
a	1	constant of fertilization function parameter
ϕ	1–20	shape parameter in the fertilization function
Fixed-cued sex change		
r_{fix}	1	shape parameter in the sex change function
L_{mat}	20 cm	length at which 50% of fish mature
L_{male}	30 cm	length at which 50% of fish change sex
q_{fix}	1	shape parameter in the maturity function
Flexible-cued sex change		
$\bar{L}$		mean length in the population
r_{flex}	1	shape parameter in the sex change function
ΔL_{mat}	4 cm	difference from the mean size at which $p_M(L) = 0.5$
ΔL_{male}	14 cm	difference from the mean size at which $p_c(L) = 0.5$
q_{flex}	1	shape parameter in the maturity function
F		fishing mortality rate
ψ_a		age-specific fishery selectivity
L_F		length at entry to the fishery
Transient calculations		
$\mathbf{w}$		stable age distribution
λ		asymptotic growth rate
λ_{init}		initial trajectory of the transient
θ		similarity of $\mathbf{N}_0$ to the SAD
T_{asyp}		time to convergence on asymptotic growth λ_1

Notes: See Alonzo and Mangel (2005) for source of parameter values if not otherwise noted. Symbols for which a value is not listed are either state variables or are varied in simulations.

asymptotic maximum length L_∞ , growth rate k , and age-at-length-0 a_0 :

$$L(a) = L_\infty \left(1 - e^{-k(a-a_0)} \right). \quad (4)$$

In the protogynous hermaphrodite scenarios, the timing of maturation, $p_{\text{mat}}(a)$ and sex change to male, $p_{\text{male}}(a)$, were modeled using either a fixed or a flexible sex change cue, using expressions originally described by

Alonzo and Mangel (2005). In both protogynous cases, all fish begin as primary females and males were only produced through sex change. Individuals are assumed to mature as females before changing sex.

The *fixed* cue scenario describes a species with an endogenous cue for both maturity and sex change, based on length or age. An example of this type of life history pattern is gag grouper (*Mycteroperca microlepis*), in which mature females and males are spatially segregated

except during spawning migrations, so there are no opportunities for the sex ratio to influence within-season sex change decisions (Heppell et al. 2006). In this scenario, the proportions of females maturing and transitioning to male is a fixed function of length (and thus age), and both the maturity, $p_{\text{mat}}(a)$, and sex change, $p_{\text{male}}(a)$, functions have a logistic form (Alonzo and Mangel 2005):

$$p_{\text{mat}}(a) = \frac{1}{1 + \exp(-q_{\text{fix}}(L(a) - L_{\text{mat}}))} \quad (5a)$$

$$p_{\text{male}}(a) = \frac{1}{1 + \exp(-r_{\text{fix}}(L(a) - L_{\text{male}}))} \quad (5b)$$

where L_{mat} and L_{male} are the sizes at which 50% of individuals mature or change sex, respectively, and q_{fix} and r_{fix} are steepness parameters.

The *flexible* cue scenario describes a species in which the probability of maturity and sex change are determined by an individual's size relative to the average size of individuals in the population. This represents the dynamics of socially cued sex-changing species, such as half-moon grouper (*Epinephelus rivulatus*), in which large males maintain social dominance over smaller individuals; when large males are removed from the population, the largest females quickly change sex and replace them (Mackie 2003), resulting in sex ratios that are more stable under exploitation. In this scenario, we also assume that maturity responds to the population size distribution; fish mature at smaller sizes when more large fish have been removed (as has been observed in the sex-changing California sheephead, *Semicossyphus pulcher*; Hamilton et al. 2007). These patterns can be described by the following equations:

$$p_{\text{mat}}(a) = \frac{1}{1 + \exp(-q_{\text{flex}}(L(a) - (\bar{L} + \Delta L_{\text{mat}})))} \quad (6a)$$

$$p_{\text{male}}(a) = \frac{1}{1 + \exp(-r_{\text{flex}}(L(a) - (\bar{L} + \Delta L_{\text{male}})))} \quad (6b)$$

where ΔL_{mat} is the difference from the population mean length at which the probability of an individual maturing is 50%, ΔL_{male} is the equivalent quantity for sex change, $\bar{L}$ is the mean length of all individuals in the population, and q_{flex} and r_{flex} are steepness parameters.

Female fecundity $E(a)$ (eggs produced at age a) depends on the mature female body size and the probability of maturity, $p_{\text{mat}}(a)$, and follows the allometric relationship

$$E(L) = u[L(a)]^v p_{\text{mat}}(a) \quad (7)$$

where u and v are constants.

While conventional models of gonochore populations consider eggs to be the limiting gamete and calculate

reproduction based on females only, highly female-skewed sex ratios often experienced by protogynous populations warrants consideration of the contribution of males to reproductive success. Although the importance of males is poorly understood empirically and a general allometric relationship between male body size and sperm production does not exist, presumably the proportion of eggs fertilized is ultimately limited by sperm production, and thus depends on the sex ratio (Warner 1997). We expressed the population sex ratio, X , as the proportion of male biomass in the population (calculated as the total biomass of males divided by the biomass of all mature individuals). For all sex-change scenarios, we presumed that the proportion of fertilized eggs $P_{f,t}$ followed a cumulative beta distribution function

$$P_{f,t} = \text{beta}(2X, a, \phi) \quad (8)$$

with shape parameters a and ϕ (White et al. 2017). We fixed parameter a to be 1, so that the function is monotonically increasing, with the parameter ϕ describing how quickly the proportion of eggs fertilizes approaches 1 as the proportional male biomass increases from zero. The factor 2 in Eq. 8 ensures that the function reaches a maximum at $X = 0.5$, i.e., a 50:50 sex ratio. Eq. 8 is known as the *mating function* (Miller and Inouye 2011).

In Fig. 1, we show examples of the mating functions estimated for three fish (in fact, to our knowledge, these are the only fish for which the mating function has been formally estimated). *Lythrypnus dalli* and *Rhinogobiops nicholsii* are small-bodied, temperate gobies, both protogynous hermaphrodites. The former has socially cued sex change and, in some circumstances, also changes back from male to female (St. Mary 1994, 1996); it also appears that a small fraction of the population may begin life as males (Drilling and Grober 2005). Sex change in *R. nicholsii* may be partially based on absolute size (Cole 1993). In both species, multiple females in a social group lay their eggs in a nest guarded by a single male; they typically have low sex ratios and highly convex mating functions (high ϕ), indicating low male importance (i.e., few males are needed to reproduce; Pang 2019). In contrast, the atherinid *Menidia beryllina* is a schooling estuarine fish and a gonochore that spawns in large groups, depositing adhesive eggs onto submerged aquatic vegetation. They have a nearly linear mating function, reflecting high male importance (possibly because high sex ratios are necessary to initiate spawning behavior) and low ϕ (White et al. 2017). In our model analysis, we used mating functions with values of ϕ ranging from 1 to 20, effectively spanning the range observed in nature (preliminary analysis indicated that model results changed little for $\phi > 20$).

Model analysis: open population

We examined the response of a fished population following reserve implementation, investigating how the

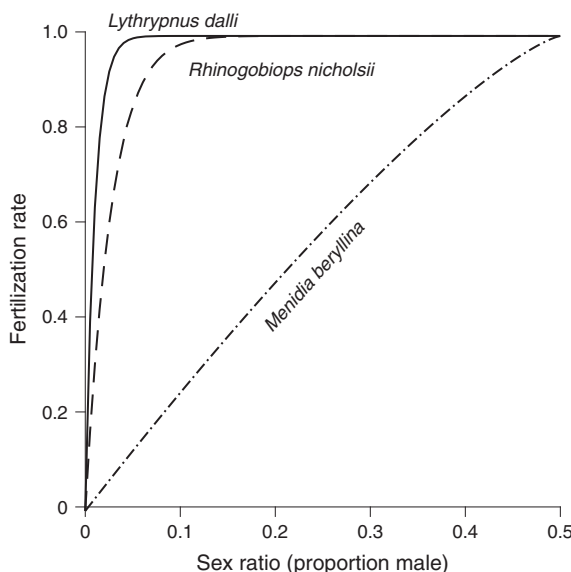


FIG. 1. Examples of the relationship between egg fertilization rate and sex ratio for species with various levels of the nondimensional male importance parameter, ϕ : bluebanded goby, *Lythrypnus dalli* (solid curve, $\phi = 50.0$; Pang 2019), black-eye goby, *Rhinogobiops nicholsii* (dashed curve, $\phi = 18.0$; Pang 2019), and inland silversides, *Menidia beryllina* (dot-dash curve; $\phi = 1.3$; White et al. 2017).

transient response was influenced by fishing intensity F , sex-change strategy (gonochore, fixed-cue sex change, and flexible-cue sex change), male importance ϕ , and the length of entry to the fishery, L_F . We simulated population dynamics that began at the unfished equilibrium value (this is determined by recruitment, R , but because we only express abundances as ratios, results are not sensitive to the value of R chosen). The population was then fished at the specified value of F for 50 yr (this was sufficient to reach a stable age distribution), then fishing ceased (i.e., MPA was put in place) and we simulated an additional 50 yr of dynamics with $F = 0$. We then considered a range of combinations of F (from 0 to 1.0 per yr), male importance ($\phi = 1$ to 20), and a length of entry to the fishery, L_F , corresponding to the average (unfished) length at maturity, the average length at sex change, and a value greater than the average length at sex change (L_F was translated to an age using Eq. 4 for actual implementation in the age-structured model). We used baseline life history parameter values for the California sheephead (*Semicossyphus pulcher*), a commercially important protogynous hermaphrodite (Alonzo and Mangel 2005, Hamilton et al. 2007, 2011; see Table 1 for parameter values).

In the open population scenario, reproductive strategies have no effect on the number of recruits entering the population, so the post-MPA trajectories in population abundance are the same for gonochores and sex-changing populations, and follow the results in White et al. (2013a,b). Therefore, in this scenario, we examined the

transient dynamics in terms of two response variables: sex ratio (commonly used to assess the degree of overfishing in sex-changing stocks) and egg production (relative to equilibrium) as a measure of the possible contribution of the population in the MPA to other populations along the coast. For the latter, we calculated the time it took the population to converge to the unfished equilibrium egg production, i.e., the duration of transient dynamics. The population approaches the equilibrium asymptotically, so we identified the time t (post-MPA) at which the population had egg production that was 99% of the long-term equilibrium value.

Model analysis: closed population

We then examined the dynamics of populations that were demographically closed, varying the same factors: fishing intensity, sex-change strategy, male importance, and the age of entry to the fishery. In this scenario, the asymptotic rate of population increase depends largely on α , the larval survival rate (see Eq. 2), which is also unfortunately mostly unknown for marine fishes (see White 2010). Because our basic question was the relative ability to detect positive increases in gonochore vs. protogynous changes, we took the approach of specifying an overall population growth rate, λ , at which the population would increase in the absence of density-dependent effects. When reduced to low density by fishing, the population would increase at that rate (after transient effects subsided) before the growth rate slowed as density increased. We chose to specify $\lambda = 1.02$, which implies the population would double in size in approximately 35 yr; this is appropriately conservative for gauging relative differences in population trajectories for long-lived temperate species that will recover from overharvest over decadal scales (also used by White et al. 2013b). Analyses by White et al. (2013b) indicated that omitting density dependence from the model does not affect predictability of short-term, transient dynamics when the population has been heavily exploited and is far from its unfished equilibrium abundance, as is the case for many of the world's fisheries (FAO 2016).

The closed population model will eventually reach a stable age distribution (SAD) $\mathbf{w}$, given by

$$\mathbf{w} = \begin{bmatrix} 1 \\ e^{-Z}(\lambda)^{-1} \\ e^{-Z^2}(\lambda)^{-2} \\ \vdots \\ e^{-Z^n}(\lambda)^{-n} \end{bmatrix} \quad (9)$$

where the term Z is equal to $M_A + \psi_a F$ when there is a constant fishing rate F and simply M_A when there is no fishing. We began simulations at the fished SAD, then examined the transient dynamics when fishing stops (i.e., the MPA is enforced) and the population converges asymptotically on the unfished SAD.

We calculated three metrics at $t = 0$ that characterize the transient dynamics: the initial trajectory (λ_{init}), the similarity of the initial age distribution, $\mathbf{N}_0$, to the unfished SAD (θ), and time to convergence on the asymptotic state (T_{asympt}). The first of these is an indicator of what the population will do initially (because it may not increase at the asymptotic rate $\lambda = 1.02$), and the second and third of these are indicators of the duration of the transient dynamics, how long it will take the population to reach the unfished SAD, at which point it will be increasing at rate λ .

White et al. (2013b) provided an analytical expression for λ_{init} , but we could not apply that formula to a model with sex change. Instead we simply calculated the initial rate of change in abundance as

$$\lambda_{\text{init}} = \frac{\sum(\mathbf{N}_1)}{\sum(\mathbf{N}_0)} \quad (10)$$

where the summation is taken over all age classes.

We expressed the similarity of $\mathbf{N}_0$ to the SAD as the vector angle θ (smaller θ equating to greater similarity between λ_{init} and λ ; White et al. 2013b), by finding the angle between the vectors $\mathbf{w}$ (unfished SAD) and $\mathbf{N}_0$:

$$\theta = \arccos\left(\frac{\mathbf{w} \bullet \mathbf{N}_0}{\|\mathbf{w}\| \|\mathbf{N}_0\|}\right) \quad (11)$$

where double bars indicate a vector norm.

We calculated the time to convergence on asymptotic behavior, T_{asympt} , or effectively, duration of the transient dynamics, by identifying the time t post-reserve implementation at which the population was consistently growing at 99% of the asymptotic population growth rate, λ .

For comparison to the results of the open population model, we also display the transient dynamics in terms of sex ratio and egg production.

All simulations were conducted using Matlab R2018b (Mathworks, Natick, Massachusetts, USA). Model code is available; see *Data Availability* section.

RESULTS

Open population model

In the open population case, higher rates of fishing led to more female-skewed sex ratios (Fig. 2a, b) and greater reductions in egg production (Fig. 2c, d) at the time of MPA implementation. Following the cessation of fishing (i.e., MPA implementation), both variables returned to their unfished equilibria (note that the equilibrium sex ratio for the sex-changing population is approximately 0.32 while, for the gonochore, it is 0.5 and does not change with fishing; the line corresponding to this is not shown in Fig. 2a, b). The trajectories depicted in Fig. 2 suggest that the return to the unfished state is slower when there had been greater fishing (compare red vs.

blue and black curves) and, in the case of egg production, faster for sex-changing species (dashed and dot-dash curves) than for gonochores. This last point is particularly true if the mating function is very steep (i.e., low male importance, $\phi = 18$ in the examples shown in Fig. 2). This occurs because in the sex-changing population, most egg production is by young, moderate-sized fish and the population very rapidly produces enough males to fertilize a majority of female eggs; in the gonochore, the older, larger individuals have much higher per capita egg production but it takes time for those age and size classes to fill in after fishing ceases. Interestingly, the type of sex change cue (fixed vs. flexible) did not have a strong influence on the results, though the flexible-cued population did show a faster increase, particularly with greater fishing, as we expected.

In Fig. 3, we illustrate the strong effects of fishing (F) and male importance (ϕ) on the duration of the transient recovery period. In general, greater fishing lead to longer transients, and for a given level of fishing, sex-changing fish had shorter transients (Fig. 3a). For a given level of fishing, transient duration was similar for sex-changing fish and gonochores if male importance was very high (shallow mating function, left side of Fig. 3b) but for even moderately concave mating functions ($\phi \geq 5$), sex-changing fish had dramatically shorter transient periods (e.g., less than one-half of the duration experienced by the gonochores; right side of Fig. 3b). Additionally, there was a dramatic effect of the length at which fish enter the fishery: for both sex-changing and gonochore fish, the transient is longer when fishing targets smaller fish (Fig. 3a, b). This was in part because a larger part of the age distribution is initially removed; in sex-changing fish, it was also because both males and females are targeted by the fishery. As in Fig. 2 there was little effect of sex change cue, with the fixed- and flexible-cue scenarios having similar durations. This seems to conflict with the faster initial increase depicted in Fig. 2 for flexible-cue, but occurs because the flexible-cued species converges on the asymptotic sex ratio (and thus asymptotic egg production) via a process that has a built-in negative feedback, slowing the rate of approach as it gets closer. By contrast, the fixed-cue sex ratio (and egg production) trajectory is simply a function of how long it takes the full complement of age classes to advance past the size at sex change, so the rate of increase is slow at first but then increases more directly to the asymptote.

Closed population model

The dynamics of the closed population exhibited most of the same key sensitivities, to harvest, male importance, and the length at which fishing begins, as the open population model. The key difference between the two model types is in the shape of the trajectory; in the closed model, the population gradually increases but can exhibit damped, deterministic oscillations if the initial

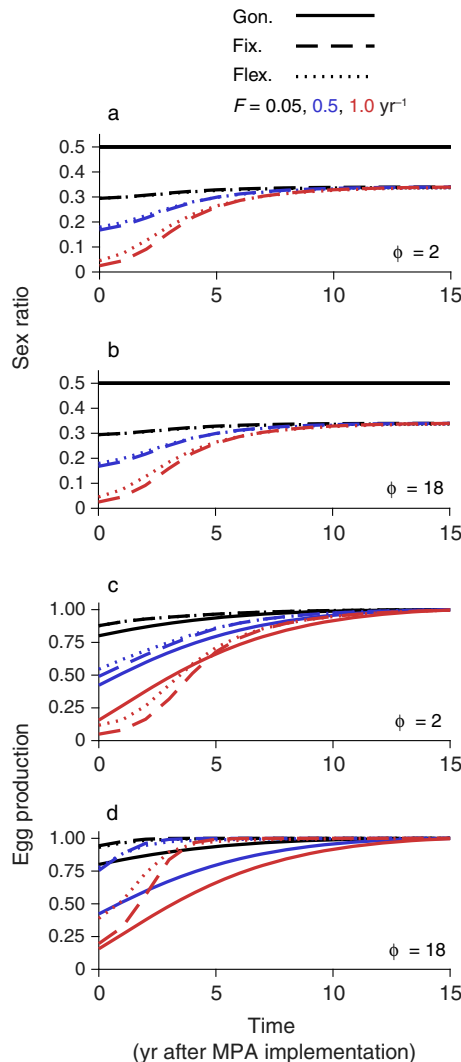


FIG. 2. Trajectories of (a, b) sex ratio or (c, d) population-wide egg production after MPA implementation in the open population model. Results are shown for the three different reproductive strategies (indicated by line type: Gon., gonochore; Fix., fixed-cue sex change; Flex., flexible-cue sex change), three fishing rates (F ; indicated by line color) and two different values of male importance ($\phi = 2$, high importance; $\phi = 18$, low importance). Egg production is expressed relative to the unfished maximum value. In panels a and b, the gonochore sex ratio is 0.5 regardless of fishing rate.

starting age distribution is sufficiently truncated by harvest (Fig. 4; keep in mind that the trajectories in abundance and egg production shown here would eventually reach a maximum if density dependence were accounted for, but those effects would not likely be important early in the dynamics of a heavily fished population). In the examples shown here, these oscillations are only noticeable for the highest level of pre-MPA fishing and persist for at least 20 yr as the population approaches its asymptotic state. Additionally, the amplitude of oscillations was much greater for sex-changing species than for

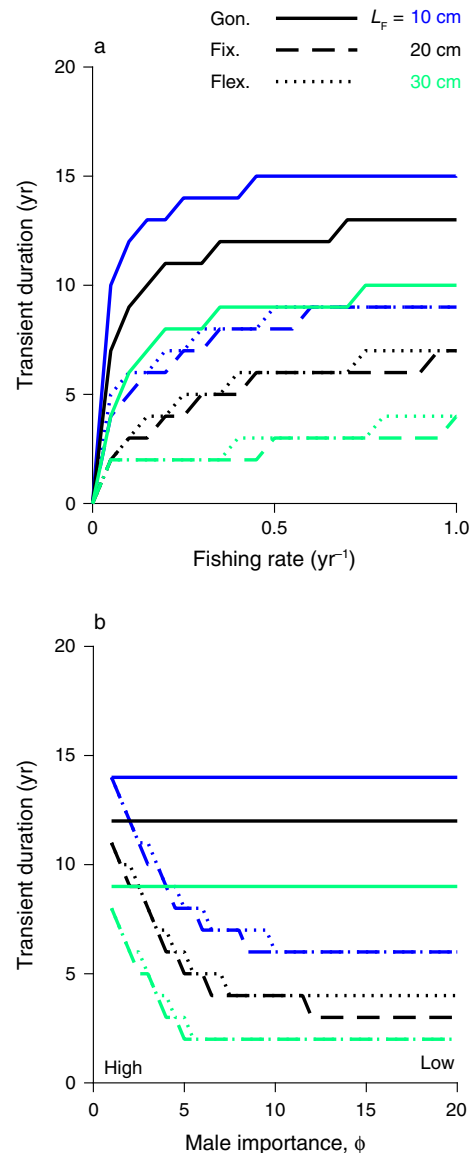


FIG. 3. Relationship between the duration of the post-MPA transient and (a) the pre-MPA fishing rate or (b) the importance of males to reproduction (ϕ) in the open population model. Results are shown for the three different reproductive strategies (indicated by line type), and three different values of the length at which fish can be harvested, L_F (indicated by line color).

gonochores, particularly in egg production. This higher amplitude can be explained by noting that the oscillation in sex ratio has the opposite phase as the oscillation in egg production (Fig. 5). Essentially, when fishing ceases and more males appear as the older size classes fill in, there is a temporary surplus of males relative to females, and egg production declines: there is more male spawning biomass than necessary, and a temporary loss of female biomass. This is reversed as the next pulse of new recruits enters the age distribution, then that pulse moves into the older, male age classes, causing another

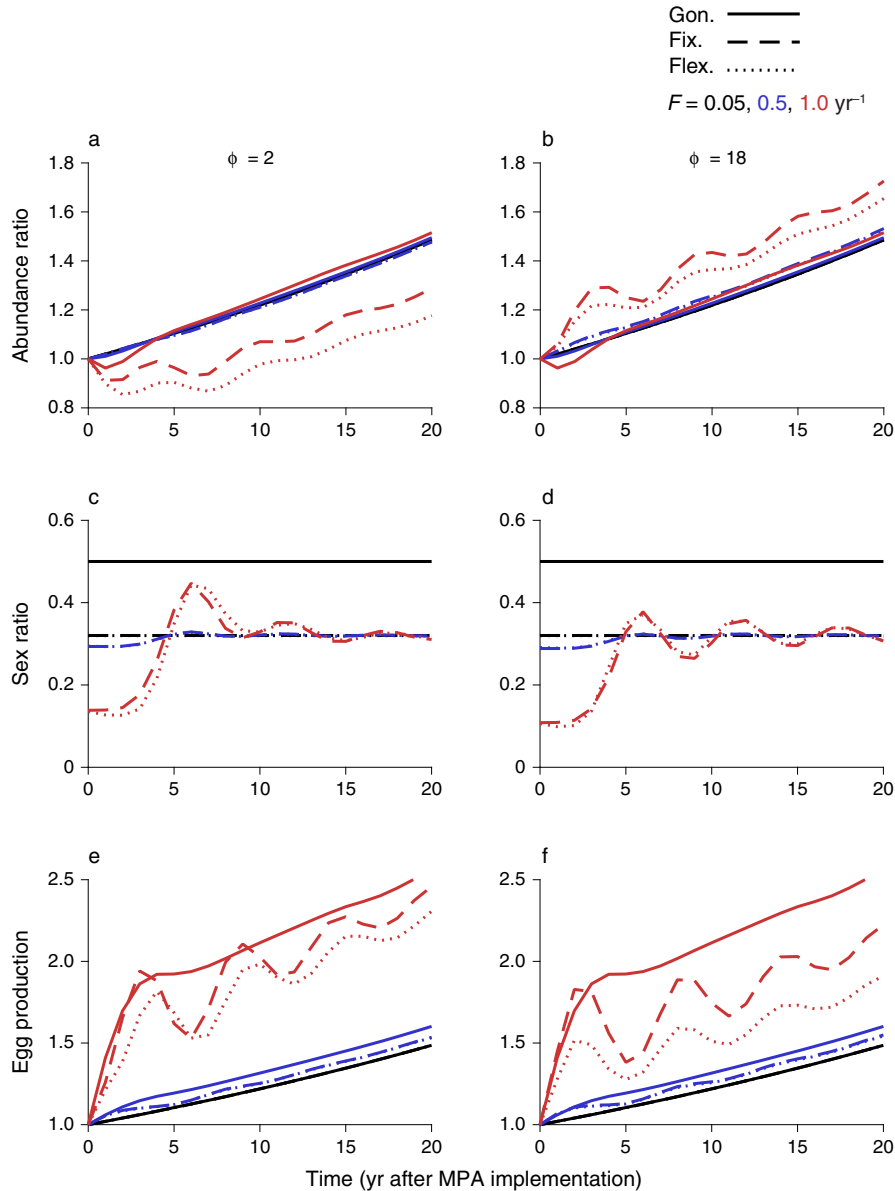


FIG. 4. Trajectories of (a, b) abundance, (c, d) sex ratio, and (e, f) population-wide egg production after MPA implementation in the closed population model. Results are shown for the three different reproductive strategies (indicated by line type), three fishing rates (indicated by line color), and two different values of male importance (a, c, e, $\phi = 2$, high importance; b, d, f, $\phi = 18$, low importance). Abundance and egg production are expressed relative to the value at time $t = 0$.

imbalance. We illustrate this in Fig. 5, comparing the age structure of a gonochore and a fixed-cue protogynous population over the first 13 yr after MPA implementation. The key difference is near year 7, when reproduction in the gonochore population slows because there are now more older female fish but fewer new juveniles entering the reproductive age classes; at the same point in the sex-changing population there are more older male fish but fewer older female fish (because of the lack of recruits several years prior) and recruitment actually declines.

The duration of the transient oscillations was longer with greater fishing, and if fishing targeted a broader size range (Fig. 6a). Somewhat counterintuitively, the transient duration was greater for the sex-changing species than for gonochores and increased with decreasing male importance (Fig. 6d). This appears to occur because, when the age structure of the closed population fills back in, the additional large males do not contribute very much to population growth (if male importance is low), so recovery depends on the smaller portion of the fished age classes that is female. This explanation is

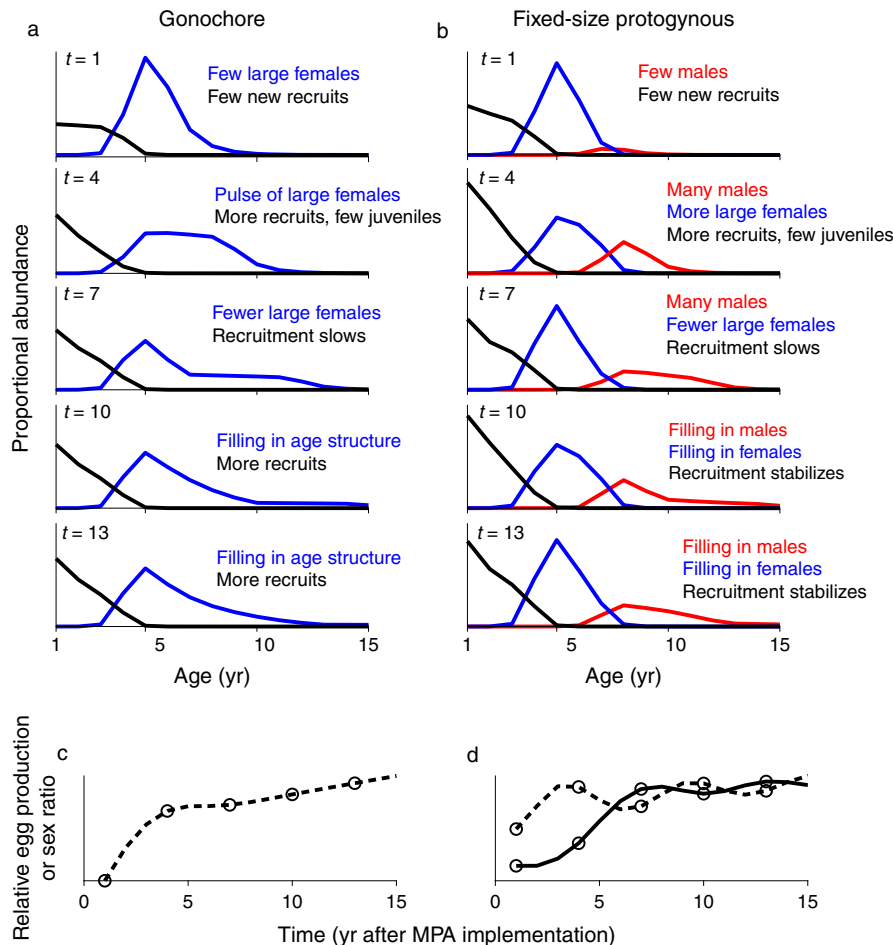


FIG. 5. Shifts in age structure and egg production during the post-MPA transient in the closed population model. (a) Age structure of juveniles (black) and reproductively mature adults (blue) in a gonochore population 1–13 yr after MPA implementation; (b) age structure of juveniles (black), mature females (blue) and males (red) in a fixed-cue sex changing population over the same 13 yr. In both cases, pre-MPA $F = 1.0$ per yr, $L_F = 20$ cm, asymptotic growth $\lambda = 1.02$, and for the sex-changing species, $\phi = 18$ (low male importance). In panels a and b, juveniles are shown at 25% of their actual abundance for ease of visualization. (c, d) Relative trends in egg production (dashed curve) and, for the sex-changing species, sex ratio (solid curve) after MPA implementation. Open symbols indicate the values in the years depicted in panels a and b.

reinforced by the observation that if fishing is restricted to very large size classes (i.e., very few females), the transient is much shorter in the sex-changing species than in the gonochore (green curves in Fig. 6d).

Additionally, the initial trajectory of the population was lower (and has a greater deviation from the asymptotic value of 1.02) when pre-MPA fishing was greater (Fig. 6b), when males had greater importance to reproduction (Fig. 6e), and when fishing targeted smaller fish (Fig. 6b, e). Similarly, the initial deviation from the stable age distribution was greater with greater pre-MPA fishing (Fig. 6c) and greater male importance (Fig. 6f). In general, both types of sex-changing populations had more positive initial trajectories and lower initial deviations than gonochores, with the flexible-cue scenario slightly “better” than the fixed-cue scenario in both cases (Fig. 6c, f).

DISCUSSION

Our analysis shows that populations of sex-changing fishes can exhibit transient dynamics of varying degree and duration following an abrupt cessation of fishing, such as when a no-take MPA is implemented. We found that, as in gonochore (non-sex-changing) species, the historical level of exploitation prior to MPA implementation had a strong influence on the duration of the transient dynamics. Populations that have been heavily exploited historically will tend to have size distributions that are truncated relative to the unfished size distribution (Barnett et al. 2018), and it will take longer for that size distribution (and reproductive output) to recover. If the population is demographically closed, the population will tend to oscillate during this time period, as reproductive cohorts move through the age distribution (White et al. 2013b).

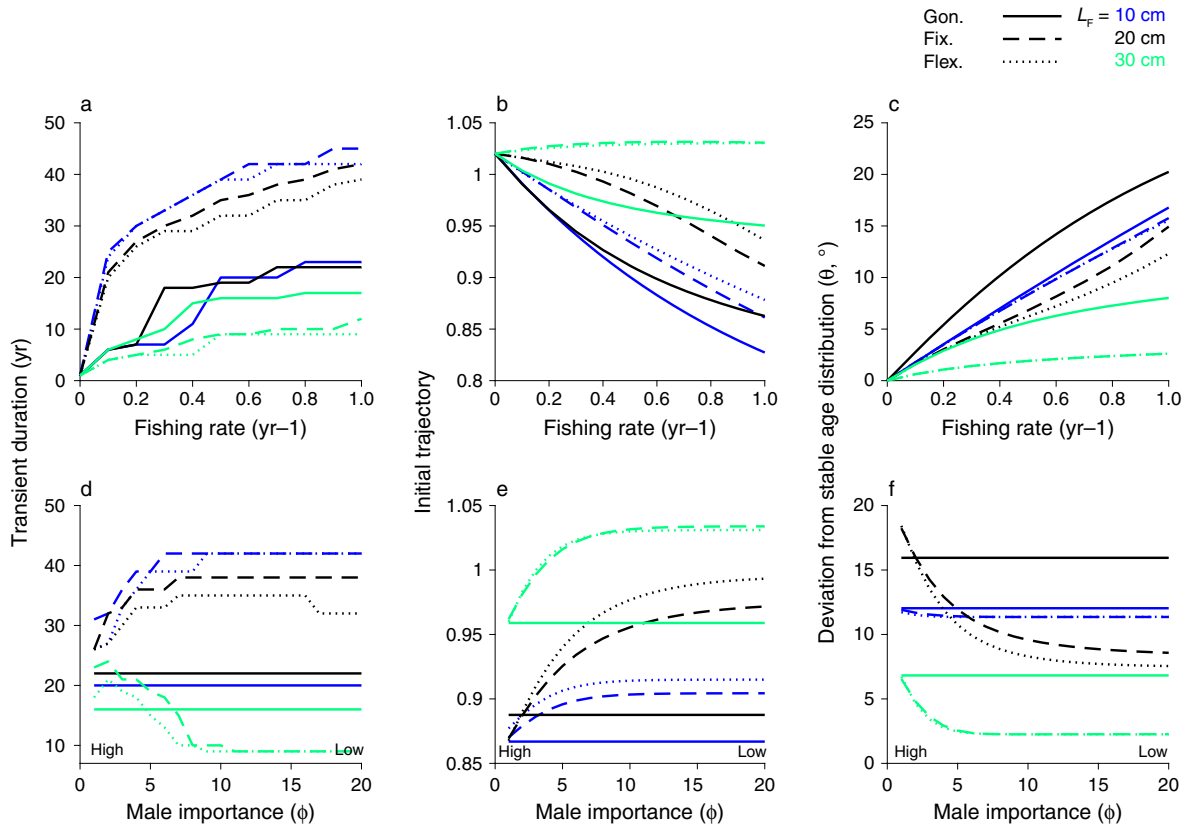


FIG. 6. Relationship between three different metrics of the post-MPA transient and (a–c) the pre-MPA fishing rate or (d–f) the importance of males to reproduction (ϕ) in the closed population model. The metrics are (a, d) the duration of the transient, (b, e) the initial population growth trajectory (for comparison, the asymptotic growth rate is $\lambda = 1.02$), and (c, f) the initial deviation of the population from the stable distribution, θ ($^\circ$). Results are shown for the three different reproductive strategies (indicated by line type), and three different values of the length at which fish can be harvested, L_F (indicated by line color).

Our results generally agree with those shown earlier by Hopf et al. (2016a), whose model analyses suggested that the fishery for protogynous coral trout would see an initial decrease, followed by an eventual increase in yield outside of no-take MPAs, and that time lag would be greater when harvest rates were greater. The parameters for Hopf et al.'s (2016a) model included a relatively steep mating function and a fishery in which fish are targeted several years before the onset of sex change. Based on those features, our analysis would predict that coral trout transient dynamics would be more similar to the gonochore population in our model (particularly in terms of initial population trajectory, based on Fig. 6b, e) than to a protogynous species with a less-steep mating function or a fishery that targeted mostly males. This corresponds to more extreme initial declines in abundance and longer transients as harvest rates were greater, as Hopf et al. (2016a) found. While Hopf et al.'s (2016a) modeling included additional spatial complexity that ours did not, our broader analysis of different protogynous life histories (e.g., different mating functions) and fishery management strategies (e.g., fishery targeting males only) revealed a wider range of possible post-MPA transient dynamics.

Understanding the potential for these types of dynamics is essential in order to set expectations for short-term, empirical assessments of populations in MPAs (White et al. 2011). For example, we show examples of a sex-changing population changing in abundance very slowly for the first several years before eventually increasing (Figs. 2b, 6a), or increasing rapidly before declining somewhat again (Fig. 6b). Either scenario could lead to an inappropriate management decision (e.g., deciding the MPA is not protecting the population effectively). Similarly, one would want to be able to predict when such lags are unlikely to occur due to a species' life history, so that a negative trend in population abundance is not mistaken for transient dynamics. Empirical monitoring programs have reported different timescales of population recovery following the placement of marine reserves, from a short period of time (under 5 yr; Halpern and Warner 2002) to decades to recovery (e.g., Russ and Alcala 2004, McClanahan et al. 2007; all of these studies include some sex-changing species). Such differences in the time scale of population responses could be explained in part by differences in the types of transient dynamics illustrated in our analysis.

We cannot make a general statement regarding whether sex-changing populations will have faster, less cyclic transient dynamics than non-sex-changing (gonochore) populations because the dynamics are strongly affected by what we term male importance (the relationship between the sex ratio and fertilization success). The recovery of population abundance and reproductive output inside MPAs will tend to be more rapid for species in which few males are needed per female for reproductive success. In contrast, when sex ratios closer to 50% male are needed for successful reproduction and fertilization, sex-changing populations will tend to exhibit responses that are similar to or slower than gonochore populations. Interestingly, despite the generally faster recovery when male importance is low, such populations also tend to have longer-lasting oscillations, because the growing “male” portion of the population size distribution contributes very little to reproduction, so reproduction is effectively compressed into a narrow age window (mature females that are too small to change sex), a condition that tends to produce cycles as cohorts of offspring pass through the age distribution, causing an “echo” effect (Botsford et al. 2014a).

Unfortunately, despite growing concern about the highly female-skewed sex ratios of many commercially and recreationally important protogynous species (e.g., Coleman et al. 1996, McGovern et al. 1998, Hawkins and Roberts 2003, Hamilton et al. 2007) and our growing understanding of the effect of sex ratios on fish population dynamics (Easter and White 2016, White et al. 2017), little is empirically known about how male depletion affects fertilization rates and at what point sperm become limiting. In general, because many protogynous sex-changing species have mating systems in which one male monopolizes all of the reproduction in a social group or spawning site (Warner 1988), we would expect that near-maximum fertilization is possible with very few males (Petersen et al. 1992). This suggests that we should focus on the set of results with low male importance (high ϕ), implying that post-MPA transient dynamics would be faster and less extreme than in non-sex-changing species. However, species without harem mating systems may be more sensitive to the loss of males and thus have slower, more extreme, transient dynamics. For example, White et al. (2017) estimated a nearly linear mating function for the group-spawning inland silverside (*Menidia beryllina*); this is not a sex-changing species but other sex-changing species could have similar group-based spawning behaviors (e.g., Nassau grouper, *Epinephelus striatus*; Whaylen et al. 2004). The impact of male importance on the short-term response of protogynous populations warrants better understanding of this relationship as a worthy target of future empirical and experimental research, which will help refine the type of analysis we have performed here. We have begun to address this gap by empirically measuring the fertilization function in a number of fish species (e.g., White et al. 2017, Pang 2019); however, much

more work needs to be done to better characterize the diversity of mating functions in nature.

Despite our lack of understanding of how disproportionate male harvest affects the reproductive output of protogynous populations, more attention has been given empirically to changes in the timing of maturity and sex change. We addressed such changes indirectly in our analysis, by adjusting whether harvest tended to target fish before or after they matured or changed sex. We found that, as one might expect, transient dynamics were shorter when fish became reproductive prior to the onset of fishing. Transient dynamics were also slightly less extreme for populations modeled with a “flexible” sex change cue, meaning that they could mature and change sex earlier in life in response to exploitation and the truncation of the size distribution, as observed in many species (e.g., Buxton 1993, McGovern et al. 1998, Hawkins and Roberts 2003, Hamilton et al. 2007). Of course, there are limitations to the benefit of flexibility in the timing of maturation and sex change; physiological constraints on the minimum age or size at maturity may limit compensation (Armsworth 2001, Alonzo and Mangel 2004), the loss of highly fecund large-bodied females to early sex change can reduce overall reproductive output due to the exponential relationship between body length and egg production (Bohnsack 1990), and females must still live long enough to change sex for sex ratio compensation via early sex change to be successful (Hawkins and Roberts 2003). Therefore, it is perhaps best not to expect flexible-cued protogynous sex changers to have substantially different population responses to fishing and, in our model, the differences between fixed-cue and flexible-cue species were not as great as that between sex-changing and gonochoristic species. Interestingly, for protandrous (male-first) fishes such as barramundi (*Lates calcarifer*), the population dynamic response to fishing is more similar to that of gonochores, because the primary effect in both cases is removal of large, egg-producing individuals, and the mating function would have little effect. However, flexibility in the timing of sex change is very important, because it allows males to begin changing sex to females prior to the onset of harvest, stabilizing egg production (Molloy et al. 2007).

As spatial management is being evaluated as a tool for recovering female-skewed sex ratios of harvested protogynous populations (e.g., Buxton 1993, Beets and Friedlander 1998, Adams et al. 2000, Hawkins and Roberts 2003), predicting the time scale over which increases in male abundance may be expected is important to informing monitoring programs. Our results indicated that the response of sex ratio generally tracked the trend in overall population abundance. However, somewhat unexpectedly, our simulations indicated that the most male-limited protogynous populations may see a rapid initial increase in male abundance, above that of the equilibrium sex ratio, in the few years immediately following MPA implementation (Fig. 4c, d). This response

is due to the cohort effects described above and by White et al. (2013b), where heavily fished populations experience a bulge in the age structure just before the age of entry to the fishery, which resonates through the older age classes (and in the case of protogynous hermaphrodites, through the males) as it moves through the now-unexploited male age classes after fishing ceases. If not appropriately recognized, empirical monitoring could note this resonant effect as a rapid and complete recovery of the operational sex ratio, even if the short-term response does not reflect the eventual conditions.

The model we used in our analysis is a fairly simple representation of population dynamics in MPAs. Like White et al. (2013b) and Kaplan et al. (2019), we sought to capture the dominant, first-order effects expected after fishing stops, namely, filling in of the age structure and concomitant increases in reproduction. This type of strategic modeling analysis is useful for understanding the primary types of deterministic responses to expect, and in this case we were able to generate basic expectations for when sex-changing populations would differ from gonochore populations inside MPAs. In a more tactical, applied analysis, such as guiding adaptive management of particular species in a particular MPA system, one would want to include other important dynamic factors, possibly including density dependence (White 2009), movement (Grüss et al. 2011), species interactions (Baskett et al. 2007), the effects of fishing outside MPA boundaries (Chan et al. 2012), the possibility of poaching within MPAs (Brown et al. 2018), and perhaps most importantly, stochastic variation in larval recruitment (Kaplan et al. 2019). For example, Nickols et al. (2019) provide a case study in how this type of tactical population dynamic modeling can set expectations for the magnitude and tempo of population recovery inside MPAs.

One question addressed by authors such as Moffitt et al. (2013) and Hopf et al. (2016a,b), but not in this paper, is the consequences of the transient pattern of increases in fish biomass inside MPAs for the fished populations outside MPAs. The basic results of Hopf et al. (2016a,b) are likely to hold in most cases (particularly if male importance is low): if there is greater fishing exploitation, then there will be a longer lag in the increase of biomass inside MPAs, and thus a longer lag in the increase in fishery yield due to spillover of larvae or adults from the MPA. A general analysis of the factors affecting that time lag is underway (C. Barcelo, J. W. White, L. W. Botsford, and A. Hastings, *unpublished data*). However, based on results like those of Nickols et al. (2019) and our growing understanding of the level of spatiotemporal stochasticity in larval connectivity pathways (Siegel et al. 2008; reviewed by White et al. 2019), it is becoming clear that in some systems, variability in recruitment could obscure the deterministic effects of MPA protection on fish abundance over time scales relevant to MPA adaptive management. With this in mind, we did not attempt to analyze the more complex

dynamics of an entire metapopulation, including MPAs and fished areas, at this time.

Generating null expectations for the biological response of populations to reserve implementation requires that appropriate empirical data be linked with theoretical models, which will provide a source of comparison for monitoring programs, in addition to improving future reserve design (Hamilton et al. 2010, White et al. 2011, CDFW and OPC 2018). Predicting both the transient and asymptotic states of exploited populations are critical to answering questions in the adaptive management process, and ignoring transient dynamics can lead to misinformed management recommendations (Ezard et al. 2010). As an increasing number of MPAs are put into place worldwide, matching the timescales of empirical and theoretical analyses (Hastings 2004) will be critical to informing monitoring programs in their analyses of the efficacy of marine reserves in meeting management and conservation goals.

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DATA AVAILABILITY

All model code is available on Zenodo: <https://doi.org/10.5281/zenodo.3546441>