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Evaluation of the effectiveness of marine reserves for transient spawning aggregations in data-limited situations

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Many coral reef fish species form predictable, transient spawning aggregations. Many aggregations are overfished, making them a target for spatial management. Here, we develop a per-recruit model to evaluate the performance of no-take marine reserves protecting transient spawning aggregations. The model consists of only 14 demographic and exploitation-related parameters. We applied the model to a protogynous grouper and a gonochoristic rabbitfish from Seychelles and tested six scenarios regarding the extent of protected areas, the level of fish spawning-site fidelity, and fishing effort redistribution post reserve implementation. Spawning aggregation reserves improve spawning-stock biomass-per-recruit and reduce the sex ratio bias in protogynous populations for all scenarios examined. However, these benefits are often small and vary among the different scenarios and as a function of sexual ontogeny. In all scenarios, increases in yield-per-recruit do not occur or are negligible. The long-term yield increases due to spawning aggregation reserves may still occur, but only if spawning-stock biomass recovery results in a recruitment subsidy. Given these limited benefits, the value of no-take reserves must be weighed against those of other management options, such as fishing effort reduction and seasonal fishery closures. The latter is particularly appropriate when spawning and non-spawning areas overlap in space.

Keywords: coral reef fish, fisheries closures, marine conservation, marine protected areas, protogynous hermaphrodites, resource management.

Introduction

Many coral reef fish species migrate to form short-lived spawning aggregations at sites located a few to hundreds of kilometres from their normal areas of residence (Domeier and Colin, 1997). Transient spawning aggregations are highly vulnerable to fishing due to their spatial and temporal predictability and to the large increase in catchability that often occurs when fish aggregate (Sadovy and Domeier, 2005). High levels of fishing effort can lead to the rapid depletion of transient spawning aggregations (e.g. Colin, 1992; Sala *et al.*, 2001; Hamilton and Matawai, 2006), and several surveys of the status of transient spawning aggregations (primarily focusing on groupers and snappers) indicate that many are declining in size or have collapsed due to overexploitation (e.g. Sadovy and Eklund, 1999; Sadovy *et al.*, 2008; Claro *et al.*, 2009). Furthermore, protogynous species (i.e. species that mature first as females then change into males) also experience declines in the relative number of males in the adult population. These changes in the female:male sex ratio (SR) are hypothesized to produce reductions in egg fertilization rates and reproductive failure (Buxton, 1993; Coleman *et al.*, 1996; Koenig *et al.*, 1996). Management measures are therefore urgently needed to ensure the persistence of transient spawning aggregations, the fish populations from which they form, and the long-term viability of the fisheries depending on them (Sadovy and Domeier, 2005).

A range of management tools have been employed for the conservation of spawning aggregations, including marine reserves and temporal fishery closures protecting spawning sites or periods from fishing, respectively (Sadovy and Domeier, 2005; Russell *et al.*, 2012). Though spawning site closures, here referred to as “spawning aggregation reserves”, are often identified as an effective

Table 1. Main features of existing models exploring the impacts of spawning aggregation reserves.

Species	Aggregation type	Geographical area	Model type	Spawning site fidelity	Sex change	Fishing effort adjusted?^{a}	Scenarios where total fishing effort is increased?	Authors
Gag grouper (*M. microlepis*)	Transient	Gulf of Mexico, USA	Spatially non-explicit population model	Individuals entirely faithful to spawning sites	Age-mediated	Yes	No	Heppell *et al.* (2006)
Gag grouper (*M. microlepis*)	Transient	Gulf of Mexico, USA	Spatially non-explicit population model	Individuals entirely faithful to spawning sites	Age-mediated or density-dependent (under exogenous control)	Yes	Yes	Ellis and Powers (2012)
California sheephead (*Semicossyphus pulcher*)	Resident	Non-specific	Spatially non-explicit individual-based model	Individuals entirely faithful to spawning sites	Size-mediated	Yes	No	Alonzo and Mangel (2004)
Common coral trout (*P. leopardus*)	Many small aggregations at many sites over a wide area	Non-specific	Spatially non-explicit population model	Individuals entirely faithful to spawning sites	Age-mediated	No	Yes	Chan *et al.* (2012)

^{a}Assume the redistribution of fishing effort in the non-protected areas after reserve implementation.

management tool, few quantitative studies of their effects on aggregating populations currently exist. Empirical evidence of the benefits associated with spawning aggregation reserves, such as an increases in aggregation size and the normalization of the female:male SR, is limited (Beets and Friedlander, 1999; Burton *et al.*, 2005; Nemeth, 2005). A number of empirical studies identify the limitations of spawning aggregation reserves for improving the reproductive capacity of populations, citing ineffective design or implementation (e.g. Rhodes and Sadovy, 2002; Pet *et al.*, 2005; Mangubhai *et al.*, 2011), and fishing pressure outside protected spawning sites as key factors undermining their effectiveness (e.g. Claro and Lindeman, 2003; Coleman *et al.*, 2004; Rhodes and Tupper, 2007).

In the absence of empirical data, theoretical studies can provide insights into the potential impacts of spawning aggregation reserves (Table 1). The effects of spawning aggregation reserves depend on many factors relating to exploitation and life history, including pre- and post-implementation fishing effort, the existence and nature of sex change in the population, and the impact of sperm limitation on reproductive success. Permanent no-take spawning area closures for a protogynous species (gag, *Mycteroperca microlepis*) helped normalize the female:male SR but were less effective for population recovery than reducing the overall fishing effort or implementing reserves protecting juveniles and non-spawning females (Heppell *et al.*, 2006; Ellis and Powers, 2012).

The effectiveness of marine reserves that are intended to protect spawning aggregations is dependent on the sexual mode of the target species. If sex change occurs after recruitment to the fishery, protogynous populations are predicted to decrease proportionally less than otherwise equivalent gonochoristic populations under the same fishing pressure and, consequently, to derive fewer conservation benefits from reserves that protect spawning aggregations (Alonzo and Mangel, 2004; Chan *et al.*, 2012). Protogynous populations, unlike gonochoristic populations, are also unlikely to receive a yield-enhancement benefit from spawning aggregation reserves (Alonzo and Mangel, 2004; Chan *et al.*, 2012; Ellis and Powers, 2012). Finally, if sex change is under exogenous control rather than endogenous (e.g. age- or size-mediated), protogynous populations will be more resilient to fishing pressure and derive even fewer benefits from large spawning aggregation reserves (Ellis and Powers, 2012). These predictions all stem from the larger proportion of females in older age classes in gonochoristic populations. Older age classes derive proportionally greater benefits from reduced fishing pressure and older females contribute disproportionately to egg production. Therefore, gonochoristic populations have greater inherent potential for benefits from closures, whereas reserve impacts on the reproductive capacity of protogynous populations are primarily due to the alleviation of sperm limitation (Chan *et al.*, 2012).

Existing modelling studies (Table 1) are consistent in predicting that protecting spawning aggregation sites will only rebuild populations and normalize the population's SR if fish do not suffer high fishing mortality outside spawning sites or at unprotected spawning sites. However, considerable knowledge gaps remain regarding the use of spawning aggregation reserves, such as the effects of spawning site fidelity on their effectiveness and their fisheries effects (Sale *et al.*, 2005; Grüss *et al.*, 2011a). Furthermore, many transient spawning aggregations are targeted by artisanal fisheries in developing countries for which species-specific data on stock–recruitment relationships, harvest rates, spawning-site fidelity, and sperm limitation due to the altered SR are extremely limited (Johannes, 1998; Sadovy, 2005; Sadovy and Domeier, 2005). There is, therefore, a need to develop generic tools for assessing the potential conservation and fisheries effects of spawning aggregation reserves in these data-limited contexts.

With these information constraints in mind, we developed a parsimonious, non-spatial, per-recruit model for evaluating the conservation (spawning stock biomass-per-recruit (SSBR), female:male SR) and fisheries (yield-per-recruit, YPR) effects of no-take spawning aggregation reserves, for gonochoristic populations and protogynous populations with age-mediated sex change. We herein present our model and demonstrate its value by using it to assess reserve scenarios for two populations that form transient spawning aggregations in Seychelles.

Material and methods

Per-recruit models avoid the need for the explicit inclusion of a stock–recruitment relationship and/or a relationship linking the proportion of males in the population to egg fertilization success, both of which are often unknown or uncertain. The information needed to run the model is often readily available: the level of annual fishing effort exerted on fish populations and the fraction of this annual effort directed towards spawning aggregations, estimates (by proxy) of catchability at spawning and non-spawning sites, and estimates for the standard growth and reproduction life-history parameters. Therefore, the per-recruit model we develop here can be widely applied for examining the effects of spawning aggregation reserves in data-limited situations.

Our model includes two life-history stages for gonochoristic populations (juveniles and adults), and three life-history stages for protogynous populations (juveniles and adult females and males). Adults can either be in a spawning or a non-spawning state, and catchability differs between spawning and non-spawning sites. We assume that fish spawn regularly and on time-scales that are considerably shorter than those for other biological processes, such as growth, so that spawning and non-spawning events can be treated as continuous processes occurring in all adult age classes. Both adult females and males are considered to leave the spawning aggregation sites at the end of the spawning period, and juveniles are considered absent from spawning sites.

Mortality/survival in the absence of spawning aggregation reserves

It is assumed that fish recruit to the fishery at or before sexual maturation due to the wide size selectivity in multigear reef fisheries and the late maturity in many aggregation-forming species (Sadovy, 1994; Sadovy and Eklund, 1999; Rhodes and Tupper, 2008). As juveniles are not harvested during spawning periods, the total mortality rate of juveniles is:

$$Z_j = M + (1 - C_s)q_{ns}E, \qquad (1)$$

where M is the natural mortality rate (year^{-1}), C_s the fraction of annual fishing effort on spawning aggregations, q_{ns} the catchability at non-spawning sites, and E the total annual fishing effort (year^{-1}). The probability of survival of an individual to sexual maturity is:

$$p(a_{50}) = e^{-[M+(1-C_s)q_{ns}E](a_{50}-a_F)}, \qquad (2)$$

where a_{50} is the age at 50% maturity, which for simplicity we equate with the age of sexual maturity, and a_F the age of recruitment to the fishery.

Adult individuals are exposed to fishing mortality at both spawning and non-spawning sites. For gonochoristic populations, the total mortality rate of adult individuals is:

$$Z_{mat} = M + ((1 - C_s)q_{ns} + C_s q_s)E, \qquad (3)$$

where q_s is the catchability at spawning sites. Natural mortality, M, is assumed the same for adults and juveniles, though changes in natural mortality with age could be included in the model.

Females of protogynous populations often spend less time at spawning sites than males (e.g. Zeller, 1998; Nemeth *et al.*, 2007; Robinson *et al.*, 2008) and the total mortality rate of adult females is:

$$Z_f = M + ((1 - C_s)q_{ns} + C_f C_s q_s)E, \qquad (4)$$

where C_f is the fraction of the spawning period females spend at spawning sites. This fraction is 1 in cases where males and females experience the same level of fishing effort at spawning sites. The probability of survival of adult females to sex change is:

$$p(a_{sx}) = e^{-[M+(1-C_s)q_{ns}E](a_{50}-a_F)} e^{-[M+((1-C_s)q_{ns}+C_f C_s q_s)E](a_{sx}-a_{50})}, \qquad (5)$$

where a_{sx} is the age of sex change. Sex change is often a gradual process in populations of protogynous species, occurring over a wide range of sizes and ages, but for mathematical simplicity we use a single mean age at sex change.

Finally, for protogynous populations, the total mortality rate of males (Z_m) is identical with that of gonochoristic populations and is given by Equation (3).

Mortality/survival in the presence of spawning aggregation reserves

On implementation of spawning aggregation reserves (hereafter, often simply referred to as "reserves" or "protected areas"), the resulting fishing mortality will depend on spawning-site fidelity and the fate of the fishing effort previously in reserve areas. We examine cases where all adult fish are either completely faithful or completely unfaithful to spawning sites and consider several scenarios for the evolution of effort after reserve creation: (i) effort previously in reserves disappears, (ii) pre-reserve effort is redistributed to spawning sites remaining open to fishing, and (iii) pre-reserve effort is fully redistributed to non-spawning sites for cases where all spawning sites are closed to fishing. In all these scenarios, it is assumed that fishers will preferentially move to other spawning sites if any remain open to fishing, only resorting to intensifying fishing in non-spawning areas if they have no other alternative.

If effort previously in reserves disappears at the time of reserve creation and fish are not faithful to spawning sites, then the fishing mortality rate of spawning individuals is simply reduced by a factor of $(1 - C_r)$, the fraction of time fish spawn outside the protected spawning areas. For example, for gonochoristic populations, the total mortality rate of adult individuals will become:

$$Z_{mat} = M + ((1 - C_s)q_{ns} + (1 - C_r)C_s q_s)E, \qquad (6)$$

Conversely, if individuals are faithful to spawning sites, then there will essentially be two subpopulations, one that experiences no fishing mortality while spawning (representing a fraction C_r of the population assuming complete mixing of recruits between the two subpopulations) and one that does experience fishing mortality while spawning [representing a fraction $(1 - C_r)$ of the population].

If the effort previously in reserves is fully redistributed to the spawning sites remaining open to fishing and fish are not faithful to spawning sites, then the fishing mortality rate of spawning individuals will be both reduced by a factor of $(1 - C_r)$ compared with the pre-reserve situation and increased by a factor of $1/(1 - C_r)$, so that global fishing mortality will be unchanged by protection.

If, on the other hand, fish are faithful to spawning sites, then there will again be two subpopulations, one that experiences no fishing mortality during spawning periods and one that has the normal fishing mortality during that time of the year increased by a factor of $1/(1 - C_r)$.

Considering the case where all spawning sites are closed, if effort previously in reserves is fully redistributed to non-spawning

Table 2. Parameter estimates for shoemaker spinefoot rabbitfish (*S. sutor*) and brown-marbled grouper (*E. fuscoguttatus*).

Parameter	Definition	*S. sutor*	*E. fuscoguttatus*
M	Natural mortality rate	0.63 year^{-1a}	0.1 year^{-1b}
E	Total annual fishing effort	95 × 10^3 trap sets per year^c	169 fishing days per year^d
C_s	Fraction of annual fishing effort on spawning aggregations	0.0822^c	0.0329^d
C_f	Fraction of the spawning period females spend at spawning sites	–	0.45^e
q_s	Spawning-site catchability	1.0758 × 10^{-4}	6.5447 × 10^{-3}
q_{ns}	Non-spawning site catchability	$q_s/10^e$	$q_s/140^e$
a_F	Age of recruitment into the fishery	0.34 years^c	9.2 years^e
a_{50}	Age of sexual maturity	0.79 years^d	9.2 years^f
a_{sx}	Age of sex change	–	25.5 years^f
k	Instantaneous growth rate at small size	0.65 year^{-1a}	0.16 year^{-1f}
L_∞	Maximum size	43.3 cm^a	80.7 cm^f
a_0	Theoretical age at zero length	−0.379 year^a	−0.2 year^f
α	Constant of proportionality of the allometric length–weight relationship	5.9 × 10^{-3g}	6 × 10^{-6h}
β	Exponent of the allometric length–weight relationship	2.75^g	3.28^h

[a] Grandcourt (2002).
[b] Hoenig (1983).
[c] Robinson *et al.* (2011).
[d] JR, pers. obs.
[e] Seychelles Fishing Authority, unpubl. data.
[f] Pears *et al.* (2006).
[g] Samboo and Mauree (1988).
[h] Grandcourt (2005).

sites, all the annual fishing effort is exerted in non-spawning areas and all individuals (juveniles and adults) are assumed subject to the same total mortality rate:

$$Z_j = M + q_{ns}E \tag{7}$$

Conversely, if effort previously in reserves disappears at the time of reserve creation (which can occur if the redistribution of effort to normal residence areas is unprofitable), the total mortality rate for all fish individuals is:

$$Z_j = M + (1 - C_s)q_{ns}E \tag{8}$$

Metrics

To evaluate the effectiveness of spawning aggregation reserves, we use two metrics: female SSBR and YPR. For protogynous populations, we also examine the SR, defined here as the number of mature females over the number of males. Female SSBR is an indicator of reproductive capacity, whereas the SR is an indicator of the chances of egg fertilization for protogynous populations. It is assumed that the egg fertilization rate decreases if females significantly outnumber males in a population. No explicit relationship is used here for this poorly understood non-linear process, though the population SR can be compared with a "critical SR", above which reproduction may fail (Coleman *et al.*, 1996; Fitzhugh *et al.*, 2006).

For scenarios with spawning aggregation reserves and absolute spawning site fidelity, the fish population essentially decomposes into two subpopulations experiencing different mortality rates. These two subpopulations reproduce separately, but are linked by larval dispersal. Here, it is assumed that all larvae produced enter a common pool from which they settle into protected or fished subpopulations in direct proportion to the percentage of protected or non-protected spawning sites. Given this assumption, population-wide average values for the three metrics are weighted averages (by fraction in reserves) of the corresponding metrics for the two subpopulations. Though population-wide average values of SSBR and YPR are useful indicators, sperm limitation due to the unbalanced SR occurs at a local level. Therefore, it is necessary to estimate the local SR at both fished and protected spawning sites.

Female SSBR and YPR are obtained by integrating the product of survival to age and weight-at-age over the relevant age ranges, whereas the SR is the ratio of integrals of survival to age over the female and male age ranges. The relevant equations for these metrics in the absence of reserves are described in Supplementary Appendix A1. In the results and figures, SSBR is given relative to the natural (unfished) SSBR (i.e. the fraction of natural SSBR or FNSSBR). Similarly, YPR is given relative to the maximum YPR in the absence of reserves.

Model application

The model is applied to populations of two species that form transient spawning aggregations in Seychelles: the brown-marbled grouper (*Epinephelus fuscoguttatus*) population of Farquhar Atoll (Robinson *et al.*, 2008) and the shoemaker spinefoot rabbitfish (*Siganus sutor*) population of the main granitic islands (Robinson *et al.*, 2011). Brown-marbled groupers are long-lived (maximum reported age ~42 years; Pears *et al.*, 2006), slow-growing, and protogynous and have a low natural mortality rate, whereas shoemaker spinefoot rabbitfish are short-lived (natural life expectancy ~2.5 years; Grandcourt, 2005), fast-growing, and gonochoristic and have a high natural mortality rate. Both populations are assumed to grow according to a von Bertalanffy growth function, and weight is an allometric function of growth (Table 2 and Supplementary Figure A1).

At Farquhar Atoll, the fishery for the brown-marbled grouper and other species is subsistence and small-scale commercial, typically involving three fishing boats that are each only used a fraction of the year. The total annual effort for the brown-marbled grouper is ~169 fishing boat days per year, of which roughly 12 occur

Table 3. Reserve scenarios simulated in the present study.

Reserve scenario	Full or partial spawning site closures?	Fidelity of fish to spawning sites?	Redistribution of fishing effort after reserve creation?
#1	Partial		
#2	Partial	X	
#3	Partial		X
#4	Partial	X	X
#5	Full		
#6	Full		X

Fidelity of fish to spawning sites?: checked, absolute fidelity; unchecked, absolute infidelity. Redistribution of fishing effort after reserve creation?: checked, the fishing effort previously in reserves is redistributed to non-protected spawning sites (partial closures) or to non-spawning areas (full closures); unchecked, the fishing effort previously in reserves disappears.

during spawning aggregations (JR, pers. obs.). Shoemaker spinefoot rabbitfish and other siganid species are fished using traps mainly set from small outboard-powered boats. The trap fishery is subject to minimum mesh size requirements but otherwise is not managed (Robinson *et al.*, 2011). The mean annual effort in the trap fishery for 2000–2006 was 95 000 sets (Seychelles Fishing Authority, unpubl. data). The number of days the trap fishery spent fishing on spawning aggregations is estimated at 30 (Robinson *et al.*, 2011).

The absolute values of catchability are highly uncertain for both groupers and rabbitfish and are difficult to estimate precisely. To derive a starting point for the value of the catchability coefficient, it is assumed that the total annual fishing mortality on spawning aggregations is roughly equivalent to the annual natural mortality rate (this is different from the instantaneous spawning-aggregation fishing mortality, which would be much greater than natural mortality, but only occurs over a small fraction of the year). Given this assumption, spawning-site catchability is obtained as:

$$q_s = \frac{M}{C_s E}, \tag{9}$$

The ratio of catch per unit effort (cpue) at non-spawning sites to cpue at spawning sites is then used to estimate relative catchability between these two periods. The assumption that annual fishing mortality at spawning sites is equivalent to the annual natural mortality rate is obviously tenuous. We address this uncertainty by varying total fishing effort, which can alternatively be interpreted as varying catchability, since these two quantities always appear together in the model.

The age of recruitment to the fishery is unknown for the brown-marbled grouper at Farquhar. Since juvenile catch is negligible for this population (JR, pers. obs.), the age of recruitment to the fishery is taken as being equal to the age of sexual maturity. The SR is assumed to be 1:1 for rabbitfish (Robinson *et al.*, 2011). All other model parameters are obtained from the literature relating to the study populations or to populations of the same species in other regions (Table 2). The model assumes that sex change takes place at a fixed age for the grouper. The potential implications of the exogenous control of sex change on the effects of fishing and marine reserves are considered in the "Discussion" section.

The six scenarios of spawning aggregation reserves described above were assessed for both groupers and rabbitfish (Table 3 and Supplementary Figure A1). To facilitate the discussion of our results, we assumed that the reproduction of the grouper may fail when the SR is superior to 50:1, a reasonable threshold considering SR estimates reported for heavily exploited aggregation-forming serranid populations (Beets and Friedlander, 1992; Sadovy *et al.*, 1994a; Coleman *et al.*, 1996). The value of the "critical SR" for the brown-marbled grouper under the assumption of age-mediated sex change may in reality be higher or lower than 50:1, but qualitative comparisons between the effects of different reserve scenarios on SR normalization are unchanged for a wide range of critical SRs. Unequivocal evidence of sperm limitation in response to the unbalanced SR is currently lacking (e.g. Coleman *et al.*, 1996; Koenig *et al.*, 1996; Armsworth, 2001; Fitzhugh *et al.*, 2006), and the "critical SR" used here is solely to demonstrate qualitative aspects of potential effects of the SR bias on reproductive success.

To disentangle the effects of slow growth and natural mortality from those of sexual mode and to explore general principles for the effects of spawning aggregation reserves, the model was also applied to three other theoretical grouper populations: a "gonochoristic" population, a "fast-growing" population, and a population "with high natural mortality". These theoretical populations have exactly the same characteristics as the brown-marbled grouper population (described in Table 2), except that the gonochoristic population does not change sex and its SR is 1:1; the fast-growing population has an instantaneous growth rate at small size k that is three times that of the brown-marbled grouper (0.48 year^{-1}; a value for k that is close to that for the common coral trout, *Plectropomus leopardus*; Chan *et al.*, 2012); and the population with high natural mortality has a natural mortality rate that is three times that of the brown-marbled grouper (0.3 year^{-1}).

The basic MATLAB code to run the model can be found in Supplementary Appendix A2.

Results

Model in the absence of reserves

The two study populations present contrasting life-history traits, but also different exploitation levels. The default annual fishing effort level used here for the grouper population, hereafter referred to as E_{base}, is around 13 times less than the level of annual effort at which YPR reaches a maximum, $E_{\max}$ (Figure 1a). The YPR of the population is at 63% of its maximum value (Figure 1a), whereas female SSBR is at 66% of its natural value (Figure 1b). This value of FNSSBR needs to be considered relative to the value that causes population collapse, which typically is in the range of 10–60% of natural SSBR and higher for long-lived fish populations (Myers *et al.*, 1999). The grouper SR at the base fishing effort level is significantly skewed with respect to the natural, unfished state (19:1 vs. 4:1 female to male ratio for fished vs. natural conditions; Figure 1c). This stems from the fact that the relationship between fishing effort and SR is roughly exponential (Figure 1c), meaning that small increases in fishing lead to a considerable increase in the SR bias. The SR is particularly sensitive to changes in model parameters and especially to changes in the age of sex change (Table 4).

Compared with the grouper population, the rabbitfish population is subject to greater levels of fishing pressure. The annual fishing effort used for the rabbitfish population, E_{base}, is close to

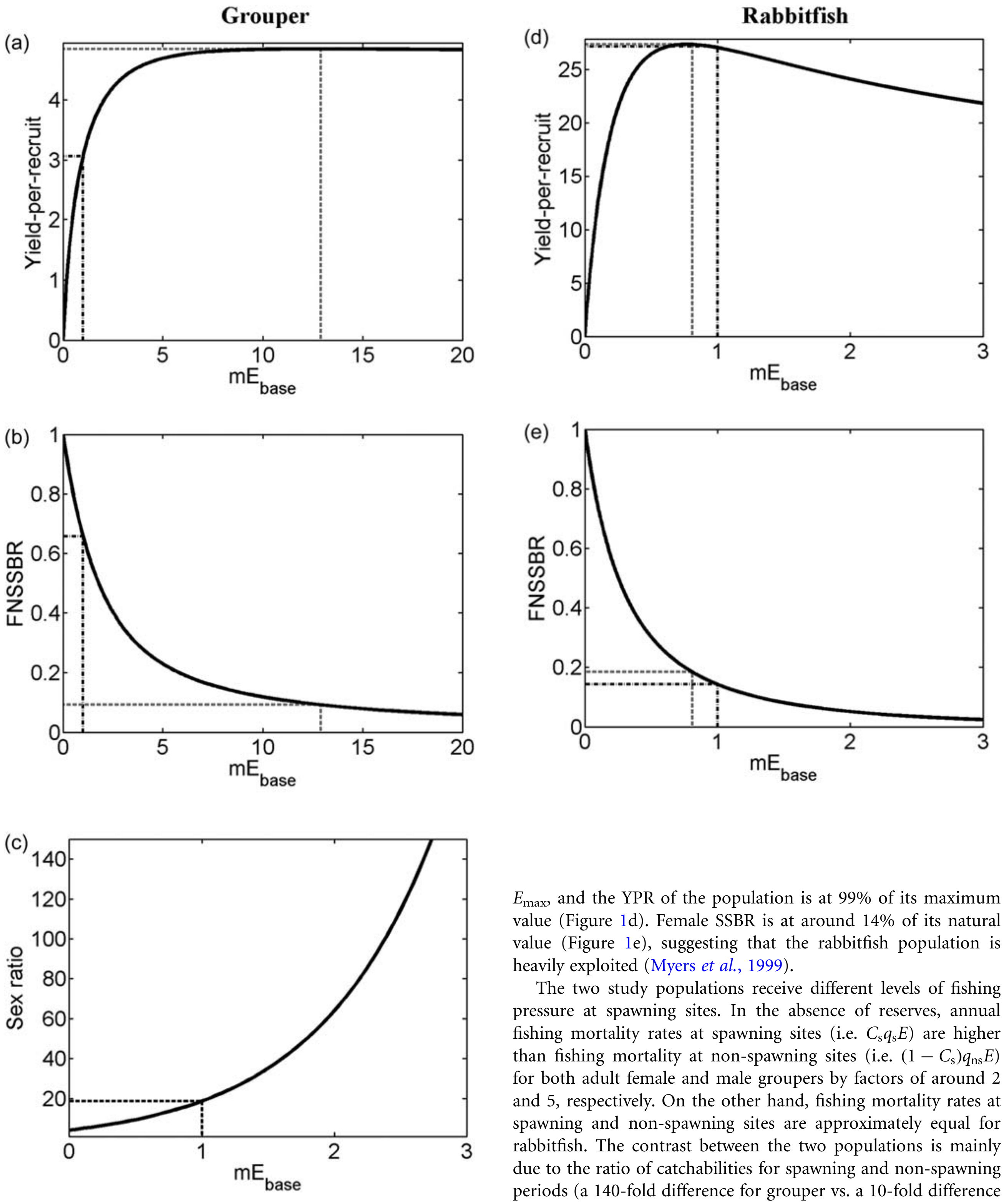

Figure 1. YPR (a and d), fraction of natural female SSBR (b and e), and the female:male SR (c) as functions of annual fishing effort. (a)–(c) are for the grouper, whereas (d) and (e) are for rabbitfish. The vertical dashed grey lines indicate the default value of annual fishing effort exerted on the population, E_{base}, and the corresponding value of the per recruit quantity, whereas the vertical dashed-dotted black lines indicate the value of annual fishing effort at which YPR reaches a maximum for the population, E_{max}, and the corresponding value of the per recruit quantity.

E_{max}, and the YPR of the population is at 99% of its maximum value (Figure 1d). Female SSBR is at around 14% of its natural value (Figure 1e), suggesting that the rabbitfish population is heavily exploited (Myers *et al.*, 1999).

The two study populations receive different levels of fishing pressure at spawning sites. In the absence of reserves, annual fishing mortality rates at spawning sites (i.e. $C_s q_s E$) are higher than fishing mortality at non-spawning sites (i.e. $(1 - C_s) q_{ns} E$) for both adult female and male groupers by factors of around 2 and 5, respectively. On the other hand, fishing mortality rates at spawning and non-spawning sites are approximately equal for rabbitfish. The contrast between the two populations is mainly due to the ratio of catchabilities for spawning and non-spawning periods (a 140-fold difference for grouper vs. a 10-fold difference for rabbitfish; Table 2).

Effects of spawning aggregation reserves

The response of female SSBR and YPR to changes in fishing effort and fraction of spawning sites protected is qualitatively similar for grouper and rabbitfish populations for the six reserve scenarios (Table 3). As such, we focus primarily on results for grouper,

Table 4. Sensitivities of per recruit quantities and SR to changes in natural mortality rate (M), fraction of annual fishing effort on spawning aggregations (C_s), spawning-site catchability (q_s), non-spawning site catchability (q_{ns}), age of recruitment into the fishery (a_F), age of sexual maturity (a_{50}), and age of sex change (a_{sx}), for brown-marbled grouper and shoemaker spinefoot rabbitfish.

	Fish population	Female SSBR	YPR	SR
M	Grouper	−0.57	−0.75	**1.61**
	Rabbitfish	−0.73	−0.62	-
C_s	Grouper	−0.25	0.32	**0.97**
	Rabbitfish	−0.38	0.02	-
q_s	Grouper	−0.26	0.32	**0.98**
	Rabbitfish	−0.45	0.02	-
q_{ns}	Grouper	−0.12	0.14	0.34
	Rabbitfish	−0.82	−0.09	-
a_F	Grouper	**1.12**	0.82	0
	Rabbitfish	0.45	0.34	-
a_{50}	Grouper	**−0.66**	−0.23	**−1.63**
	Rabbitfish	−0.40	0.07	-
a_{sx}	Grouper	0.42	−0.13	**4.64**

Sensitivities close to or greater than 1 in magnitude are indicated in bold. Sensitivities >1 in magnitude indicate than a 1% change in a given parameter results in a change in a given metric of more than 1%.

indicating differences between the two study populations wherever it is important.

Enhancement of female SSBR with spawning aggregation reserves occurs for all scenarios except when fish are not faithful to spawning sites and effort formerly in reserves is redistributed outside the protected areas (scenario #3; Figures 2 and 3). As expected, the greatest increases in female SSBR are obtained when all spawning sites are set aside as reserves (reserve scenarios #5 and 6; green curves in Figure 2). When only a fraction of spawning sites C_r are protected, increases in female SSBR are greater when the fishing effort previously in reserves disappears, rather than being redistributed to non-protected spawning sites (scenarios #1 and 2 vs. #3 and 4; black vs. violet curves in Figure 2, and Figure 3a and b vs. c and d). In contrast, when all spawning sites are protected, female SSBR levels are rather insensitive to the fate of fishing effort formerly on spawning sites due to low catchability levels at non-spawning sites (scenarios #5 and 6; green curves in Figure 2). Differences in female SSBR between the reserve and the non-reserve situations are stronger for the grouper than the rabbitfish as adult fishing mortality rates are much higher at spawning sites than in normal residence areas for the grouper.

Enhancement of female SSBR is expected to be greater when fish are faithful to spawning sites. This expectation stems from the fact that the convex, decreasing relationship between annual fishing effort and female SSBR (Figure 1b and e) implies that two separate subpopulations (e.g. using protected and unprotected spawning sites) experiencing different fishing rates will have superior average SSBR than a single subpopulation experiencing the average of the two fishing rates (via Jensen's inequality; Grüss *et al.*, 2011b). However, we do not observe the marked differences of female SSBR between the site fidelity and the non-site fidelity situations (scenarios #2 vs. #1 and, to a lesser extent, scenarios #4 vs. #3; dashed black and violet curves vs. full black and violet curves in Figures 2 and 3). Moreover, female SSBR—as well as SR and YPR—is unchanged with reserves in the non-site fidelity situation when the effort previously in protected areas is redistributed to non-protected spawning sites [Equation (7); full violet curves in Figures 2 and 3c].

Marine reserve effects on the SR vary qualitatively depending on whether fish are faithful to spawning sites or not and whether the fishing effort formerly in reserves is displaced to non-protected spawning sites. Decreases in the SR occur when all spawning sites are protected (scenarios #5 and 6; green curves in Figure 4 and Supplementary Figure A2), or when the effort previously in reserves is not redistributed to the spawning sites remaining open to fishing (scenarios #1 and 2; black curves in Figure 4 and Supplementary Figure A2, and Figure 5a and Supplementary Figure A3a and b). Decreases in the SR are largest when all spawning sites are protected due to the complete protection of males during spawning periods (green curves in Figure 4 and Supplementary Figure A2).

In contrast, the SR is unchanged in the absence of spawning site fidelity when the effort formerly in reserves is displaced to non-protected spawning sites (reserve scenario #3; full violet curve in Figure 4 and Supplementary Figure A2 and Figure 5c and Supplementary Figure A3c), whereas the SR of the fished subpopulation increases with both annual effort and C_r in the site fidelity situation (reserve scenario #4; dashed violet curves in Figure 4 and Supplementary Figure A2 and Figure 5d and Supplementary Figure A3d). In the site fidelity situation, the SR at fished spawning sites may rise above the critical level as a result of displacement of fishing effort from protected spawning sites (dashed violet curves in Figure 4 and Supplementary Figure A2 and Figure 5d and Supplementary Figure A3d). On the other hand, the SR at protected spawning sites remains close to the natural SR (Supplementary Figure A4), potentially ensuring that the overall production of fertilized eggs is not compromised if enough spawning sites are set aside as reserves (Figure 3e and f).

Spawning aggregation reserves have negligible or negative effects on YPR for all reserve scenarios (Figures 6 and 7). YPR values with and without reserves are similar for annual fishing effort levels greater than around 1.5 times E_{base} for rabbitfish and are only marginally different for lower effort levels (Figure 6c and d). Except reserve scenario #3 (no site fidelity, fishing effort redistribution), grouper YPR decreases with the fraction of spawning sites protected for any given effort level (Figures 6a and b and 7). YPR is significantly reduced compared with the no-reserve situation for the grouper when all spawning sites are protected (full and dashed green curves in Figure 6a and b).

Consequences of life history for reserve effects

The patterns of female SSBR and YPR for the different scenarios examined are qualitatively similar when comparing the three theoretical grouper populations (the gonochoristic and fast-growing populations and the population with high natural mortality) with the studied brown-marbled grouper population (Supplementary Figures A5 and A6). The gonochoristic population experiences greater increases in female SSBR and similar decreases in YPR than the baseline protogynous population for all reserve scenarios (Supplementary Figures A7c and d vs. Supplementary Figures A7a and b). More rapid growth causes a reduction in reserve efficacy in terms of female SSBR and greater decreases in YPR for the different reserve scenarios (Supplementary Figure A7e and f). The population with high natural mortality experiences much fewer benefits from reserves

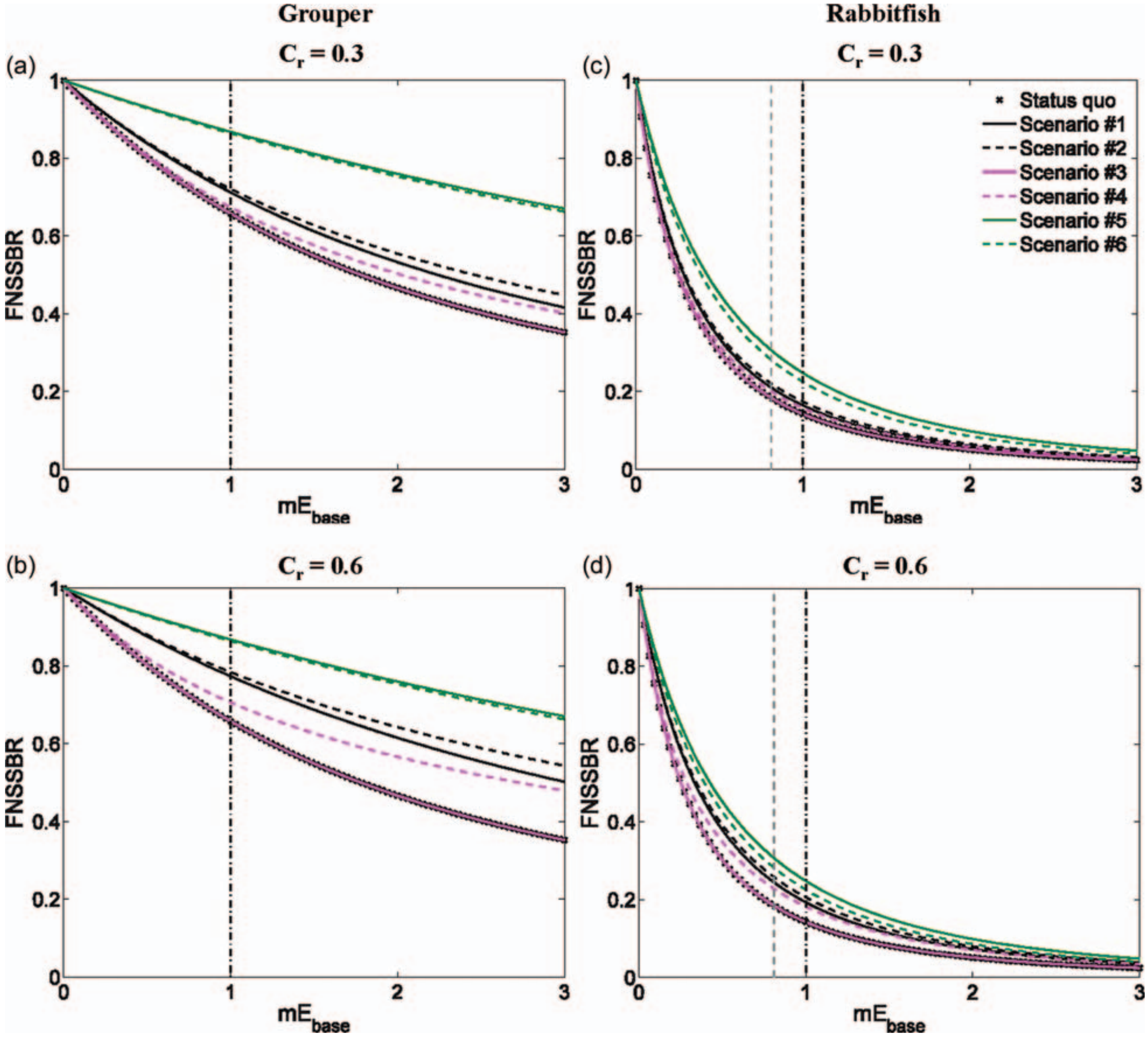

Figure 2. Fraction of female SSBR as a function of multiplier of fishing effort (mE_{base}), for the six reserve scenarios (Table 3). (a) and (b) is for the grouper, whereas (c) and (d) is for rabbitfish. For reserve scenarios #1 – 4, the fraction of spawning sites in marine reserves, C_r, is 30 and 60% for (a) and (c) and (b) and (d), respectively, whereas all spawning sites are set aside as reserves for scenarios #5 and 6. E_{base} is indicated by a vertical dashed-dotted black line. E_{max} is indicated by a vertical dashed grey line for rabbitfish.

in terms of female SSBR and much greater decreases in YPR than the baseline population for all reserve scenarios (Supplementary Figure A7g and h).

Discussion

Our model indicates that spawning aggregation reserves increase reproductive capacity (FNSSBR) and help normalize the female:male SR under a wide range of conditions. Nevertheless, increases in reproductive capacity are small often, particularly for the most realistic scenario involving fishing effort redistribution and spawning site fidelity (reserve scenario #4 in Figure 2). For example, placing 60% of all spawning sites in reserves only increases FNSSBR from 0.65 to 0.7 for the grouper and from 0.13 to 0.2 for the rabbitfish at the base fishing effort level for scenario #4. These modest increases suggest that spawning aggregation reserves have a role to play in conserving aggregation-forming populations, but that the benefits of reserves must be weighed against those of other approaches, such as global fishing effort reduction (e.g. an ~15% drop in total fishing effort produces as large an increase in grouper FNSSBR as placing 60% of spawning sites in reserves).

Placing all spawning sites in reserves is more effective at increasing reproductive capacity and lowering the female:male SR than closing only a fraction of spawning sites to fishing. Even if total fishing effort is conserved via redistribution onto normal residence areas, FNSSBR increases to 0.87 for the grouper and 0.27 for the rabbitfish at the base fishing effort level (reserve scenario #6 in Figure 2), and the grouper female:male SR remains below 10:1 for a wide range of fishing effort levels (Figure 4). These important benefits from spawning aggregation reserves are due to the significant differences in catchability between spawning and non-spawning individuals for our study populations. Our results contrast with those of Heppell *et al.* (2006),

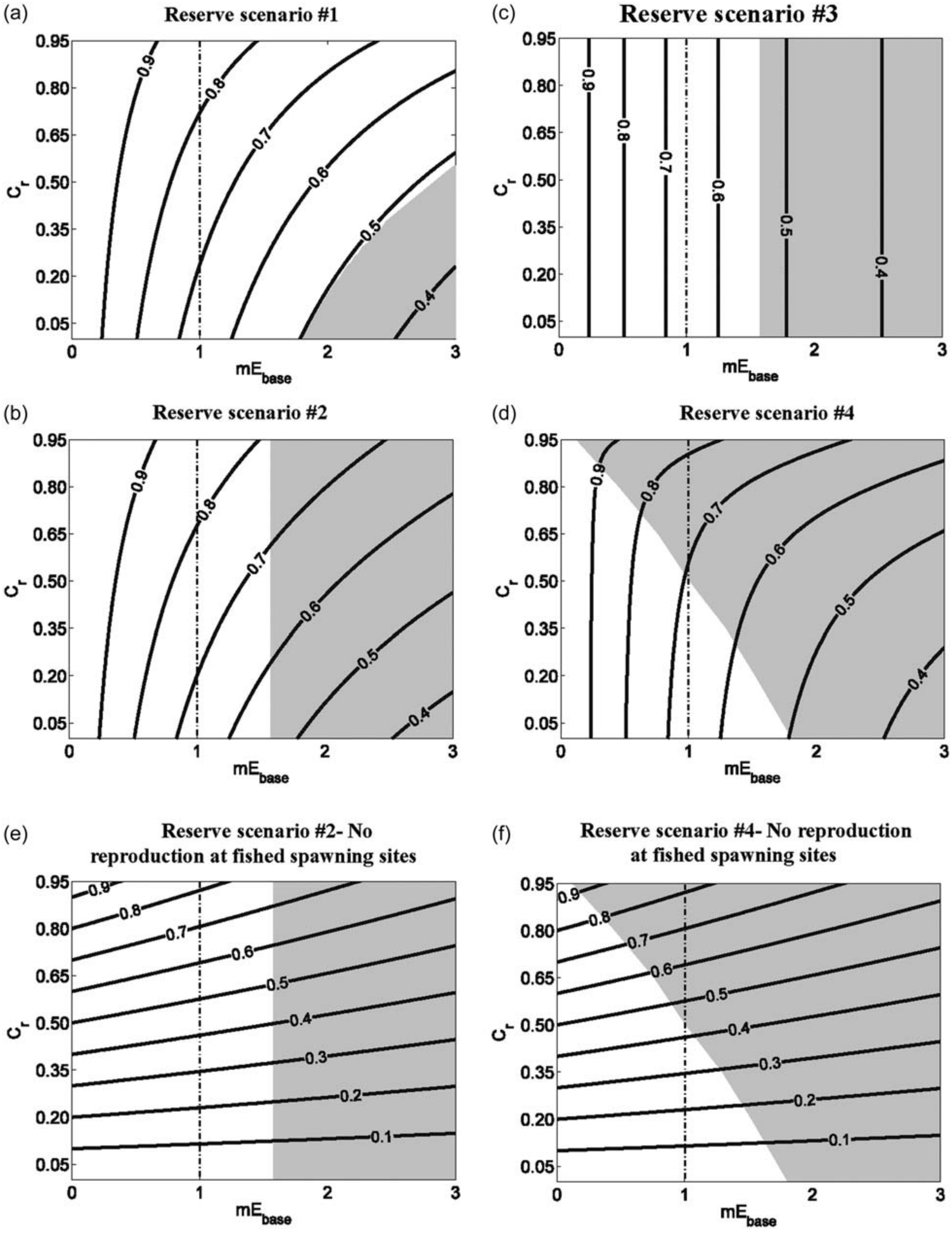

Figure 3. The grouper fraction of female SSBR as a function of multiplier of fishing effort (mE_{base}) and fraction of spawning sites in reserves (C_r) for reserve scenarios #1–4 (Table 3). (a) is for scenario #1, (b) and (e) for scenario #2, (c) for scenario #3, and (d) and (f) for scenario #4. Reproduction occurs at fished spawning sites for (a)–(d), whereas it is assumed that there is no reproduction at fished spawning sites for (e) and (f) due to a strongly imbalanced SR. For all panels, the light grey area represents the combinations of mE_{base} and C_r for which SR at fished sites is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted black line.

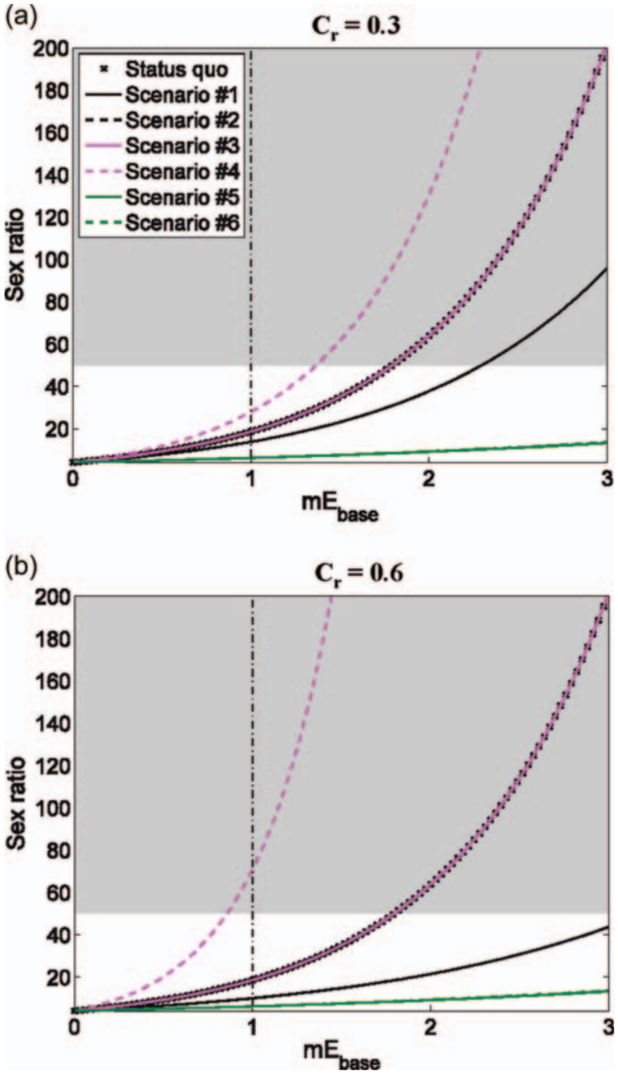

Figure 4. The grouper female:male SR for the fished subpopulation as a function of multiplier of fishing effort (mE_{base}), for the six reserve scenarios analysed in the present study (Table 3). For scenarios #1–4, the fraction of spawning sites in reserves, C_r, is 30 and 60% for (a) and (b), respectively, whereas all spawning sites are protected for reserve scenarios #5 and 6. E_{base} is indicated by a vertical dashed-dotted black line.

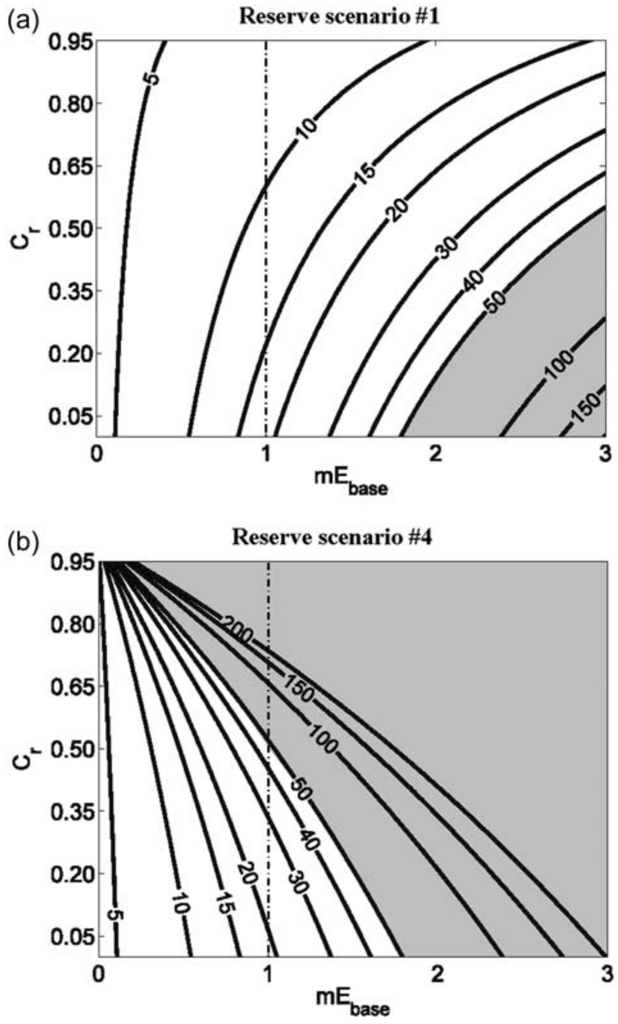

Figure 5. The grouper female:male SR for the fished subpopulation as a function of multiplier of fishing effort (mE_{base}, i.e. fishing effort in units of E_{base}) and fraction of spawning sites in reserves (C_r). Results are only shown for reserve scenarios (a) #1 and (b) #4. For reserve scenarios #2 and 3, the SR of the fished subpopulation is given by Figure 1e as it is independent of C_r. For all panels, the light grey area represents combinations of mE_{base} and C_r for which the SR of the fished subpopulation is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted black line.

who found that closing all spawning locations to fishing has a limited effect on population growth. This discrepancy stems from the fact that fishing mortality of grouper females is higher at spawning than at non-spawning sites in our model, while the opposite occurs in the Heppell *et al.* (2006) model.

Increases in YPR did not occur or were negligible in our model. Consequently, spawning aggregation reserves do not directly increase the yield for our study populations, but fishery benefits may still occur via a recruitment subsidy. Whereas changes in YPR are marginal for rabbitfish, closing all grouper spawning sites to fishing results in a 55% reduction in YPR at the base fishing effort level due to the very large (140-fold) difference in catchability between spawning and non-spawning areas (reserve scenarios #5 and 6; Figure 6). These results are consistent with yield decreases in Alonzo and Mangel (2004) and Ellis and Powers (2012), which integrate recruitment in their models. Improvement in total yield through a recruitment subsidy will only occur if populations targeted by protection efforts are recruitment limited before reserve implementation and the increase in reproductive capacity offsets lost fishing opportunities due to closing areas (e.g. Polacheck, 1990; Guénette and Pitcher, 1999; Hart, 2006; Le Quesne and Codling, 2009), as is clearly the case for any population that would collapse in the absence of reserves, but is persistent with reserves. Chan *et al.* (2012) suggest that, for scenarios of high fishing pressure, increases in fisheries yield occur for gonochoristic populations, and eventually for protogynous populations, that do not show fidelity to spawning aggregation sites but not for protogynous populations showing spawning site fidelity. This stems from the fact that in sex-changing populations the largest individuals are male, which contribute to a recruitment subsidy only through their marginal contribution to improved egg fertilization success (Chan *et al.*, 2012).

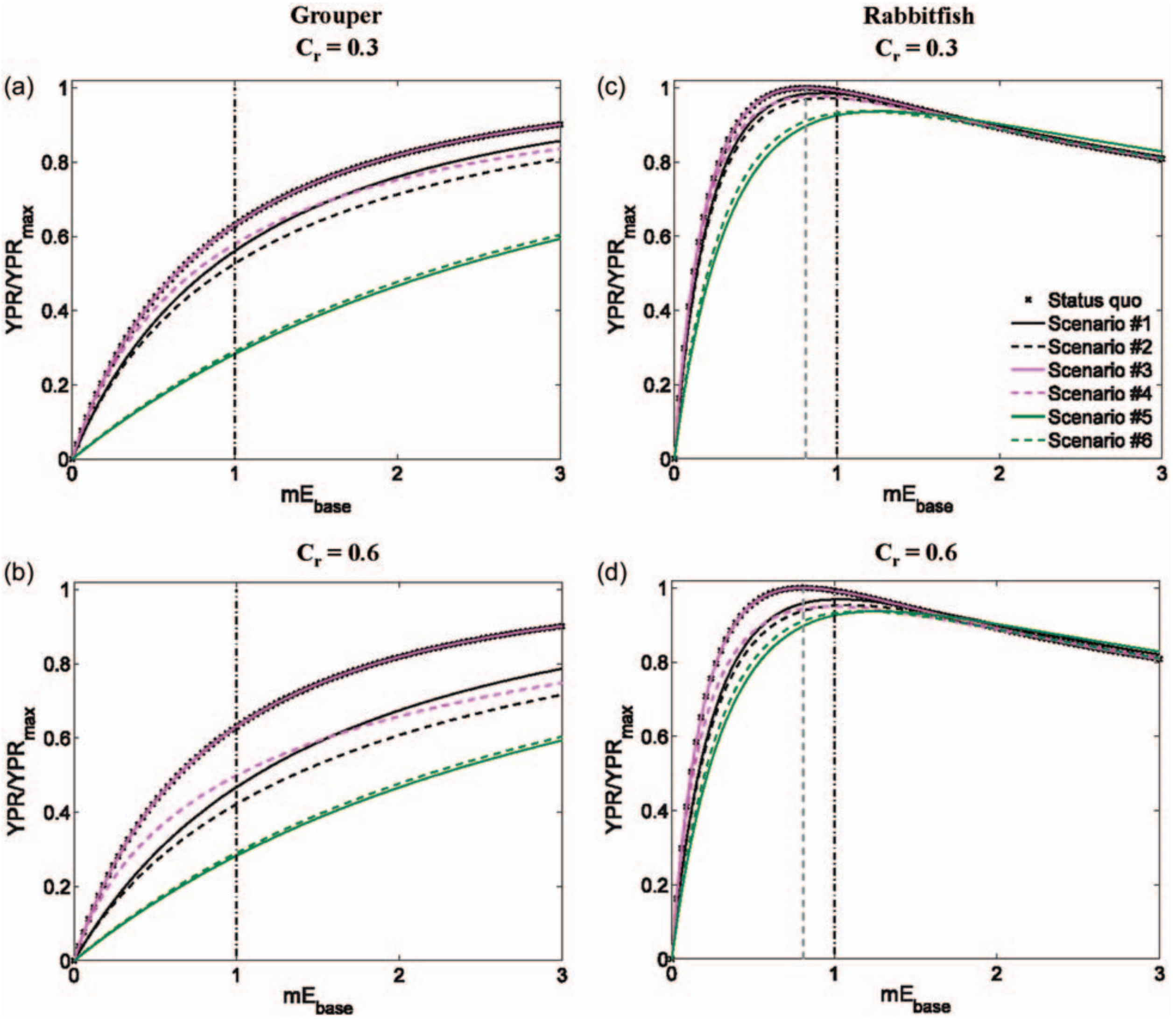

Figure 6. YPR normalized by maximum YPR in the absence of reserves (YPR/YPR$_{max}$) as a function of multiplier of fishing effort (mE_{base}) for the six reserve scenarios (Table 3). (a) and (b) are for the grouper, and (c) and (d) are for rabbitfish. The fraction of spawning sites in reserves, C_r, is 30 and 60% for reserve scenarios #1–4 for (a) and (c) and (b) and (d), respectively, whereas all spawning sites are set aside as reserves for reserve scenarios #5 and 6. E_{base} is indicated by a vertical dashed-dotted black line. E_{max} is indicated by a vertical dashed grey line for rabbitfish.

The output of our model appears counterintuitive in at least two ways. The first is that creating spawning aggregation reserves can increase the female:male SR and decrease the reproductive capacity of certain demographic segments of the population. This occurs when individuals are faithful to spawning sites and fishing effort from protected spawning sites is redistributed onto the segment of the population using unprotected spawning sites (reserve scenario #4; Figure 2b). The importance of this effect can in part be gauged by considering what happens to FNSSBR if we assume the production of fertilized eggs completely collapses at fished spawning sites (Figure 3e and f vs. b and d). This extreme assumption would significantly reduce reproductive capacity, but population persistence may still occur if the protected fraction of spawning sites exceeds the level of FNSSBR needed to ensure replacement (Botsford *et al.*, 2001); though reducing the number of viable spawning sites may negatively impact resilience to environmental variability (Mumby *et al.*, 2011).

The second counterintuitive result is that spawning site infidelity has only a marginal impact on reproductive capacity (e.g. compare Figure 3a and b and, to a lesser extent, Figure 3c and d). Grüss *et al.* (2011b) demonstrated that movement in a home range, which exposes "reserve" individuals to fishing, dramatically reduces persistence benefits of closures. Therefore, one would naively expect a significant decrease in reserve benefits due to a lack of spawning site fidelity. Here, this effect is weak because the implementation of spawning aggregation reserves eliminates some, but not all, fishing mortality. The difference in the total mortality of individuals using protected spawning sites vs. those using non-protected spawning sites is minor (e.g. total mortality of individuals using protected sites is only 0.6 times that of individuals using non-protected spawning sites for grouper fished at the default effort level), and both are close to the average mortality rate experienced by fish that lack site fidelity. These small differences in mortality explain both the need for placing significant fractions of spawning

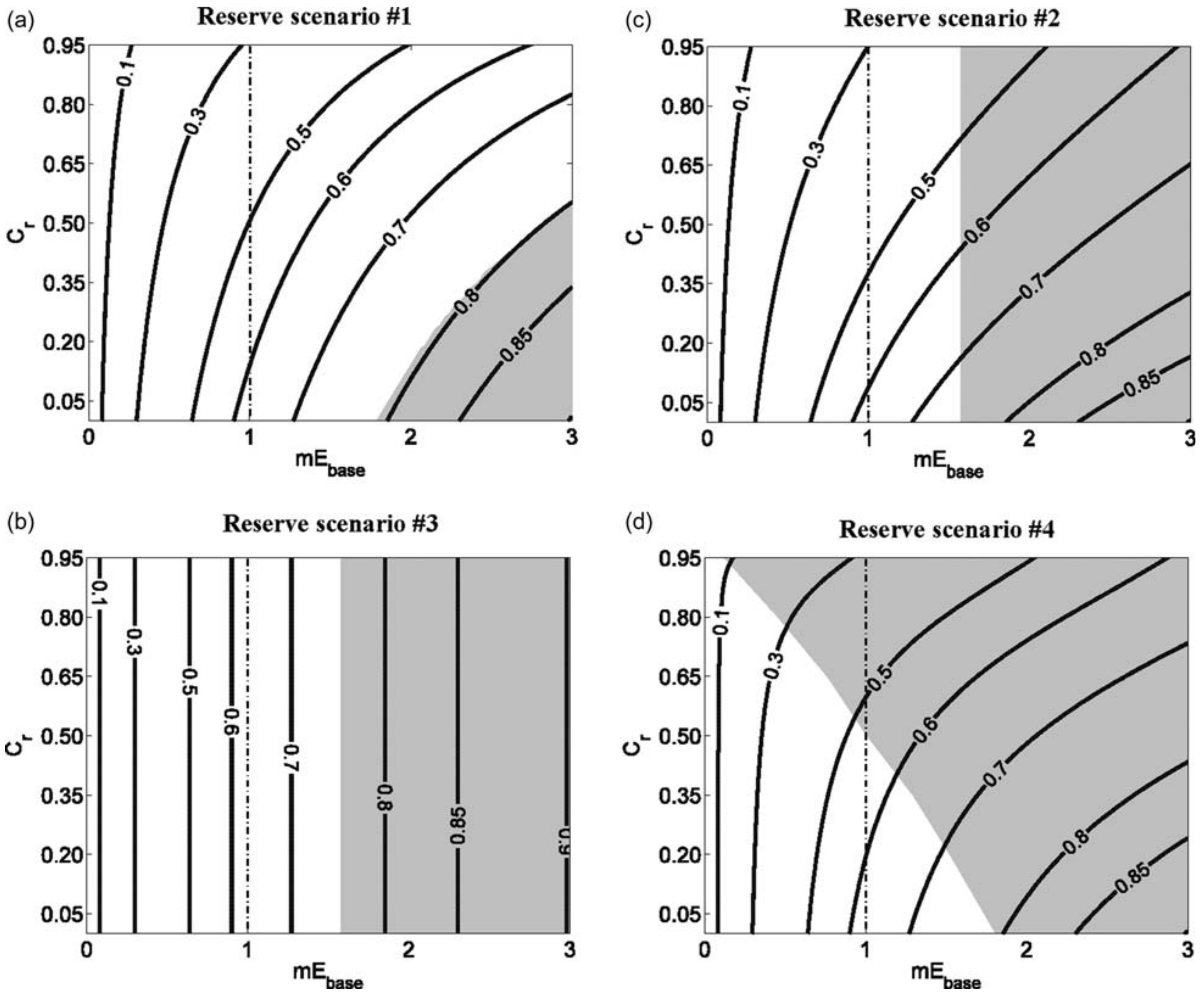

Figure 7. YPR normalized by maximum YPR in the absence of reserves (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}) and fraction of spawning sites in marine reserves (C_r). Panels pertain to the grouper population for reserve scenarios #1–4 (a–d, respectively; Table 3). For all panels, the light grey area represents combinations of mE_{base} and C_r for which the SR at fished sites is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted black line.

sites in reserves to see marked changes in fish reproductive capacity and the fact that site fidelity has a small impact. Differences between the site fidelity and non-site fidelity situations would be more marked if the fraction of annual effort on spawning aggregations was much greater and/or the difference between spawning site catchability and non-spawning site catchability was very large. Such a situation could be envisaged for some groupers that are predominantly fishable at spawning aggregations [e.g. Nassau grouper, *Epinephelus striatus* (Sadovy *et al.*, 2012); tiger grouper, *Mycteroperca tigris* (Sadovy *et al.*, 1994b)].

We found that the positive effects of spawning aggregation reserves in terms of increased biomass are stronger for slower-growing populations and for populations with lower adult mortality (Supplementary Figure A10; Gaylord *et al.*, 2005; Chan *et al.*, 2012). Consistent with Alonzo and Mangel (2004), gonochoristic populations experience greater increases in reproductive capacity and similar decreases in YPR than protogynous populations when spawning aggregation reserves are created if sex change occurs after recruitment into the fishery (as is true for the majority of protogynous aggregation-forming populations, e.g. Sadovy, 1994; Rhodes and Warren-Rhodes, 2005).

The results presented here provide a basis for management recommendations specific to two case study species in Seychelles. Though shoemaker spinefoot rabbitfish is gonochoristic, it is also fast growing and has high natural mortality, suggesting that overall benefits from spawning aggregation reserves will be small. The brown-marbled grouper, on the other hand, is a slow-growing protogynous species that should show significant benefits for reproductive capacity and SR, at the expense of a drop in YPR. The key missing element for translating these predictions into management decisions is an understanding of the exploitation status of each population, precise estimations of which are impossible due to data gaps regarding absolute catchability and minimum levels of FNSSBR needed for persistence. Minimum levels of FNSSBR tend to be higher for long-lived fish populations (Myers *et al.*, 1999), suggesting that exploitation status of the two study populations may not be that different despite large differences in FNSSBR. If both study populations are overexploited, then spawning aggregation reserves are likely of value, especially if all spawning sites are protected. Nevertheless, global fishing effort reduction via conventional fisheries management would also be effective, particularly for the rabbitfish population (Robinson *et al.*, 2011).

There are a number of important caveats to be considered when applying our model to real populations. Two were raised in the preceding paragraph: difficulty in estimating (i) absolute catchability and (ii) density-dependent recruitment relationships (or at least minimum FNSSBR for persistence). The first of these can be addressed via controlled studies of fishing effort and catch during spawning and non-spawning periods, highlighting the importance of further research along these lines. The second is a universal problem in fisheries management that is often addressed indirectly via comparisons across species (Myers *et al.*, 1999). We believe that uncertainty in recruitment processes are such that the per-recruit approach used here, followed by *post hoc* comparisons with target FNSSBR levels, is more valuable for management than a model integrating recruitment.

Sex change in our model is assumed to take place at a fixed age, whereas a recent empirical study suggests that sex change in the brown-marbled grouper from the Great Barrier Reef occurs over a wide range of ages and sizes and may be socially mediated, i.e. under exogenous control (Pears *et al.*, 2006). The existence of exogenous mechanisms controlling sex change may reduce the need for spawning aggregation reserves to balance the SR as age or size at sex change will adjust to compensate for any imbalance (Ellis and Powers, 2012). Nevertheless, factors such as the minimum size at sex change are bounded by physiological limits and are, therefore, not indefinitely plastic (Allsop and West, 2003). Assuming that sex change occurs at a fixed age is conservative in the sense that the model will indicate the maximum possible increase in the SR that is likely to occur as a result of fishing.

Though full fishing effort removal and full effort redistribution after reserve implementation provide reasonable bounds for the impact of closures on fishing, real effort evolution is likely to be a complex process that is difficult to predict (Fulton *et al.*, 2010). For example, we have not considered that reserve implementation could drive a fishing effort increase and/or increases in fishing efficiency or that reserve enforcement could be incomplete, all of which would reduce reserve benefits. Furthermore, the redistribution of the fishing effort formerly at protected spawning sites may place greater pressure on adults migrating to and from spawning sites (e.g. Fulton *et al.*, 1999; Claro and Lindeman, 2003; Rhodes and Tupper, 2007, 2008) or on other fish populations (e.g. Rhodes and Tupper, 2008; Karras and Agar, 2009). These possible effects highlight the importance of integrating spawning aggregation reserves into a global vision of total fishing mortality and available management options (Rhodes and Warren-Rhodes, 2005; Russell *et al.*, 2012).

Finally, seasonal fishery closures during reproductive periods are a viable alternative to spawning aggregation reserves, particularly when spawning and normal residence areas overlap in space. The effects of seasonal fishery closures are likely similar to those of closing all spawning sites (reserve scenarios #5 and 6), except that seasonal closures also benefit individuals not participating in aggregations during spawning events. These individuals include juveniles and also any females that do not attend aggregations faithfully each month of the spawning season (Rhodes *et al.*, 2012). Seasonal closures have the advantage of avoiding the necessity of identifying all spawning aggregation sites, though they are susceptible to uncertainty in the timing of spawning activity.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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