

Effects of sex change on the implications of marine reserves for fisheries

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Abstract. Marine reserves have become widely used in biodiversity conservation and are increasingly proposed as fisheries management tools. Previous modeling studies have found that reserves may increase or decrease yields, depending on local environmental conditions and on the specific life-history traits of the fishery species. Sex-changing (female-to-male) fish are targets of some of the most important commercial and recreational fisheries in the world. The potential for disproportionate removal of the larger, older sex of such species requires new theory to facilitate our understanding of how reserves will affect the yields of surrounding fisheries, relative to fishes with separate sexes. We investigated this question by modeling the effects of marine reserves on a non-sex-changing and a sex-changing population. We used demographic parameter estimates for the common coral trout as a baseline, and we conducted extensive sensitivity analyses to determine how sustainable yields of sex-changing species are likely to be affected by reserves across a broad range of life-history parameters. Our findings indicate that fisheries for sex-changing species are unlikely to receive the same yield-enhancing benefit that non-sex-changing fisheries enjoy from marine reserves, and that often reserves tend to reduce sustainable yields for a given overall population size. Specifically, the increased egg production and high fertilization success within reserves is more than offset by the reduced egg production and fertilization success in the fished areas, relative to a system in which fishing mortality is distributed more evenly over the entire system. A key reason for this appears to be that fertilization success is reduced, on average, when males are unevenly distributed among subpopulations, as is the case when reserves are present. These findings suggest that, for sex-changing populations, reserves are more suited to rebuilding overfished populations and sustaining fishery viability, rather than enhancing fishery yields. These results are robust over a range of sex-change regimes, stock–recruitment relationships, adult mortality rates, individual growth strategies, and fertilization-success functions. Our findings highlight the importance of considering the different contributions of males and females to population growth and fishery yields when evaluating the efficacy of marine reserves for enhancement of fished species.

Key words: density dependence; fisheries management; Great Barrier Reef, Australia; hermaphrodite; marine reserves; *Plectropomus leopardus*; protogynous sex change; sustainable fishery yields.

INTRODUCTION

No-take marine reserves have become widely used in biodiversity conservation and, more recently, as fishery management tools (Sanchez Lizaso et al. 2000, Mangel and Levin 2005). No-take reserves are areas completely and usually permanently protected from all fishing (Sale et al. 2005), based on the idea that natural populations can maintain themselves if protected from human interference (Bohnsack 1996). Establishing marine reserves allows the numerical abundance and biomass of previously harvested populations within them to increase toward pre-exploitation levels. Such protected populations can in turn benefit nearby fishing grounds in two ways: through the net emigration of adults and

juveniles across marine-reserve boundaries (termed “spillover”; Russ 2002), or through the export of pelagic eggs and larvae (termed “larval subsidy”; Little et al. 2005). Reserves also have a potential cost, however: the decrease in fishing area associated with establishment of reserves can lead to a loss in fishery yields as fishing fleets have diminished access to target populations (Gerber et al. 2003). Sustainable fishery yields are of paramount importance to commercial and recreational fishers, two of the most common users of marine environments. Thus, there is a need to understand how reserves will affect the yields of surrounding fisheries so that appropriate sustainable harvesting strategies can be developed, regardless of whether reserves are established for fisheries management or other objectives. Specifically, it is important to determine the circumstances in which benefits from reserves to long-term sustainable yields, such as through larval subsidy or emigration (“spillover”) of larger adults, are greater or less than the

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opportunity cost of closing the area to fishing (Sanchirico 2004, Hart 2006).

Approaches to understanding the benefits and costs of reserves on fisheries yields include both empirical studies and theoretical models, with the two approaches typically addressing different questions (Sladek-Nowlis and Roberts 1999). Empirical reserve studies typically address questions with a transient nature (e.g., how quickly does biomass increase upon reserve establishment?; Russ 2002), while mathematical models typically have been used to answer questions about long-term asymptotic outcomes (e.g., how do reserves affect long-term sustainable yields?; Guenette et al. 1998, Gerber et al. 2003). Some models are simple and idealized, with no age structure and simple larval-dispersal assumptions, and have been used to seek general rules of thumb applicable to a large number of populations (Mangel 1998, Hastings and Botsford 1999, Botsford et al. 2003). Others are more complex and tailored to particular fisheries, with age and size structure (e.g., Guenette and Pitcher 1999, Little et al. 2007, Mapstone et al. 2008), complex larval dispersal patterns (Man et al. 1995, Gaines et al. 2003), or fishery-specific density-dependent effects (Quinn et al. 1993).

It has become apparent that different models yield different conclusions about the effect of reserves on long-term sustainable yields, and that differences in model assumptions have important implications for model results (Rose et al. 2001, Gerber et al. 2003). If these results reflect reality, then marine reserves appear to vary in the extent to which they enhance or reduce fishery yields depending on species-specific life-history traits, demographic rates, and dispersal patterns. For instance, models in which density dependence occurs after dispersal but before recruitment to the adult population (i.e., density-dependent recruitment), tend to find that reserves enhance fishery yields; however, models with pre-dispersal density dependence, such as density dependent fecundity, find that reserves reduce fishery yields (Sanchirico 2004, White and Kendall 2007). Models with large larval-dispersal distances relative to reserve size (Gaylord et al. 2005), or with strong source-sink structure (Gaines et al. 2003), tend to find that reserves enhance yields more often than models with smaller larval-dispersal distances. Reserves also have been more likely to enhance yields in models with long-lived, slow-growing species, as opposed to short-lived, fast-growing species (Gaylord et al. 2005). And more recently, it has been shown that while models with simple life-history assumptions, such as age-independent size and mortality, produce yield equivalence with reserves, models that include realistic variation in biomass, reproduction, or mortality with age are more likely to find that reserves decrease yields (Kaplan 2009). Similarly, assumptions about fishing behavior and the interaction of reserves with other fishing regulations also influence the effects of reserves on fishery yields (Sanchirico et al. 2006, White 2009).

Despite the growing recognition that species-specific life-history and demographic characteristics have important implications for species' responses to fishing, most current fishery models and stock-assessment methods are based on the assumption that fish have separate sexes and ignore the contributions of males to reproductive success (Alonzo et al. 2008). This may be a reasonable assumption when males and females experience similar fishing mortality, because male abundance materially reduces fertilization success only when males become disproportionately rare (Heppell et al. 2006). However, this assumption is potentially problematic for species whose individuals change sex during their lifetimes. For instance, if males are only produced through sex change, and fishing targets larger individuals, then high fishing pressure can lead to disproportionate removal of males and consequential sperm limitation, leading to a greater reduction in reproductive output than similar rates of harvest in populations with separate sexes (Hawkins and Roberts 2003, Heppell et al. 2006). Understanding whether and how marine reserves may affect the dynamics of sex-changing fishes is important because many species from a wide range of families of fishes (e.g., groupers, wrasses, parrotfish, and emperors or sea-breams) are sex changing, and such species represent major components of important commercial and recreational fisheries around the world (Mapstone et al. 2008). For example, coral trout (*Plectropomus* spp. and *Variola* spp.) and red throat emperor (*Lethrinus miniatus*), part of the grouper and sea-bream families respectively, collectively comprise 82% of the \$39.5 million per year Queensland (Australia) commercial line-fishing industry (State of Queensland 2009), and they are major fishery species in other countries with significant coral reefs (Heemstra and Randall 1993). Similarly, California sheephead (*Semicossyphus pulcher*), a wrasse, comprise 88% of the \$3 million per year California live-fish fishery (California Department of Fish and Game 1995). These important fishery species occur in areas where marine reserves have been designated, but the relative benefit of this management strategy to the fish and fisheries have not been well assessed.

There are relatively few two-sex models in the literature, and fewer still that have explicitly included both effects of sex ratio and the efficacy of marine reserves as a management tool for hermaphroditic species (Alonzo and Mangel 2004, Heppell et al. 2006, Little et al. 2007, Kerwath et al. 2008, Mapstone et al. 2008). These studies, which have assumed either a fixed schedule for sex change, or density-dependent sex change, indicate that reserves could prevent the skewing of sex ratio toward female-dominated populations, and thus mitigate some of the effects of fishing on sperm limitation in harvested areas. The consequences of these effects for long-term sustainable yields, however, remain unclear. Moreover, sexual transition in sex-changing species is believed to be triggered largely by external cues

such as environmental conditions, population density, and habitat competition, or by social cues such as local sex ratio and the size of an individual relative to the other members of its social group (Warner 1988, Shapiro 1989). There also is some evidence for varying degrees of plasticity in sexual developmental strategies: some sex-changing species produce males not just through sex change (“secondary males”) but also through direct development (“primary males”) (Adams et al. 2000). The extent of plasticity and associated cues for sex change, however, are not known for many species (Alonzo et al. 2008). The two studies considering the implications for fisheries of alternative sexual development pathways in the absence of reserves have found that fishing differs in its effects on fixed and age-variable sex-changing populations (Armsworth 2001, Alonzo and Mangel 2005). The increasing prevalence of marine reserves precipitates a need to understand how the effect of reserves on long-term sustainable yields may depend on the sexual strategies of a harvested species, especially those that change sex.

In our present study we examined how different female to male sex-changing regimes influenced the effects of reserves on long-term sustainable yields outside reserves, and explored how various life-history traits affected this influence. We developed a number of age-structured models, each with a different sex-change regime and differences in the proportion of habitat in reserve. We then compared long-term sustainable yields from these populations with those from an equivalent population that did not change sex. We chose our baseline parameter values from demographic data for the common coral trout, *Plectropomus leopardus*. However, because we are interested in how the effect of reserves depends upon sex change in general, we also conducted extensive sensitivity analyses, to assess the robustness of our results to the density-dependent and density-independent components of the model, level of adult survival, shape of the growth curve, fecundity–mass relationship, and fertilization patterns. These sensitivity analyses allow us to propose several general principles for effects of marine reserves on the management of harvest species that change sex from female to male, and to provide some insight into how sex change may interact with other demographic and life-history characteristics to determine a population’s responses to the establishment of marine reserves.

METHODS

Model species

The common coral trout, *Plectropomus leopardus* (Lacepede 1802), is a high-level predator on the Great Barrier Reef (Australia). Its life history is similar to many other tropical, exploited reef species: it is long lived, exhibits sharply asymptotic growth, changes sex from female to male (but not vice versa), has relatively sedentary adults and pelagic larvae, forms spawning aggregations, and cannibalizes juveniles. In addition,

there has been considerable research into this species’ life-history characteristics, reproductive biology, and demography (Ferreira and Russ 1994, Ferreira 1995, Russ 1998, Adams et al. 2000, Samoily 2000, Mapstone et al. 2004), which provide a strong foundation for parameter estimation. Thus, it provides a useful baseline life history for our study. Moreover, *P. leopardus* is an important fishery species in its own right: it has recently comprised 70% or more of the commercial line-fishing catch (Mapstone et al. 2004, 2008), and supports a substantial recreational and charter (tourism) line fishery.

Modeling methods and parameter estimation

For our general model, we used an age-structured Leslie matrix population framework (Leslie 1945) to model population dynamics of the stock. The Leslie matrix model projects next-year’s population size based on a vector representing this-year’s population size and, in matrix notation, is simply

$$\mathbf{n}_{t+1} = \mathbf{M} \times \mathbf{n}_t \quad (1)$$

where \mathbf{n}_{t+1} is a vector that contains abundances in each age class at the start of year $t + 1$, \mathbf{n}_t is a vector that contains abundances in each age class at the start of year t , and \mathbf{M} is the projection matrix. Each vector element in \mathbf{n}_{t+1} and \mathbf{n}_t will be an abundance from a particular combination of age class, sex (male or female), and subpopulation (fished or reserve). \mathbf{M} contains the per capita recruitment terms (which encompass fecundity, fertilization success, dispersal between subpopulations, and survival to age 1) in the first four rows, and the transition terms (which encompass adult survival and sex change) in the remaining rows. Further explanation and illustration of this model structure is available in Gerber and Heppell (2004) and Gerber et al. (2005).

For fecundity, we modeled variation in fecundity with age by first calculating the length at each age using the von Bertalanffy growth function (VBGF):

$$L = L_{\text{inf}}(1 - \exp(-k[a - a_0])) \quad (2)$$

where L is the length at age, L_{inf} is the average asymptotic maximum body size, k is the growth rate, a is age, and a_0 is the hypothetical age at zero length (Haddon 2001). The VBGF is commonly used to describe the growth of species such as fishes where individuals grow to an asymptotic size and, in particular, approximates well the growth of coral trout (Ferreira and Russ 1994). Fecundity was then calculated from a power-law length–fecundity relationship:

$$f = cL^d \quad (3)$$

where f is fecundity, L is length, and c and d are fitted parameters. This functional form provides a good approximation of length–fecundity relationships for many fishes (Sadovy 1996), including *P. leopardus*

(Samoilys 2000). Fecundity is based on females only, thus Eq. 3 only pertains to females.

Density dependence was incorporated into the model through the stock–recruitment relationship. Recruitment in this study referred to the recruitment to age 1, not recruitment to the fishery (age at first vulnerability to fishing gear), as is common in many fisheries studies. This study focused on density-dependent effects of adults on recruits because such effects are common and routinely strong in nearshore fish due to phenomena such as preemption of territory space and cannibalism (Hixon and Webster 2002; Osenberg et al. 2002), both of which occur in coral trout (St. John 1995, Samoilys 1997). Specifically, we modeled per capita survival of settlers as

$$\gamma(\mathbf{n}_t) = \frac{\gamma_0}{1 - \alpha B(\mathbf{n}_{\text{hab},t})} \quad (4)$$

where γ_0 is the density-independent component of recruitment (i.e., probability of successful recruitment in the absence of density dependence), α controls how strongly recruitment success decreases as resident biomass increases, and $B(\mathbf{n}_{\text{hab},t})$ is the total biomass in the habitat where settlement occurs (in our study, either reserve or fished areas). This functional form is commonly used to describe density dependence in exploited species where recruitment increases to an asymptotic value as population biomass increases (Haddon 2001). We use biomass rather than numerical abundance because larger adults are likely to exert stronger per capita density-dependent effects due to their greater energy requirements (and thus probable greater cannibalistic effects), and their larger territories (Luppi et al. 2001).

Part of the transition term, adult survival (p), describes the natural probability of survival of an individual in any age class in an unfished population. Annual survival was calculated from the instantaneous annual natural mortality rate (m) in the standard fashion:

$$p = e^{-m}. \quad (5)$$

Most stock-assessment models assume constant natural mortality because there are insufficient data with which to estimate natural mortality on an age-specific basis (i.e., unless species-specific data were collected before exploitation of the species, estimates of natural mortality are impractical to derive from fishery data because of the interaction between fishing and natural mortality; He et al. 2011). Moreover, methods for estimating mortality rates applied to fishery species yield a single, age-independent mortality rate (Haddon 2001), and for *P. leopardus* in particular the one empirical study that has attempted to estimate age-specific mortality rates did not obtain strong evidence for variation in mortality with age (Russ 1998). Therefore, we follow most previous studies of reserve effects on age-structured populations (Guenette and Pitcher 1999, Hu and

Wroblewski 2009) and modeled the post-recruitment mortality rate as independent of age.

We compare two sexual strategies in this study. In the non-sex-changing strategy, males and females were both produced only through reproduction. In the sex-changing strategy, females were produced through reproduction, and males produced only through sex change. To incorporate exogenous cues for sex change, we modeled the proportion of females changing sex to males as a function of mean age of the population, as described below. We also considered a third, “mixed” strategy in which males were produced both by sex change, and through reproduction (as proposed for *P. leopardus* by Adams et al. [2000]). However, the results of this model were virtually identical to the sex-changing case, and thus we do not discuss it any further here. In all models, we characterize male and female subpopulations explicitly, in contrast to most marine-reserve models, which are single-sex (female only) models. We assume that males and females are sexually mature once they reach age two (Ferreira 1995, Adams et al. 2000) and we use a logistic function to model the cumulative probability of transitioning from female to male. This function commonly provides a good description of sex-specific age-frequency distributions in sex-changing fishes (Davies et al. 2006, Caselle et al. 2011), including for *P. leopardus* on the Great Barrier Reef (Mapstone et al. 2008).

To model the contribution of males to population growth, we assumed that fertilization success (ϕ , the proportion of eggs fertilized) increased as the proportion of mature male biomass, $B(\mathbf{n}_{\text{male},t})$ in the relevant subpopulation (fished or reserve) increased. This relationship was modeled as an asymptotic function:

$$\phi = 1 - e^{-rB(\mathbf{n}_{\text{male},t})} \quad (6)$$

where r is a fertility parameter describing the rate at which ϕ approaches 100% as $B(\mathbf{n}_{\text{male},t})$ increases away from zero (Heppell et al. 2006). We used proportional male biomass, rather than numerical abundance, in the calculation of ϕ to account for the greater reproductive contribution of larger males (Samoilys and Squire 1994).

The proportion of recruits that were male (the remainder were female) in the non-sex-changing populations was set to equal the mean sex ratio for *P. leopardus* (on the Great Barrier Reef) in the sex-changing populations. For the sex-changing population, the probability that an individual changed sex from female to male increased with decreasing mean age, e.g., as an effect of increased fishing pressure. Specifically, we modeled sex change as a logistic function of age:

$$p_{\text{SC}} = \frac{1}{1 + \exp(-q[a - (a_m + a_0)])} \quad (7)$$

where p_{SC} is the cumulative probability of an individual having changed sex by age a , q is a coefficient describing how strongly the rate of sex change varies with age, a is

age, a_m is the mean age of the population, and a_o is an offset term. We fixed the offset term (a_o) in order to standardize all populations, regardless of sex-change regime, to have the same ratio of male spawning biomass to total population biomass when the population was unfished (Appendix A: Table A1). Sex change began at age 2, the age where mature males first begin appearing in populations of *P. leopardus* (Adams et al. 2000).

We consider the full range of possible harvests (from no take to complete take of the age classes subject to fishing), and a range of the amount of habitat in the reserve (no reserve, 10%, 20%, and 40% of the fished area), rather than adopting an optimization approach (i.e., finding the optimum reserve size and fishing effort that maximizes yields). We chose to analyze the full range of possible fishing-mortality rates for two reasons. First, deterministic optimization is known to lead to fishing strategies that make fisheries collapse very likely (Roughgarden and Smith 1996) while stochastic optimization requires information about inter-annual variability in demography that is often poor or unavailable (Watson and Sumner 1999). Consequently, rules of thumb based on deterministic models (e.g., 10% of fishing effort, “0.1F”) remain commonly used (Berkeley 2006). Second, many reserves (e.g., on the Great Barrier Reef) are implemented for conservation purposes rather than to manage a particular target fishery, and thus reserve area is not set to optimize fishery yields (Mapstone et al. 2008).

Catch was implemented in the model by removing each year from the fished habitat a set proportion, F , of individuals age 3 and above. This simulates the widespread phenomenon of setting minimum size limits that are above age at maturity (McPhee 2008), and, in particular, it roughly corresponds to the minimum legal size limit for harvest (38 cm) of *P. leopardus* on the Great Barrier Reef. The removed proportion F was varied from 0 to 0.9. We did not implement any additional size selectivity in fishing (e.g., a propensity to release smaller fishes). This is a reasonable baseline case because many tropical groupers, including *P. leopardus*, are sold predominantly to live markets where smaller (but legal-sized) fish are actually favored, so discarding of small but legal-sized fish is unlikely (Mapstone et al. 2001, Muldoon 2009). Similarly, noncommercial fishing in many tropical nations is dominated by subsistence fishing, and thus also likely to exhibit little if any size selective fishing, and anecdotal evidence also suggests that there is very little size selectivity in the recreational fishery for our baseline population (A. Frisch, S. Sutton, *personal communications*).

Mass-at-age was calculated using a power-law length–mass relationship to convert numerical catches to biomass:

$$M = \theta L^\omega \quad (8)$$

where M is mass, L is length, and θ and ω are parameters that describe how mass changes with length. Empirical length–mass relationships for fishes commonly show this functional form (Schneider et al. 2000), including for *P. leopardus* (Ferreira and Russ 1994).

Reserve size (R) was expressed as a proportion of the total habitat area, and the population vector extended, to explicitly model the dynamics of subpopulations in the reserve and fished habitats. Four reserve scenarios were modeled: no reserve, 10%, 20%, and 40% of the habitat closed to fishing. Our baseline case assumed that once juveniles settled in a subpopulation (reserve or fished) they remained within that subpopulation (Zeller and Russ 1998). This corresponds to a case where the scale of adult movement is small, relative to distances between reserve and non-reserve patches. For instance, on the Great Barrier Reef, reserves tend to be defined at and above the whole-reef scale, whereas adult *P. leopardus* do not appear to move between reefs (Davies 2001, Zeller 1997, 1998). Coupling of the dynamics of reserve and fished subpopulations occurred via larval dispersal. We used the simplifying assumption that all larvae (regardless of where they were produced) entered a common larval pool from which they settled into fished or reserve subpopulations in proportions equal to the relative sizes of the reserve or fished areas. This assumption is commonly made in reserve modeling (see Gerber et al. [2003] for a review) and approximates reserve designs in which reserves are well interspersed among areas open to fishing, and the sizes of individual reserve patches are small relative to likely dispersal distances of larvae. For instance, larval-dispersal modeling for coral trout on the Great Barrier Reef suggests that larval dispersal distances are much larger, relative to reserve sizes (James et al. 2002).

While our baseline case assumes no movement of adults but extensive mixing of larvae across reserve boundaries, these assumptions are likely to be violated to some degree in some reserve systems. In particular, reserves are not always large, relative to the scale of adult movement. For instance, in tropical developing countries, individual reefs may consist of reserves interspersed with fished areas. Therefore, as part of our sensitivity analysis, we consider an alternative model in which common spawning aggregations form across reserve boundaries. Our baseline larval-pool assumption is likely to maximize the benefits of reserves for sustainable yields, relative to cases with high levels of self-recruitment, because it tends to maximize the larval subsidy provided to fished habitats by adults in reserves. While this may be a reasonable approximation for many sex-changing populations, there will be others for which this assumption is likely to be less reasonable. Therefore, we address possible interactions between such dispersal patterns and sex-change dynamics below (see *Discussion*).

We modeled density dependence in the presence of reserves by first calculating the biomass within reserves

by summing the biomass of all age groups within reserves and then normalizing by reserve area (i.e., dividing by R) to obtain a biomass density in the reserve. The same was done with fished areas except that $B(\mathbf{n}_{\text{fish},t})$ was divided by $(1 - R)$.

Baseline parameter values, and the ranges explored in our sensitivity analyses, are reported in Appendix A: Table A1. Baseline parameter values were chosen to correspond to a typical tropical grouper, many of which are major fishery species that change sex from female to male (e.g., black grouper, camouflage grouper, brown marbled grouper, and coral trout) (SCRFA 2010). In particular, our baseline parameterization utilized, where available, information on the demography of *P. leopardus* on the Great Barrier Reef. We assumed a longevity of 14 years, consistent with the maximum age of *P. leopardus* observed around (unfished) Lizard Island (Ferreira and Russ 1994). The von Bertalanffy growth and length–mass relationship parameters were obtained by averaging growth parameters obtained from unfished reefs across four regions of the Great Barrier Reef. These data came from the Effects of Line Fishing (ELF) Experiment, a 10-year study that collected size, density, sex ratio, growth, and mortality data for numerous fishery target species inside and outside reserves on four regions of the Great Barrier Reef (Mapstone et al. 2004). Fecundity–length parameters were taken from previous work on the reproduction of *P. leopardus* (Samoilys 2000). The natural survival probability used was the average (over all four regions) of survival on closed (no-take) reefs from the ELF data. There are no empirical estimates for the density-dependent parameters (α and γ_0), so we set the equilibrium population biomass in the absence of fishing, and then chose several combinations of γ_0 and α that yielded this equilibrium biomass. We used an intermediate combination of γ_0 and α as our baseline values and considered the “strong” and “weak” density-dependent scenarios relative to that baseline in our sensitivity analyses.

The parameters for the logistic equation describing sex change were based on analysis of sex frequencies from unfished reefs in the ELF data (Adams et al. 2000, Mapstone et al. 2004, Davies et al. 2006). Specifically, q was obtained by solving the logistic equation for the age at which 95% of the population had changed sex. The proportion of males entering the population directly through reproduction for the non-sex-changing populations was fixed to ensure that the proportion of spawning-male biomass was similar to that of the sex-changing population. This facilitated direct comparisons between results from the various models. The proportion of males entering the population directly through reproduction in the sex-changing population was set to zero. There are no known estimates of the fertility parameter (r) for the fertilization success function so we follow a previous study that models the management of sex-changing fishes (Heppell et al. 2006) and chose two

parameterizations such that fertilization patterns range from a gradual increase in fertilization success with relative male biomass, to a sharp increase in fertilization success. We used the parameterization exhibiting a gradual increase as the baseline because it represents a strong sperm-limitation effect and thus potentially leads to the largest benefit from reserves.

Each of the models was projected for 100 years, which was more than adequate to ensure that equilibrium was reached. We then normalized the equilibrium yields by standardizing them to the biomass of an unfished population, and we plotted those percentage yields against target population biomass (also normalized to unfished population biomass) for different reserve scenarios. Thus, we examine sustainable yield as a function of target population size (i.e., the population size at which management aims to maintain the fishery). Note that because fishing begins at age 3, whereas individuals mature at age 2, curves of yield against biomass will not extend all the way to zero biomass in many cases, because fishing never removes all reproductive individuals from the population. We examined how different stock–recruitment relationships, adult mortality rates, growth rates, fertilization-success functions, and spawning patterns affected our results, because these population characteristics are likely to vary among sex-changing species, and to be important for effects of marine reserves. The nature and intensity of density dependence is known to affect whether reserves enhance or diminish sustainable yields (Sanchirico 2004). Survival, longevity, and fecundity–age relationships influence the lifetime fecundity of fish recruiting to reserves, and thus the potential for benefit to fisheries yields provided by fish that recruit to reserves (Gaylord et al. 2005). The shape of the fertilization success curve determines how strongly male depletion affects population fecundity (and thus when reserves may benefit fisheries by replenishing male numbers; Heppell et al. 2006). Moreover, the parameters describing both density-dependent recruitment and the fertilization success function frequently are poorly constrained, including for *P. leopardus* (Rose et al. 2000). Finally, reserves will not always exceed the spatial scale of adult movement, and thus, in some systems, there will be greater potential for movement of adults across reserve boundaries than for our baseline population. It is well known that such “spillover” of adults may increase yields (Russ 2002), as large fish leave reserves and are caught. However, for sex-changing populations, large males leaving reserves may also be able to alleviate sperm limitation in the fished areas, and thus enhance population fecundity.

We examined sensitivity to stock–recruitment relationships by varying the combination of α and γ_0 that together produced the same equilibrium population biomass in the absence of fishing. The density-independent parameter, γ_0 , was set to 0.00005 to represent populations with weak density dependence and to

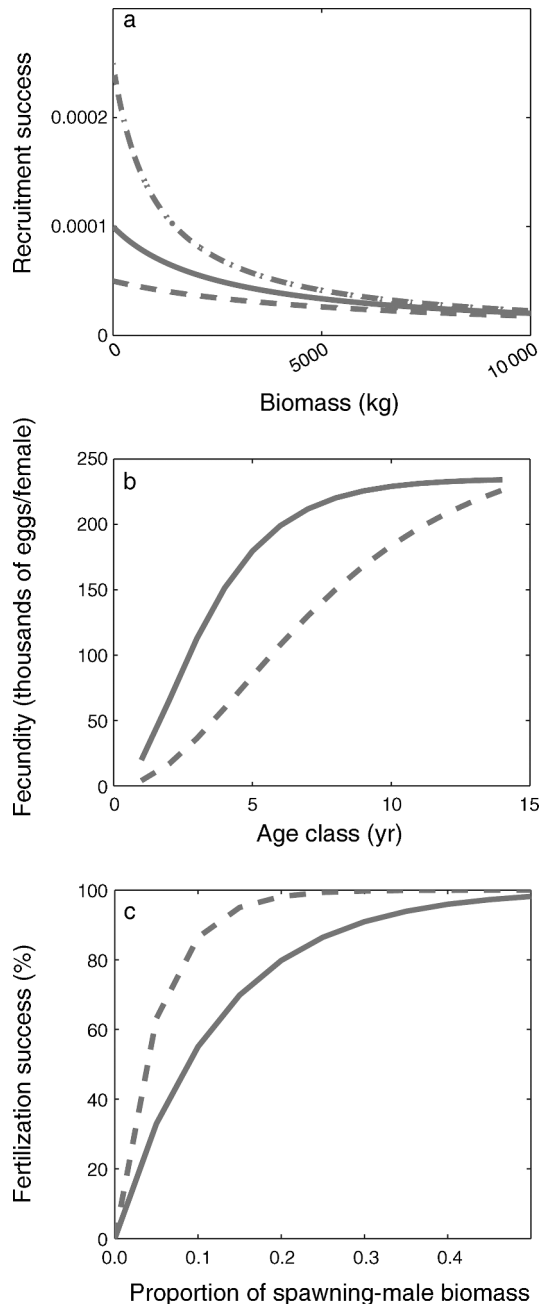


FIG. 1. (a) Recruitment success as a function of population biomass. (Recruitment success does not have units; it is just a multiplier that reduces the numbers of individuals that successfully recruit to the population.) Solid gray lines represent scenarios with the baseline density dependence ($b = 0.0001$, $\alpha = 3.9 \times 10^{-4}$), dashed lines represent scenarios with weak density dependence ($b = 0.00005$, $\alpha = 1.8 \times 10^{-4}$), and dash-dot lines represent scenarios with strong density dependence ($b = 0.00025$, $\alpha = 0.001$). (b) Fecundity (the number of eggs produced per individual female) as a function of age. The solid line is based on fast-growing coral trout, von Bertalanffy growth function, and fecundity parameters, for which maximum length and fecundity is reached at age 8. The dashed line is based on a theoretical slow-growing population for which maximum length is not reached until age 14. (c) Fertilization

0.00025 to represent populations with strong density dependence (see Fig. 1a for a graphical representation). We varied α in order to obtain the appropriate population biomass in the absence of fishing. An increase in the intensity of density dependence therefore led to both a higher density-independent component of recruitment (faster increase in recruitment as adult biomass increased away from zero) and stronger per capita negative effects of adults on juveniles (recruitment saturated quickly as adult biomass increased towards its equilibrium value). Sensitivity to different natural mortality rates was analyzed by running models using survival parameters that corresponded to doubled and halved instantaneous natural mortality rate, giving $p = 0.505$ and $p = 0.843$, respectively. *P. leopardus* grow relatively quickly, compared to many sex-changing fishery species, typically reaching maximum length, mass, and fecundity by age 8. Therefore, we assessed how slower growth influenced the effects of reserves by analyzing models using an alternative set of growth and fecundity parameters ($k = 0.2$, $c = 7.4$, $d = 2.6$), corresponding to slower growth and thus a more gradual increase of fecundity with age (Fig. 1b). A steeper fertilization-success function ($r = 20$) was used to investigate how a weaker affect of male abundance on fertilization success would affect reserve performance (Fig. 1c). We assessed the potential for migration of males across reserve boundaries to alleviate sperm limitation by considering a cross-boundary spawning aggregation model, in which reserve and non-reserve subpopulations were combined when calculating fertilization success. This represents an extreme case of alleviating sperm limitation, as would be expected if individuals formed common spawning aggregations across reserve boundaries, and thus contrasts with our baseline case in which males do not move across reserve boundaries at all.

RESULTS

Reserves had little effect on yield in the non-sex-changing case when target population biomass was high (above $\sim 70\%$ of unfished biomass) but increased yields when biomass was lower ($< 60\%$), so that the highest yields were obtained when total reserve area was large (Fig. 2a). Reserves also had little effect on yield of sex-changing populations when target population biomass was high. Reserves reduced yields, however, when population biomass was lower, so that the no-reserve scenario produced the highest yields, and larger reserves led to larger decreases in yields (Fig. 2b). When reserves were a small proportion of habitat ($\sim 10\%$) they were

← success as a function of relative male spawning biomass (as a proportion of total spawning biomass). The solid line represents a scenario with a less strongly asymptotic effect of relative male biomass on fertilization success ($r = 8$; see Eq. 6) while the dashed line represents a scenario with a more strongly asymptotic effect of male biomass on fertilization success ($r = 20$).

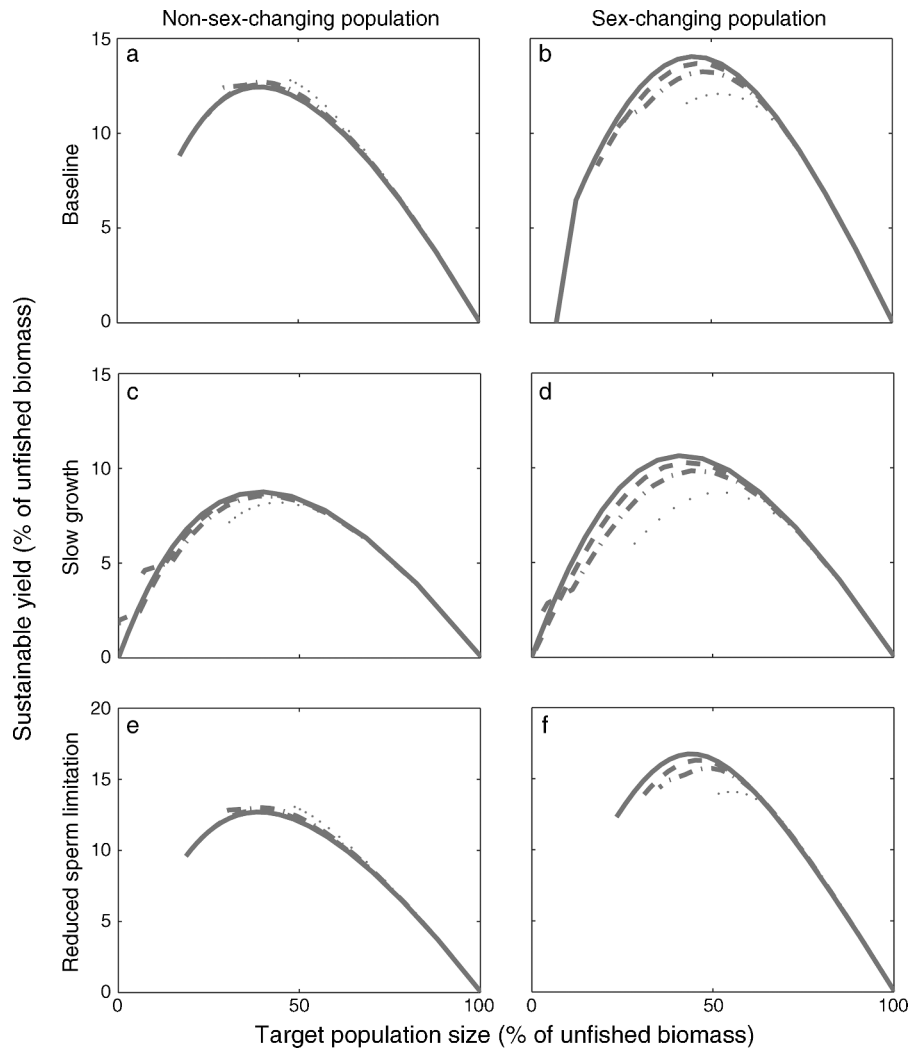


FIG. 2. Sustainable yields as functions of target population size (both expressed as a percentage of the unfished population biomass at equilibrium), for populations that do not change sex (a, c, e) vs. populations that do (b, d, f). The first row presents results from baseline parameters, the second row represents a slow growing population (changes to von Bertalanffy growth factor and associated fecundity parameters), and the third row represents a steeper fertilization success function (weaker effect of male biomass on fertilization success). Solid lines represent no-marine-reserve scenarios, dashed lines represent scenarios where 10% of the fishable area is in a reserve, dash-dot lines represent scenarios where 20% of the fishable area is in a reserve, and dotted lines represent scenarios where 40% of the fishable area is in a reserve.

able to produce equivalent or increased yields compared to models without reserves, in sex-changing populations at the low end of target population biomass (Fig. 2b), but almost complete take of fishable-aged individuals in the fished area was required for this effect to manifest.

The highest sustainable yield possible was reduced, relative to the baseline models, when a slower growth function was introduced (Fig. 2c, d). Slower growth had a qualitative influence on the efficacy of reserves in the non-sex-changing population: reserves decreased yields slightly (Fig. 2c) relative to the baseline (Fig. 2a) for small and intermediate target population sizes. Slower growth also caused an overall reduction in reserve efficacy and sustainable yield in sex-changing populations, but the increase in reserve yields at the lowest

target stock sizes (10–20% of unfished biomass) remained, leading to higher yields than scenarios without reserves for both sex-changing and non-sex-changing strategies, albeit at very low population biomass sizes.

Results were qualitatively similar to the baseline scenario when reduced sperm limitation was modeled, for both non-sex-changing and sex-changing populations (Fig. 2e, f). However, for the sex-changing population, reduced sperm limitation places a greater lower bound on target biomass levels (i.e., yield curves do not extend as far to the left under reduced sperm limitation: Fig. 2b, f).

The highest sustainable yields were always increased relative to the baseline models under strong density dependence (Fig. 3a, b) and were reduced under weak

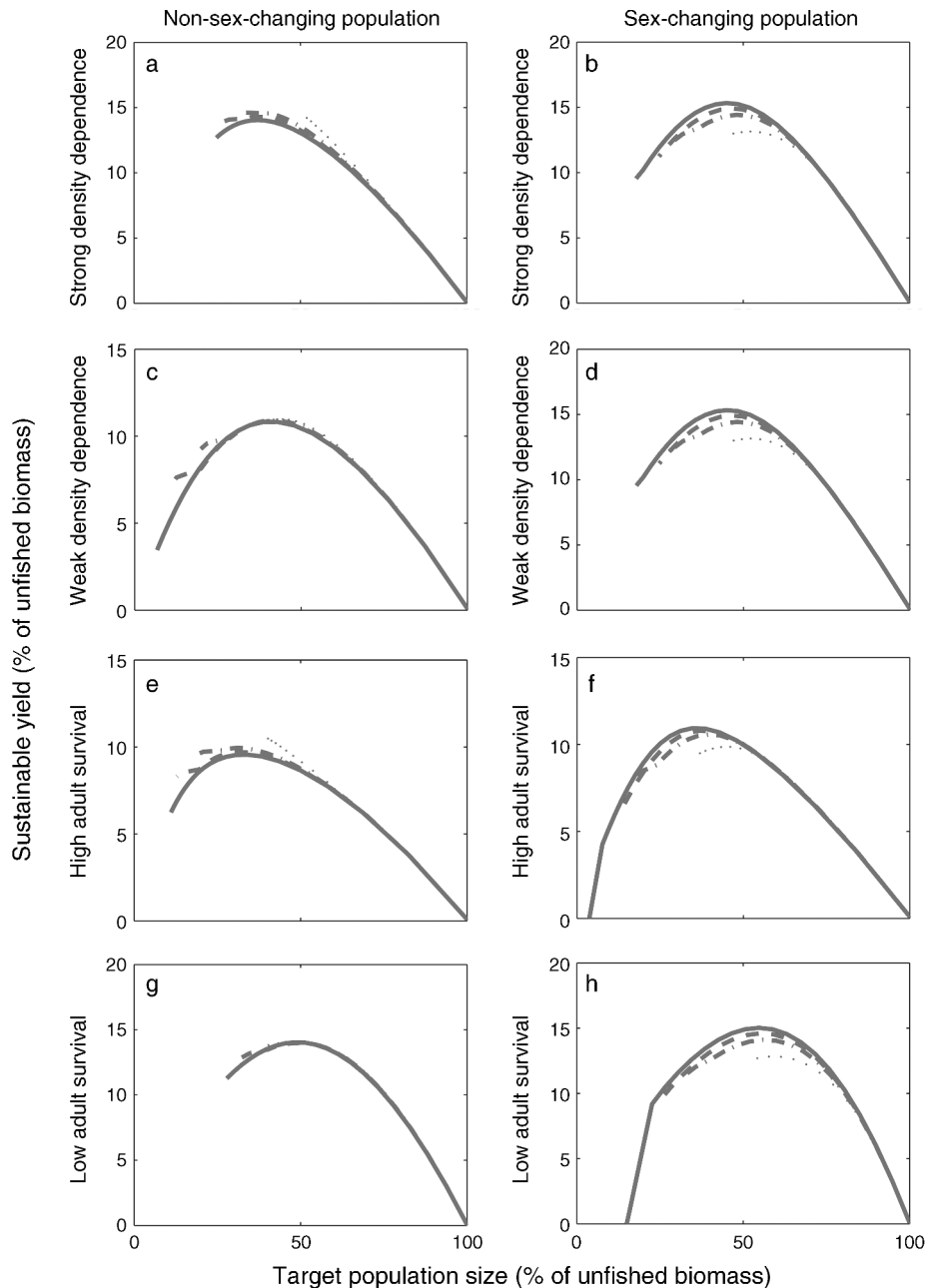


FIG. 3. Sustainable yields as functions of target population size (both expressed as a percentage of the unfished biomass at equilibrium) for populations that do not change sex (a, c, e, g) vs. populations that do (b, d, f, h). The first and second rows present results from a particular set of density-dependent parameters (high $\gamma_0 = 0.0025$, low $\gamma_0 = 0.00005$) while the third and fourth rows present results from a particular set of adult-survival parameters (high $p = 0.843$, low $p = 0.505$). Solid lines represent no-marine-reserve scenarios, dashed lines represent scenarios where 10% of the fishable area is in a reserve, dash-dot lines represent scenarios where 20% of the fishable area is in a reserve, and dotted lines represent scenarios where 40% of the fishable area is in a reserve.

density dependence (Fig. 3c, d). Overall, the qualitative effects of alternative sexual strategies on the efficacy of marine reserves were unaffected by the intensity of density dependence: yields were higher with reserves in non-sex-changing populations, and lower with reserves in sex-changing populations. Nevertheless, each sexual strategy responded to variation in the intensity of

density dependence in slightly different ways. Specifically, for non-sex-changing populations, the yield benefit of reserves was greater under strong density dependence, whereas approximate yield equivalence was observed under weak density dependence (Fig. 3a, c). For sex-changing populations, however, the difference between yields with and without reserves was very similar under

strong and weak density dependence, although, as with reduced sperm limitation, strong density dependence places a greater lower bound on target biomass levels (i.e., yield curves do not extend as far to the left under strong density dependence: Fig. 3b, d).

Variation in adult survival had qualitatively different effects on sex-changing and non-sex-changing populations. For sex-changing populations, reserves tended to produce nearly equivalent yields at large target population biomass, or decrease sustainable yields at intermediate population biomass, regardless of adult survival (Fig. 3f, h). In contrast, for non-sex-changing populations, reserves increased yields when adult survival was high (Fig. 3e), but yields were approximately equivalent when survival was low (Fig. 3g).

For the cross-boundary spawning aggregation model, the sex-changing population became qualitatively comparable to the non-sex-changing population in its response to marine reserves (Appendix B: Fig. B1). Specifically, for both populations, reserves slightly increased yields, with the largest reserve area producing the highest yields.

DISCUSSION

Most marine reserve models have predicted that reserves increase yields for non-sex-changing populations (e.g., Sanchirico 2004, Gaylord et al. 2005, White and Kendall 2007). Our results suggest, however, that sex change reduces the fisheries benefits of reserves, and can lead to reduced yields compared to the no-reserve scenarios, particularly for intermediate target population biomass levels (~35–65% of unfished biomass). At high target-biomass levels (~65% of unfished biomass or greater), we obtained near equivalence in yields with vs. without reserves, across all scenarios and for both sexual strategies. The results are qualitatively robust over a range of stock–recruitment relationships, adult mortality rates, maximum ages, growth and fecundity schedules, and fertilization-success relationships. We did find one qualitative exception for both non-sex-changing and sex-changing populations, however. For non-sex-changing populations, slow growth reduced sustainable yields more in the reserve than the non-reserve case, so that sustainable yields were slightly higher without reserves. Conversely, for the sex-changing population, allowing males from reserves to fertilize females in fished areas increased yields with reserves sufficiently that yields were slightly higher with reserves than without them.

Our results for non-sex-changing populations are qualitatively consistent with previous work that found reserves increase yields when recruitment is density dependent (e.g., Gaylord et al. 2005), but they suggest smaller reserve benefits than previous studies. The most likely explanation for this difference is our inclusion of both sexes in the model, as males contribute to yields but do not contribute directly to population fecundity. Thus, their inclusion reduces overall population fecundity, relative to a population consisting purely of

females, and thus diminishes the larval-subsidy benefit of reserves. This highlights the importance of considering the different contributions of males and females to yields and population growth when evaluating the efficacy of marine reserves.

Whether reserves increase or decrease yields depends on the trade-off between the benefit that a fish in a reserve provides to the fishery through dispersal of its offspring to fished areas (Little et al. 2005), and the opportunity cost associated with not being able to harvest that fish (Gerber et al. 2003). Reserves provide fishery benefits through two means. The first is via the buildup of large fecund females within the reserve boundaries (Gaylord et al. 2005). These females contribute disproportionately to population fecundity (compared to smaller females) and thus provide a recruitment benefit to fished areas, provided that offspring disperse beyond reserve boundaries. The benefits of larger fecund females caused reserves to increase yields for intermediate target population sizes in our non-sex-changing models. This can be seen by comparing the results of the baseline model, in which females rapidly approached maximum size and thus fecundity (Fig. 2a), with the slow growth model, in which females were smaller and less fecund, on average (Fig. 2c). In the baseline model, reserves increased yields, whereas in the slow-growth model, reserves decreased yields. Similarly, for sex-changing populations, females in the slow-growth scenario would be smaller and less fecund, on average, than in the baseline scenario, and reserves correspondingly decreased yields more in the slow-growth scenario than the baseline scenario (Fig. 2b, d). The second way that reserves benefit fisheries is by splitting a population with equal density into two (or more) populations with unequal densities. This causes a reduction in post-settlement density dependence in the population with the lower density (the fished area), which in turn increases the productivity (through enhanced per capita recruitment success) of that population (Sanchirico 2004).

Our study extends upon previous sex-change work (Armstrong 2001, Alonzo and Mangel 2004, 2005) by exploring the effects of reserves on populations with a range of sexual strategies. Female to male sex change reduces the prospect of fishery benefit from reserves, primarily by reducing the number of large fecund females in the population (e.g., Fig. 2b). In sex-changing populations, the largest fish are mostly male, which contributes to larval subsidy only via their marginal contribution to improved fertilization success. Consequently, the benefit of reserves to fisheries yield is limited relative to non-sex-changing populations for which females in reserves provide increased larval subsidies beyond the reserves throughout their lives.

The introduction of reserves not only causes an inequality of densities, it also causes a disproportionate allocation of males in the populations: there is a decrease in the proportional male biomass in the fished population,

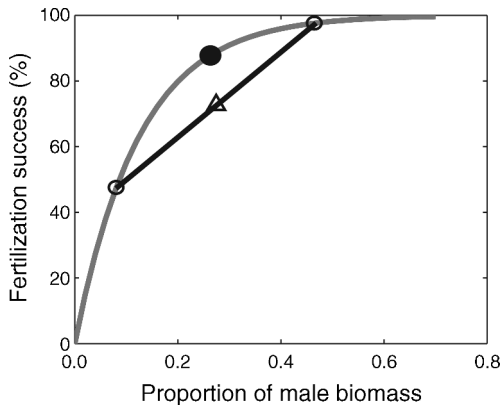


FIG. 4. Illustration of how average fertilization success is reduced when there are large spatial differences in proportional male biomass, as in reserves vs. fished subpopulations. The solid circle represents a population without marine reserves, where proportional male biomass is similar everywhere. The open circles represent fished (lower proportion of males) and reserve (higher proportion of males) subpopulations for a population with marine reserves. The open triangle represents the average fertilization success across the two subpopulations (for simplicity, this illustration assumes a 50–50 split of habitat between reserve and fished areas). Note that, due to the shape of the fertilization function, average fertilization success for the case with reserve and fished subpopulations (triangle) is lower than fertilization success for the population without marine reserves (solid circle).

and an increase in the reserve population. This disproportionate allocation of males increases the strength of sperm limitation in the fished population, while simultaneously providing limited benefits to fertilization success in reserves, which will already have a comparatively high relative male biomass. In other words, because fertilization success is a saturating function of relative male biomass, the marginal cost of decreasing male biomass where there is a lower relative abundance of males will outweigh the marginal benefit of a corresponding increase in male biomass where their relative abundance is already high. Consequently, reserves, by allocating males disproportionately between reserve and fished subpopulations, reduce the average contribution of males to reproductive output (Fig. 4), and thus lower the population's overall productivity. This interpretation is supported by our cross-boundary spawning aggregation model: allowing males from reserves to fertilize females from fished areas eliminates this fertilization effect, and thus, in contrast to our baseline case, sustainable yields are higher with reserves than without them.

Overall, our baseline and alternative fertilization-success functions produced similar qualitative effects of reserves for both sex-changing and non-sex-changing populations, suggesting that the effects of reserves on sustainable yields will be broadly similar across a range of fertilization-success relationships. However, for the sex-changing population, we did find that, under reduced sperm limitation, the lower bound on target population size was larger than in our baseline scenario (i.e., yield

curves did not extend as far to the left in Fig. 2f compared to Fig. 2b). This is consistent with the strongly asymptotic shape of the fertilization-success function under reduced sperm limitation: fertilization success remains high, even when the population is very heavily fished, compared to the baseline. Thus a comparatively larger cohort of recruits is produced when the relative abundance of males is low, as happens for sex-changing populations as target population size decreases.

Retaining a fixed equilibrium unfished biomass across different density-dependence scenarios meant that the strong density-dependence case included both an increase in the density-dependent effects of adults on recruitment success and also an increase in the density-independent component of recruitment success. In other words, the strong density-dependence case corresponded to a population with high capacity to recover from low density, via high recruitment success, but for which recruitment then decreases sharply with increases in adult biomass. This led to a sharper increase in larval-subsidy benefit from reserves as adult biomass was lowered in the fished areas. The greater larval subsidy meant that populations could withstand stronger fishing pressure (i.e., higher yields for a given target population size), and that there was a greater lower bound on target population size: populations cannot be fished down as far when the reserve population is providing a greater larval-subsidy benefit, as under stronger density dependence. Previous studies found reserves had the ability to increase yields under post-dispersal density dependence (Gaylord et al. 2005, White and Kendall 2007). Our results indicate that the magnitude of this effect is sensitive to the intensity of density dependence, but that the greater dispersal benefits from reserves under strong compared to weak density dependence holds regardless of whether populations were sex changing or not.

High adult survival consistently increased the performance of reserves relative to non-reserve cases for both sex-changing and non-sex-changing populations. With high survival, fishes recruiting to reserves survive longer, have greater lifetime fecundity, and so generate a greater lifetime recruitment subsidy to the fished population (Gaylord et al. 2005, White and Kendall 2007). In contrast, reserve benefit is reduced with low adult survival because few individuals survive to contribute significantly to reserves. This supports previous arguments that reserves would not benefit species with 'live fast die young' life histories (Gaylord et al. 2005).

The general model framework presented above has made simplifying assumptions (well-mixed larval pool, "knife-edge" fishing selectivity [i.e., fishing mortality rates equal for all fish >3 years], and no movement of adults from reserves to replenish fished areas) in order to effectively isolate interactions among key factors and to facilitate sensitivity analysis. The consequences of relaxing these assumptions, though not explicitly treated in this study, can be anticipated. The limiting case of no larval dispersal between reserve and fished areas would

mean that larvae produced inside reserves stay in reserves and do not contribute to the fishery and so yields will be reduced in direct proportion to the area closed off for reserves (Little et al. 2007, Kaplan 2009). Thus, incomplete mixing of larvae will tend to reduce reserve benefits (or increase reserve costs) relative to the complete-mixing assumption used here (Little et al. 2007). Exceptions to this general rule can occur if there is strong source-sink structure and reserves tend to be located over areas that are net exporters of larvae to areas open to fishing (Gaines et al. 2003, Sanchirico et al. 2006), provided sufficient larvae return to the "source" reserves to ensure maintenance of the populations in reserves. Sex-changing fisheries with progressively greater removal of older age classes (e.g., fisheries with significant selectivity for trophy-sized fishes) would be likely to see reduced reserve benefits, because this would tend to increase the difference between the relative male biomass in fished and reserve areas. As noted earlier, this means that, for a given overall population biomass, average male contribution to fertilization success will tend to be higher when males are more evenly distributed throughout the population (i.e., in the absence of reserves). Intermediate levels of movement by adults, particularly density-dependent migration of males, would act to mitigate some of the cost of closing an area to fishing because males would tend disproportionately to move into fished areas, and thus contribute to fishery yields (Little et al. 2009). Conversely, female migration could diminish the larval-subsidy benefits if many females cross reserve boundaries. Extensive adult movement across reserve boundaries, however, would tend to make dynamics similar to the no-reserve case, regardless of sexual strategy, because most or all individuals would become accessible to the fishery for some of their lives. In cases where adults are relatively site attached, but move across reserve boundaries to form spawning aggregations, sperm limitation is alleviated, and reserves become more likely to increase yields in sex-changing populations. In developing countries, reserves may, in some cases, be sufficiently small for species such as common coral trout to exhibit some cross-boundary interbreeding, although the extreme of complete mixing examined in our sensitivity analysis seems unlikely, given that only a minority of the population forms spawning aggregations, and that most coral trout are very site attached throughout their lives. However, for other sex-changing species whose adults move larger distances (e.g., Nassau grouper; Colin 1992), this alleviation of sperm limitation may well play a larger role.

Overall, our findings indicate that female to male sex-changing populations, unlike non-sex-changing populations, are unlikely to receive a yield-enhancing benefit from marine reserves at any given target population size, at least when reserves are large relative to the scale of adult movement. This result is robust over a range of sex-change regimes, stock-recruitment relationships, adult

mortality rates, and growth rates. The principal causes of this result appear to be the larger proportion of males in older age classes, relative to non-sex-changing populations, and the fact that fertilization success approaches an asymptote as male biomass increases. Reserves should thus be employed in female to male sex-changing fisheries for their ability to protect or rebuild overfished populations, and to sustain fishery viability, especially in the face of large uncertainty due to a lack of data, rather than for anticipated enhancement of fishery yields beyond reserve boundaries. More broadly, our findings also highlight the importance of considering the different contributions of males and females to population growth when evaluating the efficacy of marine reserves.

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SUPPLEMENTAL MATERIAL

Appendix A

A table showing parameters used in the models (*Ecological Archives* A022-042-A1).

Appendix B

A figure showing results of the cross-boundary spawning aggregation model (*Ecological Archives* A022-042-A2).