



Spatial management for protogynous sex-changing fishes: a general framework for coastal systems

Erin E. Easter*, J. Wilson White

Department of Biology and Marine Biology, University of North Carolina Wilmington,
601 S. College Road, Wilmington, NC 28403, USA

ABSTRACT: Most models of fish population dynamics ignore differences between male and female fish. Yet many harvested species are protogynous hermaphrodites (older females change sex into males), so size-selective fishing will disproportionately remove males. This shifts the sex ratio, potentially disrupting reproduction. Some modeling studies have investigated management strategies for protogynous fishes, but there is no general theory explaining how spatial fishery management should account for protogyny. We developed a spatially explicit model of a generic protogynous fish population to examine the factors affecting the population persistence of coastal (i.e. non-migratory) protogynous populations under spatial management. We varied both (1) biological factors—the cues triggering sex change and the mating function (the relationship between sex ratio and fertilization success) and (2) management factors—configuration of no-take reserves and fishery management outside reserve boundaries. We found that the number and size of reserves required for persistence depended strongly on the sex change cue and the shape of the mating function. Populations with less flexible sex change and requiring more males for fertilization needed more and larger reserves. Unfortunately, empirical mating functions are poorly known for most species and a worthy target of future research. Additionally, persistence of populations with less flexible sex change was impaired by fishery regulations that concentrated on male size classes outside of reserves. Finally, we found that increases in the sex ratio (proportion male) inside reserves are not a reliable indicator of reserve success. These results can be used to design spatial management plans and to set expectations for management assessments.

KEY WORDS: Marine reserve · Marine protected area · Sex change · Sequential hermaphrodite · Protogyny · Mating function

INTRODUCTION

Spatial management strategies, including the use of marine protected areas (MPAs), are increasingly used to address biodiversity conservation and fishery management goals (Wood et al. 2008). While many MPAs are partial-take, both empirical and model analyses have focused on no-take marine reserves in developing spatial management strategies for supporting sustainable fisheries (e.g. Halpern et al. 2009, Gaines et al. 2010). Reserve design principles are often based on the predictions of spatially explicit

models that describe the response of populations to marine reserves, usually focusing on population persistence and fishery yield (reviewed by White et al. 2011). Most such models assume sexes are fixed and in equal proportions and ignore the effects of harvest on sex-specific survival, reproductive patterns, and fertilization success (but see Heppell et al. 2006, Alonzo et al. 2008, Chan et al. 2012). The oversimplification that females solely contribute to reproductive success persists largely because females produce eggs (assumed to be the limiting gamete), and in many species, males can mate and spawn with multi-

*Corresponding author: erineaster89@gmail.com

ple females (Heppell et al. 2006). These assumptions may be appropriate for gonochoristic (separate-sex) species, because males and females are typically of similar body size, so size-selective fishing targets both sexes equally and does not affect the population sex ratio. However, this is not true for the many fish species that are sequential hermaphrodites, i.e. that change sex during their lifetime.

The most common type of sequential hermaphroditism in exploited species is protogyny (species which reproduce as females first and then change sex to male). Many commercially and recreationally important species exhibit protogyny, including California sheephead *Semicossyphus pulcher*, black sea bass *Centropristis striata*, gag grouper *Mycteroperca microlepis*, red grouper *Ephinephelus morio*, red porgy *Pagrus pagrus*, and coral trout *Plectropomus leopardus*, along with a number of aquarium trade species (e.g. bicolor parrotfish *Cetoscarus bicolor*, bluehead wrasse *Thalassoma bifasciatum*, rainbow wrasse *T. lucasanum*) and live-fish fishery species (humphead wrasse *Cheilinus undulatus*, brown-marbled grouper *E. fuscoguttatus*) (reviewed by De Mitcheson & Liu 2008).

The complex life history of protogynous hermaphrodites creates a challenge for spatial management, as mathematical models have historically focused on gonochore fish populations. Size-selective fisheries are of particular concern for protogynous species, as the take of the largest (and thus predominantly male) individuals may skew sex ratios and lead to sperm limitation (Coleman et al. 1996, McGovern et al. 1998, Hawkins & Roberts 2004, Hamilton et al. 2007), reducing the reproductive output of the population. Fishing mortality, even when distributed evenly among age classes, may skew sex ratios towards females in protogynous populations by reducing the number of individuals reaching the age or size class threshold for changing sex (Heppell et al. 2006). Extreme shifts in the sex ratio are assumed to lead to sperm limitation and thus reduce the reproductive output of the population (Alonzo et al. 2008), although the empirical relationship between sex ratio and fertilization success (the mating function, sensu Miller & Inouye 2011) is largely unknown. Under spatial management, the sex ratio will differ between fished and unfished areas, creating heterogeneity in reproductive output that is not accounted for in spatial models of gonochores (Chan et al. 2012).

The response of protogynous fish populations to spatial management likely also depends on the cues that trigger sex change (Alonzo & Mangel 2005). Generally, the signals that initiate sexual transition

are grouped into endogenous cues (a fixed developmental schedule, such as size, condition, or age) or exogenous cues (flexible social or environmental cues; Armsworth 2001). Most models of protogynous fish population dynamics have shown that if sex change is determined by a fixed developmental schedule, size-selective fishing effort may be more detrimental to the sex ratio than in an exogenously cued population, in which removal of males will trigger sex change, compensating for the shift in sex ratio (Alonzo & Mangel 2005, Ellis & Powers 2012). While exogenously cued sex change may prevent deleterious shifts in the sex ratio and consequent sperm limitation, protogynous populations often experience sexual maturity and transformation at smaller sizes or younger ages and slower growth rates when fisheries are size selective for the largest individuals, which likely reduce the average body size and sex-specific fecundity (Hamilton et al. 2007). Discrepancies exist in the literature regarding the effect of fishing effort and marine reserve implementation on the various sex change patterns; however, a consensus suggests that simply knowing that a population exhibits protogyny is not enough to develop successful management strategies (Alonzo & Mangel 2005, Ellis & Powers 2012; but see Grüss et al. 2014).

Existing research on spatial management strategies for protogynous hermaphrodites has largely focused on tactical or system-specific situations, such as reserve designs for a particular species or population (e.g. Huntsman & Schaaf 1994, Heppell et al. 2006, Little et al. 2007, Mapstone et al. 2008, Chan et al. 2012, Ellis & Powers 2012), which limits the applicability of model results and the general theory derived by those studies. For example, Heppell et al. (2006) and Ellis & Powers (2012) both modeled gag grouper *M. microlepis* populations under different management scenarios in the northern Gulf of Mexico, finding that enacting spawning site reserves resulted in the greatest sex ratio improvements by reducing fishing mortality on both adult males and females. Their analysis focused largely on the details of the study species' life history (i.e. annual spawning migrations and the role of an inshore fishery for females). Modeling the common coral trout *P. leopardus* on the Great Barrier Reef (Australia), Chan et al. (2012) investigated the differences between a gonochore and protogynous population, considering a single sex change rule, specifically with the goal of understanding how marine reserves will affect fishery yields in each population. Chan et al. (2012) found that sex-changing populations in no-take reserve scenarios did not receive the yield-increasing benefits

of marine reserves compared to non-sex-changing populations because males are likely to be disproportionately distributed between reserves (high proportion of males) and unprotected areas (low proportion of males). They concluded that the disproportionate distribution reduced the average contribution of males to fertilization success and thus lowered productivity. That result arose because the mating function they used had negative concavity, so the average fertilization over space was lower than one would expect from the average sex ratio over space (an instance of Jensen's inequality; Ruel & Ayres 1999). However, while noting the potential importance of males to reserve performance, Chan et al. (2012) did not fully explore the sensitivity of their results to the shape of the mating function in their model.

In contrast to the complex and situation- or species-specific nature of such tactical models, which are often used to make local management decisions (Gerber et al. 2003, White et al. 2010a, 2013), strategic models are generally simpler and address broad questions, such as what fraction of the coastline should be placed within reserves, to generate general spatial management rules of thumb which are more widely applicable (Botsford et al. 2003, Gerber et al. 2003, White et al. 2010b, Moffitt et al. 2011). Strategic models can also provide guiding principles which aid in interpreting the results of tactical models (Gerber et al. 2003, White et al. 2011). Most existing theoretical models for the spatial management of protogynous stocks have been tactical in nature, and as such, general principles derived from strategic models describing the factors that determine when and why protogynous populations should be managed differently from gonochores are lacking. We examined how spatial management theory for coastal environments should accommodate species with protogynous life histories, considering a broader range of life histories, maturation and sex change rules, and mating function parameters than previously noted studies to draw more broadly applicable conclusions. We compared models of generic protogynous hermaphrodite populations with various sex change cues (both fixed and flexible) to a model of an otherwise identical gonochore population in various spatial management and fishery scenarios. We investigated the sensitivity of our results to 2 key sources of biological uncertainty, the sex change cue (endogenous vs. exogenous) and the mating function relating the sex ratio to fertilization success (i.e. how important are males to reproduction), and 2 management factors that may affect reserves, the intensity of fishing outside reserve boundaries and size-based

fishing regulations outside reserves. From these simulations, we updated 2 key guidelines for spatial management (minimum reserve size and total reserve area) to ensure persistence of protogynous hermaphrodite populations. In our analysis, we focused on coastal or reef-dwelling protogynous fishes for which size and spacing guidelines would be applicable. Protogynous fishes with ontogenetic or spawning migrations will require distinct spatial management approaches (e.g. Heppell et al. 2006, White 2015) that we do not address here. Our analysis explored the generality of our prescriptions for spatial management and the need for better empirical characterization of uncertain biological factors.

METHODS

We used a discrete-time, spatially explicit, age-structured model of a generic protogynous hermaphrodite population (adapted from White & Rogers-Bennett [2010] and Alonzo & Mangel [2005]) to predict adult sex ratio, fertilization rate, and biomass as a function of size-specific fishing mortality. We focused on equilibrium dynamics (static population size and sex distribution), so simulations were started with arbitrary initial conditions and run for 1000 time steps (sufficient to reach equilibrium, for simulations with persistent populations); we then analyzed results at the final time step. The population occupied a 1-dimensional, infinite coastline (to eliminate edge artifacts) with homogeneous habitat, simulated as a circular array of n spatial cells, each defined as reserve or non-reserve (similar to the models of Botsford et al. 2001, White et al. 2010b). All variables used in the model are defined in Table 1, and all fixed parameters and their values are given in Table 2. Matlab model code is available at https://github.com/jwilsonwhite/protogynous_spatial_model.

The basic structure of the model is as follows: in each time step, the subpopulation within each spatial cell ages 1 yr and experiences somatic growth and both natural mortality and age-specific fishing mortality. The population spawns larvae, with reproductive output dependent on the sex ratio within the patch and the mating function. The larvae disperse to other cells in the landscape and experience intra-cohort density-dependent mortality at settlement. Finally, the population sex ratio is adjusted based on the updated population size distribution and sex ratio, depending on the particular sex change cue being simulated. We now provide details on each element of the model.

Table 1. Model variables and their definitions

Symbol	Definition
Larval dispersal/recruitment	
d_{ij}	Probability of dispersal from cell j to cell i
$S_{i,t}$	Settler density in cell i at time t
$\mathbf{N}_{t,j}$	$n \times 1$ vector of fish abundance in each age class at time t in cell j
$\mathbf{f}(L)$	$n \times 1$ vector of female fecundity as a function of length, L
$R_{i,t}$	Number of recruits to age 1 in cell i at time t
Growth and reproduction	
L_a	Length at age a
$\mathbf{f}(L)$	Vector of eggs produced at each body length L_a
$f(L_a)$	Eggs produced at body length L_a
$P_{t,j}$	Proportion of fertilized eggs at time t in cell j
$B_{t,i}$	Proportional male biomass
Adult survival	
F_i	Size-specific fishing mortality in cell i , represented in terms of FLEP
LEP	Lifetime egg production; mean reproductive effort of a new recruit
FLEP	Fraction of unfished LEP realized by a fished population
CRT	Critical replacement threshold; minimum value of FLEP required for population persistence
$s(L_a)$	Fishery harvest selectivity
$\sigma_i(L_a)$	Annual adult survival in cell i
Maturity and sex change	
$S_{i,t}$	Frequency of smaller mature individuals in cell i at time t
$p_M(L_a)$	Probability of maturation at length L
$p_c(L_a)$	Probability of sex change at length L
Marine reserves	
C_R	Fraction of coastline within reserve
W_R	Width of individual reserve (km)

Larval dispersal and recruitment

To represent pelagic larval dispersal, larvae produced in each spatial cell dispersed to adjacent cells according to a Gaussian dispersal kernel in which the probability of dispersal from cell j to cell i , d_{ij} , is a function of the distance between cells j and i and follows a normal probability distribution with parameters μ (mean displacement from cell j) and σ (standard deviation of the kernel, or the mean dispersal in one direction). The effects of variation in μ and σ on marine reserve design are well known for models of gonochore populations (e.g. White et al. 2010b), so

here for simplicity we focused on the case with no advection ($\mu = 0$) but varied σ .

With the incorporation of sex change and the contribution of both females and males to reproductive output, the number of settlers arriving at cell i at time t , $S_{i,t}$, is:

$$S_{i,t} = \sum_{j=1}^n d_{ij} P_{t,j} \mathbf{N}_{t,j} \mathbf{f}(L)^T \quad (1)$$

where $\mathbf{N}_{t,j}$ is an $n \times 1$ vector of fish abundance in each age class at time t in patch j ; $\mathbf{f}(L)$ is an $n \times 1$ vector of female fecundity as a function of length, L (see below, Eq. 4); and $P_{t,j}$ is the proportion of eggs fertilized at time t in patch j (see below, Eq. 5), which depends on the population sex ratio. The probability of larval dispersal from j to i , d_{ij} , is given by the dispersal kernel described above. Note that bold upright symbols indicate matrices, lowercase italicized symbols are scalars, uppercase indicates state variables, lowercase indicates parameters (either Roman or Greek characters), and T is the transpose operator.

The number of recruits to age 1 at cell i , $R_{i,t}$, is comprised of the number of settlers S_i that survive density-dependent mortality according to a Beverton-Holt function:

$$R_{i,t} = \frac{\alpha S_{i,t}}{1 + \frac{\alpha}{\beta} S_{i,t}} \quad (2)$$

where α is density-independent survivorship (describing the slope of the settler-recruit curve at low population density), and β is the asymptotic maximum number of settlers $S_{i,t}$ that can survive to recruit in a cell.

Larval dispersal was the only mode of movement between habitat cells that we considered. Many fishes also exhibit adult movement within home ranges that could extend beyond the boundaries of a single marine reserve, but the general effects of that type of movement on reserve performance are already well characterized (e.g. Moffitt et al. 2009, 2011, 2013). There is no reason to expect that a sex-changing life history would alter the generally negative effects of adult movement on population persistence within reserves, so we kept our analysis simple by avoiding that additional movement mode.

Adult survival

Post-recruitment individuals experienced age- and density-independent natural mortality μ_A and fishing mortality F as a function of age ($F = 0$ within any re-

Table 2. Fixed model parameters and their values based on available data for California sheephead *Semicossyphus pulcher*. See Alonzo & Mangel (2005) for sources of parameter values

Parameter	Parameter value	Definition
Larval dispersal/recruitment		
μ	0	Mean larval displacement from cell i
σ	10, 100 km	Standard deviation of the Gaussian dispersal kernel (mean dispersal in 1 direction)
Growth		
k	0.05 yr ⁻¹	von Bertalanffy growth rate
L_{∞}	90 cm	von Bertalanffy asymptotic length
L_0	8 cm	Larval size at recruitment
Population		
μ_A	0.35 yr ⁻¹	Natural adult mortality
α	0.0001	Density-independent Beverton-Holt settler survival
β	1	Asymptotic Beverton-Holt maximum recruit density
CRT	0.25	Critical replacement threshold (minimum value of fraction of unfished lifetime egg production required for persistence)
Fishing		
r	1 cm	Steepness of selectivity curve
L_f	20 cm	Length at which there is a 50% chance a fish will be removed
Reproduction		
v	7.04	Constant in allometric fecundity relationship
w	2.95	Exponent in allometric fecundity relationship
γ	1	Constant of fertilization function parameter
ϕ	1–20	Male importance; shape parameter in the fertilization function
Gonochore		
L_M	20 cm	Length at which 50% of fish mature
Rule 1: fixed		
L_c	30 cm	Length at which 50% of fish change sex
ρ	1 cm	Shape parameter in the sex change function
q	1 cm	Shape parameter in the maturity function
Rule 2: relative size		
ΔL_c	14 cm	Difference from the mean size at which $p_c(L) = 0.5$
ρ	1 cm	Shape parameter in the sex change function
ΔL_M	4 cm	Difference from the mean size at which $p_M(L) = 0.5$
q	1 cm	Shape parameter in the maturity function
Rule 3: size frequency		
F_c	0.67	Frequency of smaller mature individuals where $p_c(L) = 0.5$
ρ	50	Shape parameter in the sex change function
F_M	0.6	Frequency of smaller individuals at which $p_M(L) = 0.5$
q	50	Shape parameter in the maturity function

serve). Fishing mortality F was represented in terms of the lifetime egg production (LEP, calculated as the sum of the product of survival to age a and fecundity at age a over all ages) it produced in the gonochore species, relative to the natural, unfished LEP (fraction of LEP, FLEP), following White et al. (2010a). The critical replacement threshold (CRT), described as the minimum value of FLEP required for population persistence, was parameterized so that CRT = 0.25 in all model simulations. The level of fishing was expressed relative to the CRT, and results are comparable across species with similar LEP and CRT values, allowing for descriptions of both generic populations and real species with empirically determined life history parameters (White & Rogers-Bennett 2010, White et al. 2010a). For a given fishing scenario, we calculated the relationship between F and FLEP in a non-spatial gonochore population and then used that relationship to find the desired F for a specified FLEP in the spatial model for use in all of the reproductive life histories. In the absence of reserves, the value of F_i in each spatial cell was simply that value F . When there were reserves, we made the conservative assumption that fishing effort inside reserves was entirely reallocated outside of reserves, so that $F_{\text{total}} = nF$ and the fishing rate F_i in each non-reserve cell i was $F_i = F_{\text{total}}/(1 - C_R)$, where C_R is the proportion of the coastline protected within the reserve. We took the approach of expressing F relative to gonochore FLEP because LEP is not well suited to describing the effects of fishing in a sex-changing fish, yet the FLEP approach is well suited for characterizing harvest rates relative to population persistence thresholds and is conceptually identical to the various biological reference points used in fishery management (e.g. spawning potential ratio, White et al. 2010a).

Annual adult survival in each cell i was calculated from constant natural

mortality μ_A and size-specific fishing mortality F_i , where fishery harvest selectivity $s(L_a)$ is given by:

$$s(L_a) = \frac{1}{1 + e^{-r(L_a - L_f)}} \quad (3)$$

where r is the steepness of the selectivity curve, and L_f is the length at which there is a 50% chance a fish will be removed (cf. Alonzo & Mangel 2005). Then, annual adult survival $\sigma_i(L_a)$ in cell i is:

$$\sigma_i(L_a) = e^{-[\mu_A - F_i s(L_a)]}. \quad (4)$$

Growth and egg production

Growth in length followed a von Bertalanffy relationship:

$$L_a = L_\infty [1 - e^{-k(a - a_0)}] \quad (5)$$

where L_a is the length at age a , L_∞ is the asymptotic maximum length, k is the growth rate, and a_0 is the effective age at length 0. Weight was an allometric function of length. We assumed that female fecundity $f(L)$ (the vector of eggs produced at each body length L_a) was proportional to mature female biomass, so each vector element $f(L_a)$ was:

$$f(L_a) = p_M(L_a) v L_a^w \quad (6)$$

where v and w are constants, and $p_M(L_a)$ is the probability of maturity (see below, 'Maturation and sex change').

Mating function

The contribution of males to reproductive output is poorly understood, and a general empirically based allometric relationship between male body size and sperm production does not exist (Alonzo & Mangel 2004), but presumably the probability of egg fertilization is determined by the sex ratio. The only 2 such relationships of which we are aware are for the bluehead wrasse *Thalassoma bifasciatum*, in which a few males can effectively fertilize the eggs of hundreds of females (Warner et al. 1995, Petersen et al. 2001, Alonzo & Mangel 2004), and the inland silversides *Menidia beryllina*, in which per-female production of fertilized eggs increases linearly with the proportional male sex ratio, suggesting a strong dependence on the availability of males (S. M. Brander et al. unpubl.). We assumed that fertilization depended on the proportional male biomass $B_{t,i}$ rather than the numerical sex ratio, following Chan et al.

(2012), because the former accounts for the greater sperm contribution of larger males. We assumed that this biomass sex ratio was the operational sex ratio, i.e. we did not consider the possibility of social hierarchies that could skew the operational sex ratio. We further assumed male and female biomass have the same allometric relationship and the biomass sex ratio $B_{t,i}$ is male biomass divided by the sum of male and female biomass. We assumed the proportion of fertilized eggs $P_{t,j}$ could be described by a cumulative beta distribution function with shape parameters γ and ϕ :

$$P_{t,j} = \text{beta}(B_{t,i}, \gamma, \phi) \quad (7)$$

where we assume γ is a constant set to 1, so the curve has negative concavity over its entire domain, and ϕ is treated as a fertility parameter describing how quickly the proportion of eggs fertilized approaches 100% as $B_{t,i}$ increases from zero (Fig. 1). This functional form describes a plausible relationship between sex ratio and fertilization success (similar to the relationship used in past models; e.g. Chan et al. 2012), with ϕ representing male importance: for $\phi = 1$, fertilization increases linearly with sex ratio (males are very important, as in silversides), while for larger values, e.g. $\phi = 20$, the curve is saturating and asymptotes near 100% fertilization with a low sex ratio (i.e. a very small number of males can fertilize all eggs, as in bluehead wrasse; Fig. 1).

Maturation and sex change

We compared gonochoristic and 3 alternative protogynous sexual strategies using life history equations developed by Alonzo & Mangel (2005). In the gon-

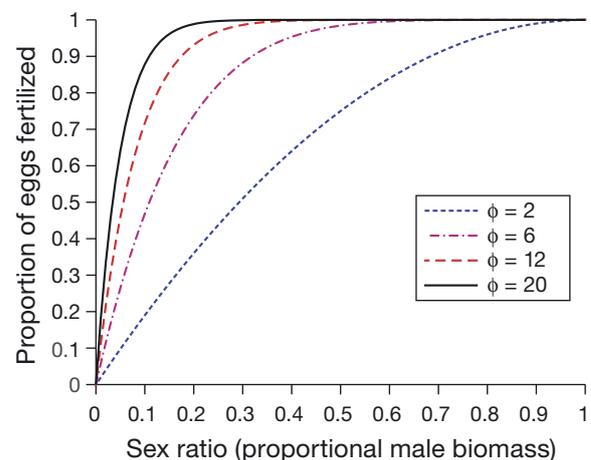


Fig. 1. Example of the relationship between egg fertilization rate and sex ratio (proportional male biomass) for various levels of the male importance parameter, ϕ

chore case, the sex ratio was assumed to be 0.5 (proportion male biomass), and sex assignment was determined at birth. The timing of maturation as expressed by $p_M(L_a)$, was determined by the absolute length of the individual:

$$p_M(L_a) = \frac{1}{1 + e^{[-q(L_a - L_M)]}} \quad (8)$$

where L_M is the length at which 50% of juveniles were anticipated to mature, and q determined the steepness of the maturation probability function.

While similar previous studies of protogynous hermaphrodites, including Heppell et al. (2006) and Chan et al. (2012), each considered just one protogynous mating function and sex change cue, we modeled one fixed and 2 flexible transition rules (rules 1, 2, and 3, respectively, next paragraphs) for the timing of maturation $p_M(L_a)$ and sex change $p_c(L_a)$. We used equations from Alonzo & Mangel (2005) for $p_c(L_a)$. Based on evidence from California sheephead that the timing of maturity may also respond to changes in the size distribution in fished populations (Hamilton et al. 2007), we applied the same functional forms to $p_M(L_a)$.

Rule 1: fixed. Representing an endogenously cued sex change function, the proportion of females maturing and transitioning to male was fixed, where the probability of maturation $p_M(L_a)$ and the probability of sex change $p_c(L_a)$ were determined by the absolute length of the individual (as in Eq. 8 for gonochores):

$$p_c(L_a) = \frac{1}{1 + e^{[-\rho(L_a - L_c)]}} \quad (9)$$

where L_c is the size at which 50% of mature females change sex. The equation for $p_M(L_a)$ is identical, with parameter q in the place of parameter ρ .

Rule 2: relative size. The probability of maturation and sex change was determined by the mean length of all individuals in the cell:

$$p_M(L_a) = \frac{1}{1 + e^{[-q(L_a - (L_i + \Delta L_M))]} \quad (10)$$

where ΔL_M is the difference from the population mean length at which the probability of an individual maturing is 50%, and L_i is the mean length of all individuals in cell i . Then

$$p_c(L_a) = \frac{1}{1 + e^{[-\rho(L_a - (L_i + \Delta L_c))]} \quad (11)$$

where ΔL_c is the difference from the mean at which the probability of sex change is 0.5.

Rule 3: size frequency. The probability of maturation and sex change was determined by the frequency of smaller mature individuals at the mating site:

$$p_M(L_a) = \frac{1}{1 + e^{[-q(S_{i,t} - F_M)]}} \quad (12)$$

where $S_{i,t}$ is the frequency of smaller mature individuals in cell i at time t and F_M is the frequency at which the probability of maturing is 0.5, and

$$p_c(L_a) = \frac{1}{1 + e^{[-\rho(S_{i,t} - F_c)]}} \quad (13)$$

where F_c is the frequency at which 50% of the individuals are expected to change sex. Note that the sex change parameters q and ρ take on different values in the different sex change scenarios (Table 2).

Spatial reserve scenarios

Population persistence is essentially achieved through replacement (each individual replaces itself with ≥ 1 offspring during its lifetime), and both theoretical and empirical results suggest that persistence of non-sex-changing metapopulations can be achieved through 2 processes: (1) network persistence, where persistence is achieved by replacement via larval exchange among all local populations, or (2) self-persistence, where individual local populations persist via sufficient retention of locally produced larvae (Hastings & Botsford 2006, White et al. 2010b). Consequently, spatial management with reserves that support persistent populations can be achieved by either (1) having many small reserves, all well connected by larval dispersal and with the fraction of coastline in reserves greater than or equal to the CRT required for persistence in non-spatial management (network persistence), or (2) having one or more individual reserves large enough to retain a proportion of locally produced larvae greater than or equal to the CRT (self-persistence; White et al. 2010b, 2011). Following the example of earlier studies (e.g. Moffitt et al. 2013), we simulated results for both network-persistent reserve systems and self-persistent reserve systems, with the understanding that those 2 scenarios define the extremes of a continuum of possible reserve configurations (many small vs. few large) in a spatial management plan.

Model analysis: Population persistence thresholds

Our primary objective was to determine how the reduction in sex ratio due to fishing affects the minimum reserve requirements (reserve size or total reserve area) for sustaining persistent protogynous hermaphrodite populations. Because we expressed

fishing rates in terms of FLEP, our calculations of persistence thresholds are insensitive to the particular values chosen for most demographic parameters shared by gonochoristic and sex-changing species (e.g. length at age, natural mortality rate; White et al. 2010a,b). However, several life history features unique to hermaphroditic species are not captured by FLEP: (1) the cue triggering sex change (fixed size, relative size, or size frequency); (2) ϕ , the parameter describing the relationship between sex ratio and fertilization success; and (3) the size of recruitment to the fishery (L_f) relative to the size at which sex change occurs. Therefore, we determined how each of those life history attributes affected minimum reserve requirements for population persistence.

We first characterized the general effects of ϕ and sex change cue on population dynamics by varying the level of fishing effort, simulating scenarios ranging from sustainably fished (F equivalent to gonochore FLEP = 0.3 in fished areas; this is greater than the CRT of 0.25, so reserves are not necessary for gonochore population persistence) down to severely overharvested (F equivalent to FLEP = 0 in fished areas). Note that in all of these cases, F is calculated to give the corresponding FLEP in the non-spatial, no-reserve case. As reserve area increases and fishing effort is redistributed, F_{total} remains the same but F_i in each cell increases, and the realized FLEP is lower than the target. In these initial simulations, we chose reserve scenarios that would allow either self-persistence or network persistence in the gonochore population (see next 2 sections below for descriptions of each scenario).

We then found the minimum fraction of coastline in reserve C_R that allowed network persistence among many small reserves or the minimum reserve width W_R that allowed self-persistence within a single large reserve. We made this calculation using the baseline life history parameters for each of the 3 sex change modes (plus gonochores), varying male importance from very low ($\phi = 20$) to extremely high ($\phi = 2$). Our model differs from that of Heppell et al. (2006) and Chan et al. (2012), who considered only 2 mating functions (i.e. male importance values) that fall roughly in the middle of our range. We investigated a wider range of possible mating function shapes, including extremely low values of ϕ that actually correspond to the nearly linear mating function observed in inland silversides *M. beryllina* (S. M. Brander et al. unpubl.).

Spatial management can also involve coordination between reserves and fishery regulations outside of those reserves. Therefore, we additionally investi-

gated the influence of fishery management outside reserve boundaries on the reserve requirements for population persistence (C_R and W_R). Specifically, we analyzed the role of fishery size limits by varying the mean size of entry to the fishery (L_f) from the baseline value, the mean size at maturity in the gonochore population (20 cm, reflecting the common goal of allowing fish to reproduce before harvest), up to the mean size at sex change in an unfished protogynous population (30 cm, reflecting the parallel goal of allowing fish to change sex before harvest). Although there is no fishing inside the reserve, it is reasonable to expect that changing fishery management outside reserves to target either one or both sexes could shift the dynamics of the system. When changing L_f , we recalculated the relationship between F and gonochore FLEP before determining the F used in simulations. This describes a realistic scenario where increasing the length limit increases the intensity of fishing on larger fish, rather than reducing overall effort (Cox & Walters 2002).

When estimating the minimum values of C_R and W_R , we calculated persistence in 2 ways: (1) scorched earth, where no reproduction occurred outside of reserve boundaries (i.e. FLEP = 0 in fished areas; this is a conservative approach that assures reserves are independent of conditions beyond their boundaries and was achieved by simply setting reproduction to zero outside of reserves), and (2) a more realistic scenario in which the exploited population outside of the reserves was achieving some reproduction (but less than the CRT; FLEP = 0.2) and contributing recruits to the metapopulation. In the following paragraphs, we describe how we made these calculations for network-persistent and self-persistent reserve scenarios.

Network persistence

To simulate a network-persistence scenario, we held W_R (the width of an individual reserve) small enough relative to the larval dispersal distance so that self-persistence was not possible ($\sigma = 100$, $W_R = 0.1\sigma$). We then varied the fraction of the coastline protected within reserve, C_R , from 0 (no reserve) to 1 (complete protection) to determine what minimum fraction of the coastline C_R was required for population persistence. Note that this required varying the size of the coastline, n , to accommodate different C_R values for a constant W_R , but because the coastline is circular, this did not create an artifact in the results. The criterion for network persistence is calculated by first estimating eggs per recruit (EPR), the number

of eggs produced by a new recruit over its lifetime when the population is at equilibrium. For sex-changing scenarios, we estimated this value using the equilibrium values of the length-dependent probability of sex change and fertilization success. We then generated an egg production matrix \mathbf{C} by multiplying each row of the dispersal matrix \mathbf{D} by the value of EPR for the corresponding spatial cell. The elements c_{ij} of \mathbf{C} then give the total number of eggs per recruit produced in j that disperse to i . This matrix has dominant eigenvalue λ_C , and network persistence requires that $\alpha\lambda_C \geq 1$, where α is the slope of the Beverton-Holt function at the origin (White 2010). In other words, each recruit must replace itself within the metapopulation within its lifetime (Hastings & Botsford 2006). Previous work has shown that gonochores achieve network persistence in the scorched earth scenario when $C_R \geq \text{CRT}$ (White et al. 2010b), i.e. 25% in our model.

Self-persistence

To simulate the self-persistence scenario, we held C_R below the level needed for network persistence ($C_R \geq 0.25$ is needed for persistence given the CRT, so we chose $C_R = 0.1$ for these simulations), imposed a shorter dispersal distance ($\sigma = 10$), and varied W_R (as a proportion of σ) to determine the size of an individual reserve required for self-persistence. For these simulations, we again varied n so that C_R remained constant as W_R increased relative to σ . Self-persistence was determined in the same manner described above for network persistence, but only the submatrix of the connectivity matrix \mathbf{C} corresponding to the cells within the reserve was included. Gonochores are expected to be self-persistent in reserves when $W_R \geq \sigma$ (larval dispersal distance) if $\text{CRT} = 0.35$ (Botsford et al. 2001, White et al. 2010b) but may persist in a smaller reserve if the CRT is smaller or if the FLEP is greater than zero outside reserves (White et al. 2010b).

Model parameterization

Baseline parameter values were taken from Alonzo & Mangel (2005) and based on previous research (Warner 1975, Cowen 1985, 1990) on California sheephead *Semicossyphus pulcher* (Labridae), a commercially and recreationally important protogynous hermaphrodite wrasse that is common in the rocky reefs and kelp forests of southern California, USA. Parameter values are reported in Table 2.

While sheephead demographics were used in the model, it is important to note that model results are not limited to this species and, rather, are dependent on the shape of the fertilization success curve, which we parameterized to capture a range of possible fertilization patterns, and the factors cueing sex change, which are generally less studied than the growth, survival, and reproduction of protogynous species. We normalized model outputs by expressing biomass as a proportion relative to the biomass of an unfished gonochore population.

RESULTS

General patterns of protogynous population dynamics in reserves

The general effects of fishing on protogynous hermaphrodites in our model matched our expectations from the non-spatial models of Alonzo & Mangel (2004). For a moderate value of male importance ($\phi = 6$) and the baseline size at entry to the fishery ($L_f = 20$ cm), a high but sustainable (without reserves) rate of size-selective fishing (FLEP = 0.30) reduced biomass and perturbed the sex ratio in fished areas, while inside reserves biomass remained high and sex ratios remained similar to those of unexploited protogynous populations (numerical sex ratio of ~34% male for fixed size and relative size strategies and ~27% male for the size frequency strategy). This general pattern held for both network-persistence scenarios (i.e. $C_R = 0.25$, $W_R = 0.1\sigma$; Fig. 2a,b) and self-persistence scenarios (i.e. $C_R = 0.1$, $W_R = \sigma$; results not shown). Although sex ratios were reduced outside of the reserve for all protogynous cases, the effect of fishing differed between the sex change scenarios. The fixed-cued protogynous population was the most sensitive to fishing, had the lowest equilibrium biomass (Fig. 2a) and the lowest equilibrium sex ratio outside of the reserve (<7% male; Fig. 2b), and exhibited the greatest difference in sex ratio between the protected and harvested zones, reflecting the inability to compensate for the disproportionate loss of males by early maturation and sexual transition. The relative size-cued population sustained higher biomass (just greater than that of the gonochore) under the same fishing rate (Fig. 2a) and maintained more males in fished areas (nearly 10% male; Fig. 2b), as individuals were able to shift the timing of maturation and sex change to earlier ages in response to size-selective (and thus sex-selective) harvest. The size frequency-cued population showed

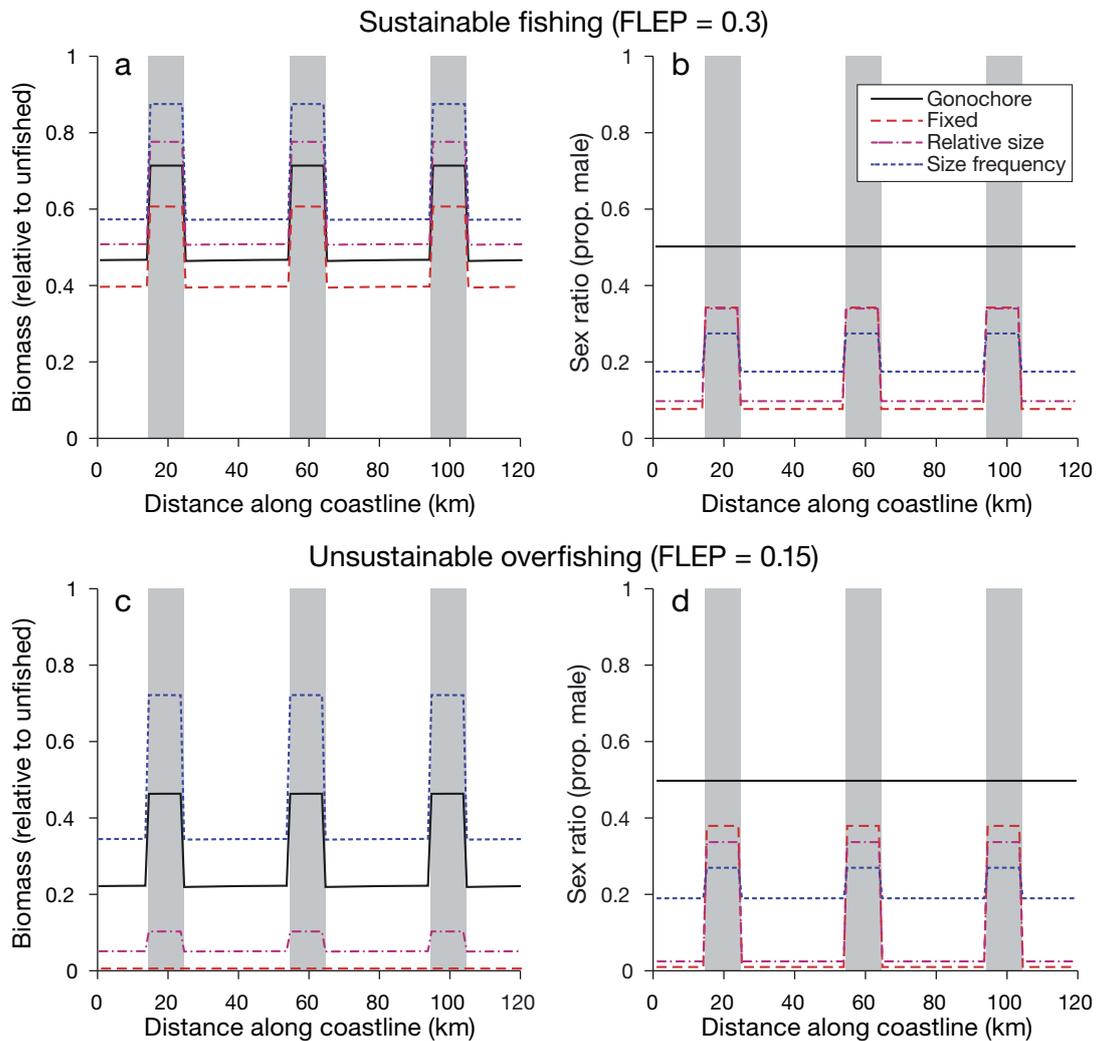


Fig. 2. (a,c) Population biomass (expressed as a proportion of unfished biomass) and (b,d) sex ratio (% male) of populations with different life histories along a coastline with marine reserves. The figure shows a segment of the infinite (circular) coastline containing no-take reserves that cover $C_R = 25\%$ of the coastline; each reserve has width equal to 10% of the larval dispersal distance, so network persistence is possible but self-persistence is not. The non-reserve area was fished at a harvest rate that was either (a,b) sustainable without reserves (equivalent to $FLEP = 0.3$) or (b,c) unsustainable without reserves (equivalent to $FLEP = 0.2$). Protogynous populations (with fixed, relative size, or size frequency cues, indicated by line type) had intermediate male importance ($\phi = 6$)

a more consistent sex ratio along the length of the coastline than fixed size- and relative size-cued populations, did not experience a dramatically reduced male population in the fished areas (Fig. 2b), and actually sustained higher equilibrium biomass than the gonochore along the entire coastline (Fig. 2a).

The differences among reproductive strategies became more evident when fishing was intense enough to cause the population to collapse in the absence of reserves ($FLEP = 0.15$). With that level of fishing, fixed size- and relative size-cued protogynous populations exhibited drastically depleted populations, with the fixed size population near zero in

the network scenario (Fig. 2c). Those 2 sex change cues also exhibited even greater reductions in sex ratio in fished areas (<5% male). Interestingly, these populations had a greater proportion of males within the reserve (~34 to 38% male; Fig. 2d) than in the less fished scenario ($\leq 34\%$; Fig. 2b). This increased sex ratio is likely an effect of the population being closer to collapse: very few larvae are spawned outside of the reserve, so recruitment is lower along the entire coast (including inside the reserve) than in scenarios with less fishing. However, larvae that do settle in the reserve have a long lifespan, resulting in a large number of old, large males there. This combination of

factors produces a shifted age structure (towards the older, predominantly male age classes) within the reserve, relative to scenarios with less fishing and higher larval recruitment. However, this effect did not materialize in the size frequency-cued population, which maintained sex ratios similar to those of the less fished population (Fig. 2b), with a substantially greater sex ratio (20% male) in fished areas and

once again higher biomass than the gonochores along the entire coastline (Fig. 2c).

The differing responses to fishing of the 4 reproductive strategies can be summarized by examining the coast-wide average biomass and sex ratio (Fig. 3; nearly identical results for the self-persistence simulations are not shown). For the moderate level of male importance ($\phi = 6$) shown in Fig. 2, biomass decreases

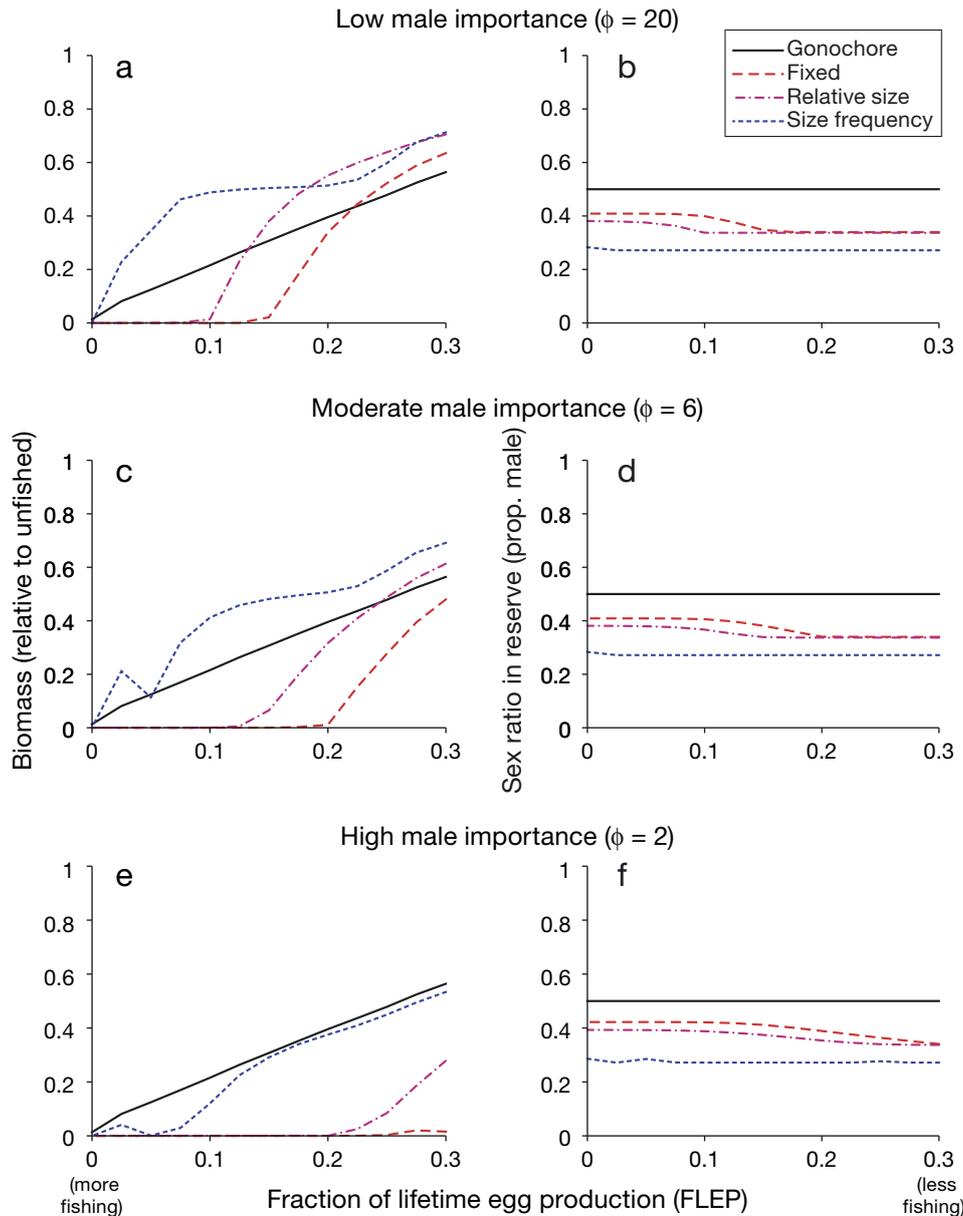


Fig. 3. (a,c,e) Population biomass (expressed as a proportion of unfished biomass) and (b,d,f) sex ratio (% male) of populations with different life histories along a coastline with marine reserves and varying intensity of fishing. The coastline contains no-take reserves that cover $C_R = 25\%$ of the coastline; each reserve has width equal to 10% of the larval dispersal distance, so network persistence is possible but self-persistence is not (as in Fig. 2). The fishing rate in non-reserve areas was equivalent to the indicated gonochore FLEP; FLEP < 0.25 results in gonochore population collapse without reserves. Protogynous populations (with fixed size, relative size, or size frequency cues, indicated by line type) had (a,b) low; (c,d) intermediate; or (e,f) high male importance (indicated by the mating function parameter ϕ)

faster with increased fishing for the fixed size- and relative size-cued protogynous populations, while the size frequency-cued population responded similarly to the gonochore population (Fig. 3c). The sex ratio inside reserves also increased as FLEP decreased (i.e. fishing increased) for the fixed size- and relative size-cued populations, reflecting the increase within reserves seen in the spatial distribution (Fig. 2).

The value of the male importance parameter, ϕ , had a strong influence on population dynamics. In general, when males were more important to fertilization success (smaller values of ϕ), the loss of males in fished areas had a more severe effect on reproduction. The relative size-cued and especially the fixed size-cued population collapsed more rapidly with increased fishing (Fig. 3e), with sex ratios that were skewed heavily towards females in harvested zones and towards males in reserves (Fig. 3f). In contrast, if very few males were required for fertilization (e.g. $\phi = 20$), the protogynous populations declined much more gradually with increased fishing (Fig. 3a), and the reserve sex ratio only increased at very high fishing rates for the fixed size- and relative size-cued populations (Fig. 3b). The latter occurred because male depletion in fished areas had a smaller effect on overall reproductive output and consequent age structure (and sex ratio) shift.

Thresholds for population persistence under spatial management

Scorched earth: No reproduction outside reserves

As the patterns in Figs. 2 & 3 suggest, differences in reserve protection requirements between gonochore and protogynous hermaphrodite populations depended on both sex change cue and the parameter describing male importance, ϕ . The protogynous populations with fixed size- and relative size-cued sex change required substantial protection to persist when males were of greatest importance ($\phi = 1$) and no reproduction was occurring outside of the reserve (up to 55% of the coastline or a reserve >1.7 times the dispersal distance; Fig. 4). The level of protection required for these populations to persist quickly dropped as males became less important; however, both fixed size- and relative size-cued populations still had greater persistence thresholds ($C_R > 0.35$ or $W_R \geq$ dispersal distance) than the gonochore and the size frequency-cued population, even when very few males were required for fertilization success. The size frequency-cued protogynous population had inter-

mediate reserve requirements that fell between the relative size-cued and the gonochore populations (Fig. 4). In this scorched earth scenario, protogynous populations always required more protection than the gonochores. This is because in gonochore populations, large, old female fish accumulate in reserves, and their large size corresponds to very high egg production. In a protogynous species, the large fish that accumulate in reserves are predominantly males, which do not contribute to an exponential increase in egg production in the same way that large females do (once the biomass sex ratio is sufficiently high for most eggs to be fertilized). Under scorched-earth conditions, all fish are assumed to be harvested prior to spawning outside the reserves, so we do not consider the effects of size limit regulations.

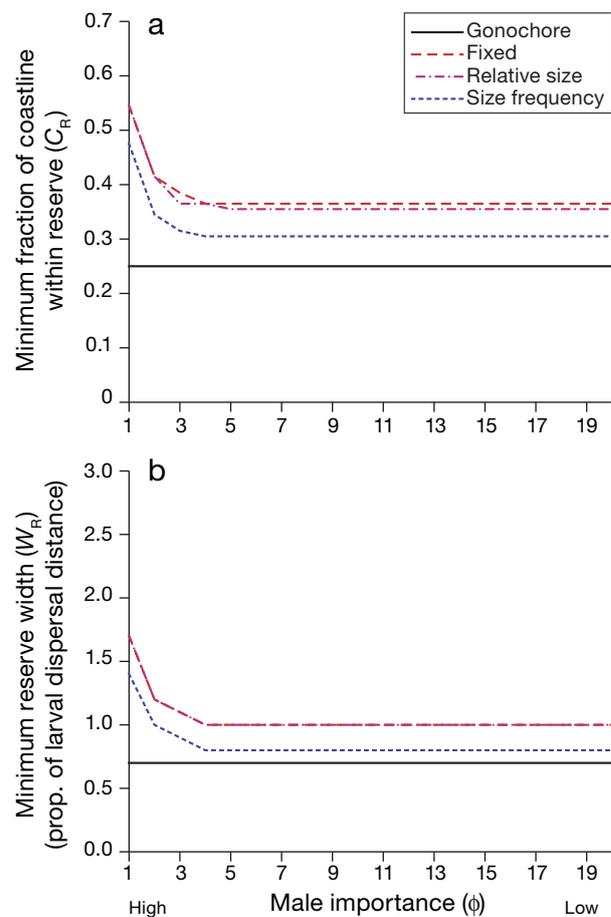


Fig. 4. (a) Minimum fraction of the coastline within reserve, C_R , to achieve network persistence or (b) minimum reserve width, W_R (as a proportion of larval dispersal distance), to achieve self-persistence as a function of male importance (mating function parameter ϕ) for populations with different reproductive life histories (indicated by line type). This scenario represents scorched earth, where harvest was sufficiently intense that no reproduction occurred outside of the reserve (FLEP = 0)

Some reproduction outside reserves

Allowing the exploited population outside of the reserves to achieve some reproduction (FLEP = 0.2) under the baseline fishery size limit ($L_f = 20$ cm) resulted in lower network and self-persistence thresholds (compared to the scorched earth scenar-

ios) for all of the life histories (Fig. 5a,b). In fact, as males became less important (larger ϕ), the protogynous populations no longer needed reserves to persist in this scenario, unlike the gonochores. The reserve area and size requirements declined faster with ϕ for the 2 more flexible sex change cues (Fig. 5a,b).

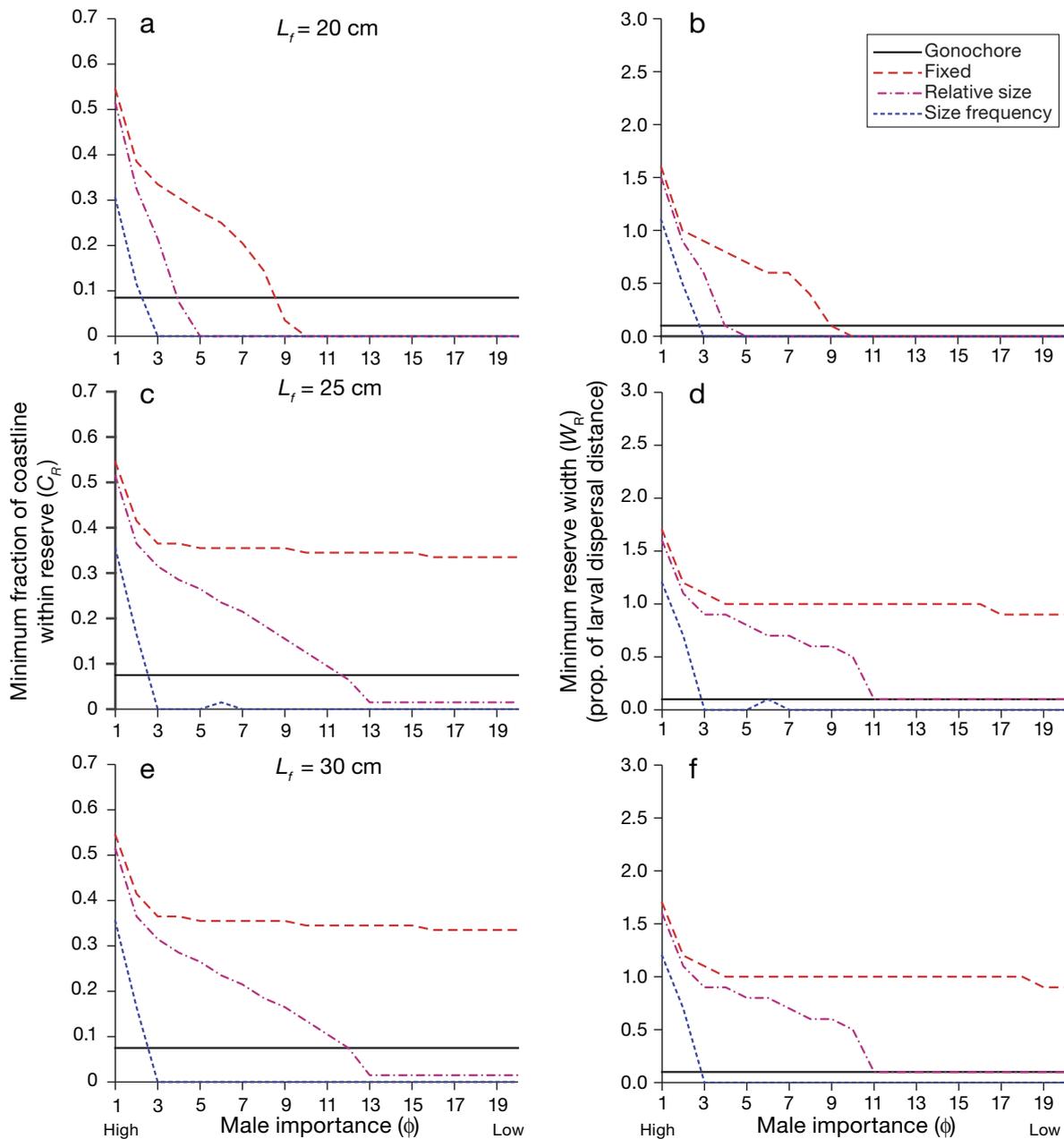


Fig. 5. (a,c,e) Minimum fraction of the coastline within reserve, C_R , to achieve network persistence or (b,d,f) minimum reserve width, W_R (as a proportion of larval dispersal distance), to achieve self-persistence as a function of male importance (mating function parameter ϕ) for populations with different reproductive life histories (indicated by line type). In this scenario, fishing is unsustainable (persistence is not possible without a reserve for the gonochore) but less intense than scorched earth (FLEP = 0.2). The minimum harvest size limit in fished areas was (a,b) 20 cm (equivalent to unfished size at maturity); (c,d) 25 cm; or (e,f) 30 cm (equivalent to unfished size at sex change)

Fishery regulations outside marine reserves

Population persistence thresholds when there was reproduction outside reserves (FLEP = 0.2) changed substantially when the minimum size limit of the fishery was increased from 20 to 25 or 30 cm (Fig. 5c–f). Essentially, for larger minimum size limits, the persistence thresholds for the 2 protogynous populations with less flexible sex change (fixed size and relative size) became more similar to those of the scorched earth scenario. This shift in persistence requirements occurred because increasing the minimum size limit of the fishery concentrated all of the fishing effort on the larger sizes, thus removing a larger proportion of the males from the population. Consequently, there were too few males to contribute to reproduction outside reserves (particularly when the sex change cue was fixed), even for very low levels of the male importance parameter. Note that the persistence requirements for the size frequency-cued and gonochore populations were not affected by the change in fishery size limits (Fig. 5c–f).

DISCUSSION

We used a spatially explicit model of a generic species to determine how spatial management guidelines should be adjusted to ensure population persistence in protogynous hermaphroditic fishes. Our simulations confirmed that protogynous stocks cannot always be managed similarly to gonochore populations (Huntsman & Schaaf 1994, Alonzo & Mangel 2004, 2005, Heppell et al. 2006, Alonzo et al. 2008, Chan et al. 2012) and may require either greater or less protection in marine reserves than gonochores to ensure population persistence, depending on their specific life history traits. The main new results emerging from our analysis were as follows. (1) The necessary level of reserve protection required for persistence of protogynous populations depended strongly on the relationship between the sex ratio and fertilization success (the mating function), which is empirically unknown for most fishes (Alonzo & Mangel 2005, Heppell et al. 2006). (2) The nature of the cue triggering sex change also affected reserve requirements, where species with less flexible sex change cues required more or larger reserves. (3) The size of reserves required by those less flexible populations was also more sensitive to changes in the minimum harvest size limits for the fishery outside reserve boundaries, requiring more protection when fishing was con-

centrated on predominantly male size classes. (4) Importantly, our simulations also revealed that sex ratios within reserves may not be informative metrics of reserve performance for protogynous species.

Although our model was constructed using parameter values for a particular species, and thus specific details in our results may not apply exactly to all protogynous stocks, it is important to note that major differences in our model results were due to variation in the sex change cue and value of male importance (ϕ) only. Thus, similar to the conclusions of Alonzo & Mangel (2005), Huntsman & Schaaf (1994), and Heppell et al. (2006), our work confirms that simply knowing that a species exhibits protogyny and that males are disproportionately removed by fishing is necessary but not sufficient to predict how that population will respond to fishing pressure or how best to design spatial management for that stock. However, we also addressed a second major factor affecting the response of protogynous species to size-selective harvest: When does the loss of males become a concern (Rankin & Kokko 2007)?

Importance of the mating function

Our work builds on previous studies of protogynous hermaphrodite population dynamics (Alonzo & Mangel 2005, Heppell et al. 2006, Chan et al. 2012) by simulating a range of spatial management scenarios and sex change functions and further considering the contribution of males to reproductive success. However, unlike our finding that population persistence within reserves depended strongly on the level of male importance (i.e. the concavity of the mating function), Chan et al. (2012) found that the effects of reserves were generally similar among the 2 mating functions (i.e. male importance value) they considered. We investigated a wider range of possible mating function shapes, from scenarios where very many to very few males are required to achieve high levels of fertilization, and also examined more than one sex change strategy. Thus, we likely captured a fuller range of biologically plausible results for real species. In particular, the low values of ϕ that produced extreme results in our simulations actually correspond to the nearly linear mating function observed in inland silversides *Menidia beryllina* (S. M. Brander et al. unpubl.), whereas the 2 mating function shapes considered by Chan et al. (2012) would both fall in the middle of the distribution of values we used. Given the importance of the mating function on spatial man-

agement in our simulations, we recommend greater focus on the empirical determination of fertilization rates and mating functions.

Effects of fishery management on reserve performance

Our results indicated that even with marine reserves in place, it is important for spatial management strategies to consider the influence of fishery management outside of the protected zones. Our results indicated that if protogynous populations are heavily exploited outside of reserves (such that reproduction is greatly reduced), persistence will require more reserves or larger reserves than those required by gonochores. Alternatively, if fishing is less intense so that there is some reproduction occurring outside reserves, protogynous species can have lower protection requirements than gonochores and may not require reserves for persistence at all. That result depends on the mating function (as males become less important, reserve requirements drop) and on fishery size regulations: when the minimum size limit was higher and the fishery concentrated on larger size classes, the populations with less flexible sex change rules required more or larger reserves. This is because the fishery primarily removes males (particularly when the population cannot respond by adjusting the sex ratio), depleting the sex ratio and impairing reproduction outside reserves. Note that this result was obtained because we assumed that higher minimum size limits were associated with higher fishing mortality rates, so that the gonochore FLEP was the same regardless of the size limit (i.e. the size limit is a catch control, not an effort restriction). If instead we had assumed that raising the size limit simply removed fishing effort on smaller size classes, we would have found a relaxation in persistence requirements. Nonetheless, our results do suggest that spatial management of protogynous fishes should take into consideration the possibly counter-intuitive effects of minimum size limits that may concentrate effort on males rather than spreading it across both sexes. However, one factor we did not account for is the potential for different fisheries with different size targets (e.g. plate size vs. trophy fishing) in protogynous species with extreme sexual dimorphism, such as the California sheephead.

While our scorched earth scenario represents a hypothetical extreme, evidence of reproductive failure in protogynous stocks has been documented. For example, Hawkins & Roberts (2004) noted that some

Caribbean parrotfishes (family Scaridae) at the most heavily fished islands may have been failing to reproduce due to a lack of terminal-phase males and suggested that those populations were dependent on larval dispersal from elsewhere. Because it is thought that many protogynous species respond to localized spawning cues from males, heavy exploitation of males has the potential to cause females to go unspawned (male limitation), reduce fertilization as males try to appropriate sperm among a large number of females (sperm limitation), or lead to large-scale reproductive failure (Coleman et al. 1996). Thus, scorched earth may be a more realistic possibility for overexploited protogynous species, especially migratory ones, than it is for gonochores, where that assumption has been criticized (White et al. 2010b).

Implications for monitoring and adaptive management

In addition to predicting the effect of different life histories and fishery regulations on marine reserve requirements to achieve population persistence, our simulations identified considerations that must be taken in empirical assessments of how well reserves are meeting specific goals. Often, after:before or inside:outside ratios of key metrics (such as biomass) are used to assess the effectiveness of marine reserves (White et al. 2011), although Moffitt et al. (2013) recently showed that inside:outside biomass ratios are not reliable indicators of reserve success. In the case of protogynous hermaphrodite stocks, evaluations have increasingly focused on the difference in sex ratio after:before or inside:outside reserves (e.g. Beets & Friedlander 1999, Adams et al. 2000, Hawkins & Roberts 2004, Kleczkowski et al. 2008). Our simulations showed that empirical assessments may actually detect a greater proportion of large, old males within reserves when population biomass is severely depleted and the population is only persistent because of reserve protection. In contrast, scenarios with lower exploitation rates and higher biomass that could support sustainable populations without reserves may have smaller inside:outside differences in sex ratio. Consequently, the inside:outside difference in sex ratio is not necessarily a reliable indicator of population health or fishery sustainability. It has been noted that changes in total biomass might not reflect the population stability of protogynous hermaphrodites, as the disproportionate removal of males may reduce fertilization rates while female

biomass or egg production remain unaffected (Punt et al. 1993, Alonzo & Mangel 2004). The opposite may occur in reserves, as males will accumulate inside reserves (supposedly indicating reserve success) even if the reserves are too small or too few to ensure population persistence, and the loss of recruits to unprotected areas results in overall lower reproductive output and population decline. Because of these potential effects, managers must exercise caution when using increases in total or male biomass to reflect population recovery.

Model limitations

While we have shown that spatial management of protogynous fishes could be improved with knowledge of the mating function and ecological cues triggering maturation and sex change, we acknowledge that this information is not available for many species (particularly the mating function). In data-limited situations, a simpler framework that does not require a mating function, such as the per-recruit model used by Grüss et al. (2014), could be used. Nonetheless, our results show that management would benefit from utilizing that information if it is available. Additionally, our work specifically focused on coastal protogynous species rather than those that undertake migrations to offshore spawning habitats (such as gag grouper *Mycteroperca microlepis*). There has been recent work developing spatial management guidelines for gonochore species with ontogenetic or spawning migrations (White 2015), so extending that work to migratory protogynous species could be a valuable next step.

As the focus of our study was largely on the biology (i.e. the cues for maturation and sex change and mating function) rather than the economics of coastal protogynous fisheries, our analysis centered on population persistence, not yield, and included the somewhat simplistic assumption that total fishing effort was held constant following the introduction of reserves. However, fishing effort may respond dynamically to reserve implementation (Sanchirico & Wilen 2001), and reserve success can be affected by harvester behavior (e.g. Kellner et al. 2007). It is important to note that we focused on population persistence, because spatial management using reserves is frequently concerned with identifying reserve configurations that will sustain populations regardless of management outside the reserves (e.g. Botsford et al. 2001). For the scenarios we modeled in which the fishery would be overharvested without

reserves, reserves would generally be expected to improve yield (Neubert 2003, Neubert & Herrera 2008, White et al. 2008, 2010a, Moeller & Neubert 2013). Fishery yield would likely be optimized for some combination of reserve size, harvester behavior, and (lower) exploitation rate that we did not consider in our study (White et al. 2008).

Finally, our study focused on the ecological aspects of fishing and did not consider the possible role of fishery-induced evolution on protogynous species (Law 2000). For example, fishery-induced shifts in the size at maturity and sex change have been reported for California sheephead *S. pulcher* (Hamilton et al. 2007). In that case, it is not possible to tell whether the shifts were plastic responses to fishing pressure (such as would occur in our model) or long-term evolutionary changes. In the latter case, reserves could have the additional benefit (not included in our model) of potentially rescuing the population from fishery-induced selection (Dunlop et al. 2009), although protogynous species have not yet been specifically examined in eco-evolutionary fishery models.

CONCLUSIONS

Overall, our findings indicate that the interaction between biological factors (sex change cue and mating function) and fishery management determines whether and how marine reserve designs must be adjusted to accommodate protogynous life histories. Under the most conservative assumptions about reproduction outside reserves, protogynous species always required more or larger reserves than gonochores. However, under the potentially more likely scenario that there is reproduction outside reserves, protogynous species required more or larger reserves than gonochores when males became limiting, either because the mating function was less concave or because minimum size limits concentrated fishing on predominantly male size classes. When males were less important or fishing was spread among males and females, protogynous species required less protection than gonochores (particularly for species with more flexible sex change cues). The 2 spatial dispersal scenarios we modeled (self-persistence and network persistence) produced similar results, indicating that our general findings are not strongly affected by the details of larval connectivity. In addition, our work indicates that conventional metrics (such as sex ratio) used in evaluating the efficacy of marine reserves may not accurately reflect

the response and recovery of protogynous stocks and that additional metrics such as the fertilization rate or age structure may be more informative to adaptive management. Because many commercially and recreationally important species exhibit protogyny and are thus potentially threatened by size-selective exploitation, it is critical to examine the life history variables that influence the response of those populations to spatial fishery management.

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Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

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